Grzimek's
Animal Life Encyclopedia

Second Edition

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Volume 16
Mammals V

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Volume 16: Mammals V

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Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E. O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa—regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in supermarkets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"—places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade—the hunting of endangered wild animals for large scale human consumption—is pushing many species, including our closest relatives, the gorillas, bonobos and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought specialists from various disciplines to write the sections with

which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 215 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Gzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909-1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series is being completely revised and updated for the first time in over 30 years. Gale is expanding the series from 13 to 17 volumes, commissioning new color images, and updating the information while also making the set easier to use. The order of revisions is:

Vol 8–11: Birds I–IV
Vol 6: Amphibians
Vol 7: Reptiles
Vol 4–5: Fishes I–II
Vol 12–16: Mammals I–V
Vol 1: Lower Metazoans and Lesser Deuterostomes
Vol 2: Protostomes
Vol 3: Insects
Vol 17: Cumulative Index

Organized by taxonomy

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science through which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the lower metazoans and lesser deuterostomes, in volume 1, the series progresses through the more complex animal classes, culminating with the mammals in volumes 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. In the case of the Mammals volumes, introductory chapters describe general characteristics of all organisms in these groups, followed by taxonomic chapters dedicated to Order, Family, or Subfamily. Species accounts appear at the end of the Family and Subfamily chapters To help the reader grasp the scientific arrangement, each type of chapter has a distinctive color and symbol:

● =Order Chapter (blue background)

⏢ =Monotypic Order Chapter (green background)

▲ =Family Chapter (yellow background)

△ =Subfamily Chapter (yellow background)

Introductory chapters have a loose structure, reminiscent of the first edition. While not strictly formatted, Order chapters are carefully structured to cover basic information about member families. Monotypic orders, comprised of a single family, utilize family chapter organization. Family and subfamily chapters are most tightly structured, following a prescribed format of standard rubrics that make information easy to find and understand. Family chapters typically include:

Thumbnail introduction
- Common name
- Scientific name
- Class
- Order
- Suborder
- Family
- Thumbnail description
- Size
- Number of genera, species
- Habitat
- Conservation status

Main essay
- Evolution and systematics
- Physical characteristics
- Distribution
- Habitat
- Behavior
- Feeding ecology and diet
- Reproductive biology
- Conservation status
- Significance to humans

Species accounts
- Common name
- Scientific name
- Subfamily
- Taxonomy
- Other common names
- Physical characteristics
- Distribution
- Habitat
- Behavior

Feeding ecology and diet
Reproductive biology
Conservation status
Significance to humans
Resources
Books
Periodicals
Organizations
Other

Color graphics enhance understanding

Grzimek's features approximately 3,000 color photos, including approximately 1,560 in five Mammals volumes; 3,500 total color maps, including nearly 550 in the Mammals volumes; and approximately 5,500 total color illustrations, including approximately 930 in the Mammals volumes. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges.

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal skins from University of Michgan Zoological Museum library. In addition to species illustrations, *Grzimek's* features conceptual drawings that illustrate characteristic traits and behaviors.

About the contributors

The essays were written by scientists, professors, and other professionals. *Grzimek's* subject advisors reviewed the completed essays to insure consistency and accuracy.

Standards employed

In preparing these volumes, the editors adopted a conservative approach to taxonomy, relying on Wilson and Reeder's *Mammal Species of the World: a Taxonomic and Geographic Reference* (1993) as a guide. Systematics is a dynamic discipline in that new species are being discovered continuously, and new techniques (e.g., DNA sequencing) frequently result in changes in the hypothesized evolutionary relationships among various organisms. Consequently, controversy often exists regarding classification of a particular animal or group of animals; such differences are mentioned in the text.

Grzimek's has been designed with ready reference in mind and the editors have standardized information wherever feasible. For **Conservation status,** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN web page at <http://www.iucn.org/>.

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Antelopes, cattle, bison, buffaloes, goats, and sheep
(Bovidae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae

Number of genera, species
46–47 genera, 137–138 species

Photo: Wild yak (*Bos grunniens*) grazing in the Langtang National Park in Nepal. (Photo by Mark Boulton/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The Bovidae are the largest family within the Artiodactyla (even-toed ungulates) and are comprised of six subfamilies, which include antelopes, cattle, duikers, gazelles, goats, and sheep. Their common characteristic is their unbranched, non-deciduous horns. The high frequency of convergent evolution within these animals suggests that this might not be a monophyletic group.

Based on tooth characteristics, some scientists suggest that the first Bovidae can be recognized from the late Oligocene. However, most agree that members of this family first appear in the fossil record during the Miocene, after which they rapidly diversified and became widely distributed. This rapid diversification during the Miocene, which resulted in all extant lineages being present by 16–17 million years ago, is supported by estimates based on molecular genetic evidence. Largely as a result of their rapid diversification, the phylogenetic relationships within the Bovidae are perhaps some of the most difficult to elucidate of all ungulates.

The earliest fossil attributed to the Bovidae is *Eotragus*, found in 18-million-year-old Miocene deposits from Pakistan. It is recognized as a bovid by its horn cores, and it also possessed high-crowned cheek teeth typical of modern members of this family. Boselaphines first appear in the middle Miocene of Africa and Europe, perhaps earlier in Pakistan, and in the late Miocene in China. The boselaphines probably gave rise to the Bovini towards the late Miocene. Also in the late Miocene, *Gazella*, probably originating from an ancestor similar to the African *Homoiodorcas*, became widely distributed throughout Eurasia, and around this same epoch, modern antelopes first appeared in Africa. The first Caprinae probably evolved from *Tethytragus* found in Europe, with the first fossil sheep, *Oioceros*, occurring in the late Miocene. *Leptobos* and *Parabos* are the first cattle and are found in early Pliocene deposits from about five million years ago, when the ovibovines also are first known.

The family Bovidae is comprised of six subfamilies (Antilopinae, Bovinae, Caprinae, Cephalophinae, Hippotraginae, and Neotraginae) with a total of 137 species in 46 genera (sometimes the subfamilies Aepycerotinae, Alcelaphinae, Peleinae, and Reduncinae are recognized). Not included in these totals are the short-horned water buffalo (*Bubalus mephistopheles*) from northeast China, which became extinct in the Shang Dynasty (1800–1200 B.C.), and the controversial "linh duong" (*Pseudonovibos spiralis*) from Vietnam and Cambodia. The validity of this latter animal is controversial because DNA evidence has suggested it is related to Antilopinae, to Bovinae, and to Caprinae, and one DNA analysis indicated

Topi (*Damaliscus lunatus*) usually live in herds of 15 to 20 animals. (Photo by David M. Maylen III. Reproduced by permission.)

that the horns of at least some specimens had been made from domestic cattle horn. Some authors recognize *Capricornis* as the genus to which serow belong; in this case, there would be 47 genera within the Bovidae.

Physical characteristics

Shape, size, and color

Body shape of members of this family varies from relatively small, slender-limbed species such as the gazelles to the massive, stocky wild cattle. The forequarters are either larger than the hind, as in many large species like wild cattle, wildebeest, and tragelaphine antelopes, or the reverse, as in smaller species inhabiting dense tropical forests such as duikers (Cephalophinae).

Bovids encompass an extremely wide size range, starting with the diminutive dwarf antelopes (*Neotragus*), which weigh as little as 4.5 lb (2 kg) and stand 10–12 in (25–30 cm) at the shoulder, with a total body length of 22–24 in (55–62 cm), and ending with Asian water buffalo (*Bubalus bubalis*), which weigh as much as 2,600 lb (1,200 kg), and the wild cattle such as gaur (*Bos gaurus*), which are up to 85 in (220 cm) at the shoulder, and the yak (*Bos grunniens*), whose total length can reach 128 in (325 cm).

The variety of body coloration of bovids is also extensive, ranging from the predominantly white or very pale, creamy white seen in addax (*Addax nasomaculatus*) to the purple-black of adult male Indian gaur and the orange-yellow coat of golden takin (*Budorcas taxicolor bedfordi*). However, most bovids are some shade of brown. The body coloration can consist of a solid shade; in some, the belly is lighter, while in others, the pelage is patterned. In some species, the patterned coloration is for crypsis and camouflage, such as light stripes against a darker ground that help break the body outline. Such a pelage pattern is seen in the aptly named zebra duiker (*Cephalophus zebra*) and the sitatunga (*Tragelaphus spekii*). In others such as gemsbok (*Oryx gazella*), contrasting colors and body markings are used for intraspecific displays. The sexes often are differently colored, with males usually having the darker pelage. Frequently within species, there are also age-specific colorations. For example, for the first few weeks or months after birth, the pelage color of young is quite different from that of adults, such as in the orange-brown coat of young bison (*Bison bison*), which contrasts to the dark burnt-sienna brown of the adults. In species such as blackbuck (*Antilope cervicapra*) or sable antelope (*Hippotragus niger*), adult males are much darker colored than are subadult males and other age-sex classes.

Other distinguishing characteristics

One pair of unbranched horns characterize bovids, except for the unique chousingha (*Tetracerus quadricornis*) from India, also known as the four-horned antelope. All male bovids have horns, and so do females in several species, although they are almost always smaller. Whether females are horned or not seems to be depend on the degree of intraspecific resource competition, which will be relatively greater in species forming large groups. As Charles Darwin, and later others, argued, horns evolved primarily through sexual selection involving intraspecific competition, and are used for fighting and display purposes.

Horn shape varies greatly among the Bovidae, from short, sharply pointed horns of steenbok (*Raphicerus campestris*) to

A mother roan antelope (*Hippotragus equinus*) nuzzles her newborn. (Photo by Animals Animals ©Jim Tuten. Reproduced by permission.)

African buffalo (*Syncerus caffer*) watching for predators, adopt a defensive position. (Photo by Harald Schütz. Reproduced by permission.)

the long, spirally twisted horns of tragelaphines to the relatively massive but simple curved horns of water buffalo. Horns are comprised of an inner bone core attached to the frontal bones of the skull, and an outer keratinized sheath, separated by two thin layers of tissue, the epidermis and the dermis. The inner bone core increases in size each year until maturity, when the growth slows or ceases. The outer horn sheath grows each year but is not shed, so the annual sheaths grow inside each other, forming a series of cones stacked one inside the other. The demarcation between each successive year's growth is distinct in some species such as wild sheep (*Ovis*), and forms a ring where one year's sheath stopped growing and the next began. Counting these annual rings can give a reliable estimate of the animal's age, but this technique does not work for all species, or sometimes not even for both sexes of the same species.

Bovids walk on the their hooves (unguligrade) and all have typical paraxonic limbs, in which two well-developed digits on both front and hind feet, the third and fourth digits, bear the weight of the body. The second and fifth digits are either absent or, more often, small, forming the so-called lateral hooves, or dewclaws. The third and fourth metapodials, the only ones completely present, are fused into a single functional unit sometimes referred to as the cannon bone. Keratinous hooves sheath the terminal bone of each toe. Other adaptations of the bovid limb include a reduction in size of the distal end of the ulna, which is also fused to the radius of the fore limb, and a similar reduction of the distal end of the fibula on the hind limb.

The bovid skull lacks a sagittal crest, and the orbits that form a complete circle with a postorbital bar at the rear are located at the sides and toward the top of the head. The lacrimal canals have a single opening within the orbit, and there are often pits or preorbital vacuities in front of the orbit. The dental formula is (I0/3 C0/1 P3/2–3 M3/3) $\times$ 2 = 30–32. All species lack both upper incisors and upper canines. The lower canines are usually incisiform (incisor-like), adding to the cropping function of these front teeth. Plants such as grasses and forbs (e.g., herbs and wildflowers) are brought into the mouth by the lips and tongue, where they are severed by the lower incisors pressing against the hard cartilaginous pad of the upper palate, followed by a quick upward jerk of the head. Tougher plants such as shoots of shrubs are severed by the premolars and molars. Depending on diet, the incisors can be wide (spatulate) and relatively uniform in size, as in grazers, or narrower and often of various sizes, as in browsers. There is a large, clearly defined gap (diastema) on the lower jaw between the canine and the first of the premolars. The structure of the premolars and molars depends on the dietary habits. In obligate grazers, they are al-

Brahma cattle (*Bos indicus*) bred for tolerance to heat, in Costa Rica. (Photo by Animals Animals ©Ken Cole. Reproduced by permission.)

most always high crowned (hypsodont), while in browsers, they are usually low crowned (brachydont). Some mixed grazer-browsers have mesodont molars. In all three types, the enamel of the molars and some premolars is folded into crescent-shaped (selenodont) loops and ridges, which are highly effective for grinding plant material into small particles to aid digestion.

All Bovidae are ruminants, having a four-chambered stomach, and regurgitate and re-chew their food (chew cud) as another means of increasing digestive efficiency.

Female Bovidae have either one or two pairs of functional mammae. Many species of bovids have glands that produce secretions used in intraspecific communication. They are especially common in many of the African antelopes, which use the secretions for marking territorial boundaries.

Distribution

Current and historical ranges

As a result of human transport and introductions, both wild and domestic species of Bovidae are distributed worldwide, except for Antarctica. However, the family is native only to Africa, North America, Europe, and Asia.

For almost all species of Bovidae, their current range is generally similar to their historic range. However, most are not as numerous and many species have become increasingly confined to pockets, forming a more patchy distribution within their former range. The reductions in abundance and distribution are almost always due to human activities, which remove or reduce populations or which destroy or dramatically alter habitats. Many species throughout the world are now found only in protected areas such as national parks and game reserves. For example, North American plains bison (*Bison bison*) were found across the Great Plains from the western mountains to the eastern forests. They were slaughtered by the thousands in the nineteenth century and reduced from an estimated total population of more than four million to fewer than 2,000. Today, numbers have increased to several thousands through concerted conservation efforts, but they are very much restricted to a few local protected sites within their historical range. Similarly, saigas (*Saiga tatarica*) once occupied much of the steppes of central Asia, but were severely depleted through human exploitation. After protection, they regained much of their former range, only to once more be decimated by hunters killing them for their horns for use in the medicinal trade.

Habitat

Being obligate herbivores, Bovidae eat a wide variety of plant types, and so members of this family are found in a wide range of habitats where they can find sufficient food. Each species tends to favor specific habitats or, more often, mixes of habitats, with some species being more adaptable than others. In many ecosystems, these bovids are the primary prey of large carnivores and thus are key components of many animal communities.

Members of the Bovidae are found in almost all major terrestrial ecosystems and habitat types. Depending on species, they can be found in open habitats such as deserts, grasslands, savanna, steppe, alpine and arctic tundra, as well as dense habitats such as swamps, riparian forests (i.e., forest near rivers and streams), shrublands, forested parklands, and tropical forests. However, bovids are probably most numerous and diverse in subtropical and tropical savannas and grasslands. Although different species specialize on particular habitats, as a family, Bovidae occupy habitats from low-elevation valley floors to mountain tops.

Some species prefer open habitats, others prefer forests, and still others occupy both. Typical open-habitat dwellers include species such as American bison, saiga, wildebeest, and various antelopes and gazelles. Shrublands are home to species like lesser kudu (*Tragelaphus imberbis*) and nilgai (*Boselaphus tragocamelus*). Swamps and floodplains are favored by Asian water buffalo and anoas, as well as African species like the Nile lechwe and sitatunga. Gemsbok occupies deserts and other arid regions, as do Barbary sheep (*Ammotragus lervia*). In tropical forests, there is a range of bovids from the various large cattle such as gaur and banteng in southern Asia, to smaller species such as the newly discovered saola or Vu Quang ox (*Pseudoryx nghetinhensis*) of Southeast Asia, and the bongo (*Tragelaphus eurycerus*) of Africa. Familiar species found in mountains and other high-elevation habitats include the yak of the Himalaya mountains and Tibetan Plateau, the wild mountain sheep (*Ovis*), whose members are found throughout the mountains of Eurasia and North America, and the wild goats and related ibex (*Capra*).

The birthing season is a time when females of many species seek out specific habitats that provide them greater security for giving birth and for protecting the newborn young. Depending on species, such secure habitats for parturition can range from dense brush to steep cliffs. The mating season, or rut, in some species of Bovidae, also occurs in particular ar-

eas, but it is uncertain whether this is due to some special attribute of the habitat, or simply reflects where they happen to be at that time.

Behavior

Social organization

Bovidae exhibit a range of sociality in their grouping behavior. Some species are solitary or near solitary, such as the bongo and dik-diks (*Madoqua*) of Africa. Species at this end of the group size spectrum are often territorial, living alone or in groups of two to three animals, usually in closed forests and dense shrublands. In other species, the basic unit of two to three is similar, but larger temporary groups form at certain periods in the year. Some, like klipspringer (*Oreotragus oreotragus*), live as mated pairs for most of the year. Bovids living in open habitats almost always occur in medium to large sexually segregated groups, with adult males living separately from females and young for most of the year. Group size across the whole spectrum appears to be dependent more strongly on habitat structure than on characteristics of the species; the larger groups are more commonly encountered in open habitats such as grasslands and savannas, and smaller groups in dense forests where visibility and, consequently, group cohesion are reduced. The largest bovid groups have been recorded in North American plains bison in the early nineteenth century, and today, the largest to be seen are the migratory herds of blue wildebeest (*Connochaetes taurinus*) in the Serengeti of Tanzania. In both cases, these "supergroups" were comprised of several thousands of individuals, probably comprised of smaller, more stable units, although group membership can be quite fluid. The primary benefit of living in groups is reduced predation due to dilution (decreased probability of being killed) and to increased vigilance (many eyes to detect predators).

Several species of Bovidae, particularly many of the African antelopes, are territorial, either defending territories year-round or only during the mating season. Other bovids occupy undefended home ranges that are, for the most part, used from year to year. Year-round territoriality can occur in any species inhabiting areas with relatively predictable, high-quality food supplies that are economically worth defending. This behavior is found in small forest-dwelling bovids such as the Cephalophinae and dwarf antelopes, as well as in larger African species such as the various kobs and reedbucks (*Redunca*). In species holding territories for reproductive purposes, the male owner most often advertises his presence by making himself conspicuous, for example, by standing on a high point of ground (e.g., topi, *Damaliscus lunatus*), and often marks points on the boundary using secretions of glands such as the antorbital gland just in front of the eye, or with dung and urine.

Social behavior

Bovids are generally highly social ungulates with a range of communication systems and displays. Many are vocal, with vocalizations ranging from the lion-like roaring of plains bison (*Bison bison*) to grunts, snorts, whistles, and barks. When on the move, an almost constant, relatively quiet grunting is typical of the large-herd-forming species such as bison and wildebeest.

Bongos (*Boocercus euryceros*) inhabit the lowland rainforest of West Africa and the Congo Basin to Central African Republic and southern Sudan. (Photo by David M. Maylen III. Reproduced by permission.)

Bovid horn structure is closely related to fighting style. Horn size and shape vary and are grouped into four types. The relatively short, smooth, sharp-pointed horns of species such as duikers (*Cephalophus*) and North American mountain goat (*Oreamnos americanus*) are used for jabbing. These are the most dangerous horn types; the smoothness and sharpness mean that they are capable of inflicting lethal wounds. Species having such horns attempt to avoid unnecessary physical contact and rely more heavily on threat displays. Two other horn types are the heavily ridged and twisted forms found in impala (*Aepyceros melampus*) and blackbuck (*Antilope cervicapra*), and the relatively long, curved and relatively slender, ridged horns of oryx (*Oryx*) and sable antelope (*Hippotragus niger*); both these horn types are used for head-to-head wrestling. The ridges and twisted shapes help catch and hold an opponent's horns, and the combatants wrestle in an attempt to twist the opponent off balance and allow them to stab with the horn points. The fourth type is the relatively massive, solid horns of species such as African buffalo (*Syncerus caffer*) and bighorn sheep (*Ovis canadensis*), which are employed to butt heads. Species with this style use their horns like clubs, and sheep and goats often increase the force of the blow either by running at each other, standing on the hind legs and then dropping into the clash, or, in some cases, using the advantage of higher ground. Fighting with conspecifics for status, territory, or mates is the primary function

The African, or Cape, buffalo (*Syncerus caffer*) can spend over ten hours a day eating. (Photo by Rudi van Aarde. Reproduced by permission.)

of horns, but they can occasionally be used secondarily in defense against predators.

Displays are used by many animals, including bovids, to communicate in a range of social interactions. Lateral displays are common in many Bovidae, and often emphasized by adaptations that enhance the size (real and apparent) of the lateral profile. In the American bison (*Bison bison*) and gaur (*Bos gaurus*), the thoracic spines are elongated, permanently increasing the dimensions of their body profile. Other morphological adaptations that enlarge the lateral profile include dewlaps, the flap of skin hanging from the neck and chest of eland (*Taurotragus oryx*) and the zebu breed of domestic cattle (*Bos taurus*), and manes of long hairs. In greater kudu (*Tragelaphus strepsiceros*) and urial sheep (*Ovis vignei*), for example, the mane falls from the underside of the neck, and in nyala (*Tragelaphus angasii*), it extends along the underside of the belly as well. A temporary increase in lateral profile is achieved in some species such as the roan antelope (*Hippotragus equinus*) and chamois (*Rupicapra rupicapra*). They have a narrow band of long guard hairs running over the shoulders and onto the back, which can be raised (piloerection) to increase apparent body size. This effect can be emphasized because these erectile hairs are often of a contrasting color to the rest of the body, thus drawing attention to the display. Striking body coloration patterns, often involving contrasting colors or shades, are commonly used in displays by members of the Bovidae.

Activity patterns and migratory movements

Rumination imposes regular, alternating periods of feeding bouts, followed by rest-rumination periods. Depending on habitat type and to a lesser extent group size, after feeding, the animal will move to more predator-secure habitats to rest and ruminate. The diurnal pattern of these activities can also be affected by predation pressure, especially hunting by humans, with the result that animals become crepuscular, feeding primarily around dawn and dusk. Nocturnal feeding also occurs, but seems to be most frequent during moonlit nights.

Bovids usually make seasonal use of their environment by occupying different habitats at different times of the year. Most seasonal movements or migrations are related primarily to food availability. In temperate regions, bovids move to different areas, often according to the seasons, attempting to find the best foraging conditions available to them. Thus in winter, they congregate in areas where there is not only adequate food, but also shallow snow, shelter from harsh climatic conditions, and habitat or terrain to avoid predators. In spring, the animals move to sites where snow melts early and forage begins to grow. In summer, further movements occur to sites where there is abundant and nutritious forage that will allow the animals to acquire sufficient energy to meet not only their immediate needs, but also enough to deposit fat for winter. Males need high-quality habitat so they can store fat that supports them during the rut. In mountainous areas, the migrations are usually altitudinal and related to snow accumulation and plant growth. Animals in these areas often spend the winter at low elevations where snow depths are usually shallow and forage more available. In spring, the animals migrate upward, following the greening of new vegetation as the snowline retreats. Snow accumulation in fall and early winter then forces them to lower elevations, unless they can forage along snow-free windswept ridges. In the tropics, migrations occur as animals take advantage of new forage growth during rainy seasons. In exceptional cases, populations may make extremely long-distance migrations each year. For example, blue wildebeest in Serengeti have an annual migration of almost 2,000 mi (1,200 km) round trip. These migrations in tropical regions achieve the same ecological benefits as those in temperate regions. Animals move about their environment to exploit seasonal foraging opportunities and thus increase their reproductive success or reduce their mortality.

Feeding ecology and diet

All members of the Bovidae are obligate herbivores, and are either grazers, browsers, or mixed grazer-browsers. Body size in Bovidae affects food requirements and feeding styles because of the relationship between size and metabolic requirements. Small species require relatively more energy and higher-quality food than do large species. In general, small bovids tend to be selective (concentrated) feeders, eating the most nutritious and digestible plant species and parts, whereas large species are usually less selective bulk feeders, which consume large quantities of low-quality forage.

Bovids have various adaptations for foraging. Besides their modified lower incisors and canines, and in grazers, their high-crowned (hypsodont) cheek teeth, the shape of the mouth is also important for feeding. Browsing species tend to have narrow muzzles and pointed pre-maxillae, grazers have broader muzzles with square pre-maxillae, and in mixed

grazer-browsers, the muzzle and pre-maxillae are, not surprisingly, intermediate. Most bovids have elongated skulls with the eyes located laterally and toward the top of the head. This elongated skull not only helps with foraging in some species, but might also benefit them to more easily detect predators while feeding. Browsing bovids will often stand on their hind legs to gain access to higher levels of shrubs. Many also have long slender necks that also help them to browse higher up a shrub or bush; the gerenuk (*Litocranius walleri*) has relatively the longest neck of all bovids and it, too, will stand on its hind legs when browsing particularly tall bushes.

Reproductive biology

Female bovids usually give birth to their first young when two or three years old, while most males, although capable of breeding around this same age, usually do not begin to fully participate in reproductive activities until older. Typically, females are interoparous, giving birth to one, sometimes two, young each year throughout their life. Males are usually semelparous, spending their early years growing large bodies and weapons (hooves and horns), and concentrating their mating activity to a limited number of years toward the end of their life.

Births are usually timed to coincide with the beginning of the annual plant growth cycle, so that females can benefit from the nutritious forage for lactation, and the young have a long time to grow before the onset of more difficult conditions in their first winter or dry season.

Parental care

Only females provide parental care in the Bovidae. Adult males, for the most part, live separately, either alone or in groups with other males, and thus take no part in rearing young. Females may remain in the group to give birth or leave to seek a secluded area with dense cover as concealment against predators. Like other artiodactyls, the young may be hiders and followers in the first week or two of life, either remaining hidden during the day while the mother feeds elsewhere, or remaining near her.

Mating systems and courtship

The majority of bovids are polygynous, with a male mating with more than one female. Only some of the small species such as dik-diks and dwarf antelopes form pair bonds, with a male and female usually remaining together in a territory held year-round. The more common polygynous-mating systems are temporary, with a male defending one or several females at once against other males in order to mate with them. When a male defends a single female at a time, as in most caprins, this is called a tending pair. When the male defends a group of females, this is termed a harem. Males in several species also defend mating territories, which contain resources such as rich food patches and security from predators. These resources attract females so that the male can then attempt to keep them on his territory so he can court and mate with them. Usually, the territories with the best resources are held by the most dominant males. Owning a territory not only attracts females, the male often has the added benefit of being able to mate with less interference. Examples of species holding mating territories include the various African gazelles (*Gazella*) and the springbok (*Antidorcas marsupialis*).

A klipspringer (*Oreotragus oreotragus*) pair. (Photo by Harald Schütz. Reproduced by permission.)

Another mating system, lekking, is very rare in mammals. It has been observed most often in the Bovidae, but only in four African forms, all belonging to the subfamily Reduncinae: Uganda kob (*Kobus kob thomasi*), white-eared kob (*K. k. leucotis*), Kafue lechwe (*K. leche*), and topi. Lekking involves males defending very small territories, often only a few feet (meters) in diameter, located at a specific location called an arena. Many males gather on the same arena, each defending its own small patch of ground, which contains no resources that could attract females. The males defend their territories during day, and females come to them. Once a female enters a territory, the male tries to keep her from moving off long enough so that he can copulate with her. Lekking is not only rare, but is not seen in all populations within a species, nor is it performed each year. It seems to occur more frequently when a population is at high density. At lower densities, each male either holds larger resource territories to attract females, or defends a harem without holding a territory. Lekking is a good example of the flexi-

The Tajik markhor (*Capra falconeri heptneri*) inhabits the Himalayas. (Photo by R. Van Nostrand/Photo Researchers, Inc. Reproduced by permission.)

bility of social organization in general and of mating systems in particular.

Typically, only males perform courtship; only in rare circumstances do females court males. Although courtship behaviors are species-specific, there are general patterns in common. A male generally approaches females in postures that are non-threatening, and once a female accepts his presence, he will perform additional courtship patterns of increasing physical contact. During this time, the male assesses whether the female is in estrus or not by testing her urine and by her receptive behavior. Such behavior occurs until he is able to mount and copulate with the female. While in many species there may be only three of four distinct courtship patterns, much more elaborate courtship repertoires are found in the Caprinae.

Conservation status

A total of 122 species within the Bovidae is listed in the IUCN Red List of Threatened Species. The listing statistics for this family are: Extinct: 4 species; Extinct in Wild: 2 species; Critically Endangered: 7 species; Endangered: 20 species; Vulnerable: 25 species; and Lower Risk: 64 species. Hence, 58 of these 122 species, or 47%, are listed in categories of conservation concern.

In most cases, threats to wild Bovidae come from loss of habitat as human populations increase and require more land for agriculture and exploitation of natural resources. Hunting for meat probably plays a slightly lesser role, although it does have significant and negative impacts in many areas, such as Africa, where poaching involving setting of hundreds of snares in an area can indiscriminately kill many different species. Increased access through the development of roads and jeep trails also adds to the risk of animals being killed, as does the ready availability of weapons that have accompanied the proliferation of armed conflicts around the world.

Most countries have protected area systems that help in the conservation of bovids and their habitat. They also have various laws regulating hunting. The main issue, however, is how well these laws and protected areas are enforced. In some parts of the world, trophy-hunting programs are established for conservation purposes. Only a limited number of animals are killed and the funds generated by this activity are used to benefit the animals harvested, often by creating incentives for local people to help protect the species and its habitat.

Significance to humans

Many species of bovids have attracted artists throughout the ages. Paleolithic artists commonly depicted bison and sometimes ibex, creating exquisite paintings and etchings on the walls of caves and other rock surfaces, as well as on portable artifacts. Later, petroglyphs and rock paintings of bovids have been found in Africa, Central Asia, and North America. A mythological creature, the Minotaur, a creature half human, half bull, comes from the Bronze Age Minoan culture of Crete, which flourished from around 2000 to 1400 B.C. Frescos and other artifacts from Crete show scenes of bull jumping, evidently a gymnastic sport practiced by both men and women, in connection with bull-worship rituals. The Minoans also sacrificed bulls, and bulls continued to figure in later Greek mythology. Human interactions with bulls continue to this day in the form of Spanish bullfights and Pamplona's annual running of the bulls.

Bovids have provided four of the world's most important domestic species of livestock: cattle, sheep, goats, and water buffalo. Wild goats were kept in captivity about 11,000 years ago in the Euphrates valley of southern Turkey, and goats and sheep were probably first domesticated about 10,000 years ago, with cattle perhaps a bit later. Some of the earliest sites of animal domestication are from the Middle East, an area referred to in archaeological literature as the "fertile crescent." However, there was very probably more than one center of bovid domestication, with the Indus basin and central Asia being the most likely. There were probably as many as three centers for the domestication of domestic goats, while for cattle, buffalo, and sheep, there were at least two centers.

A congregation of eland (*Taurotragus oryx*) in Kenya. (Photo by Harald Schütz. Reproduced by permission.)

Bovids are commonly hunted for meat and other products by local peoples in many parts of the world. Trophy hunters also seek out many species of Bovidae, primarily those species with large horns. In the southern Mediterranean, different forms of bull fighting have been popular, and even exported to Mexico. Perhaps these are derived from earlier activities in Greece and Crete.

"Bezoar stones," calcified concretions sometimes found in the stomachs of goats and ibex, were prized in the Middle Ages for testing whether food was poisoned. Aphrodisiac properties are still assigned to the horns of some species, and have most recently resulted in a major decline in saiga populations on the Russian steppe. This same "medicinal" trade is also beginning to impact wild sheep and goat populations in parts of Central Asia.

Bovids are not generally thought of as dangerous to humans, except perhaps domestic bulls and African buffalo. However, many species in this family are large and have dangerous weapons (hooves and horns), and adult males during the rut can be dangerous.

Domestic livestock, especially domestic goats, are often accused of being a major cause of habitat loss and degradation due to their overgrazing and over-browsing. This merely reflects their hardiness and wide feeding habits. The true responsibility for such habitat damage belongs to the humans who own them, but for many people forced to live in marginal areas, there is little choice but to eke out a living as best they can, even if this means degrading the vegetation on which they ultimately depend.

A Tibetan antelope, or chiru (*Pantholops hodgsonii*), searches for vegetation under the snow in Chang Tang, Tibet. (Photo by George Schaller. Bruce Coleman, Inc. Reproduced by permission.)

Resources

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David M. Shackleton, PhD
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Bovids I
Kudus, buffaloes, and bison
(Bovinae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subamily Bovinae

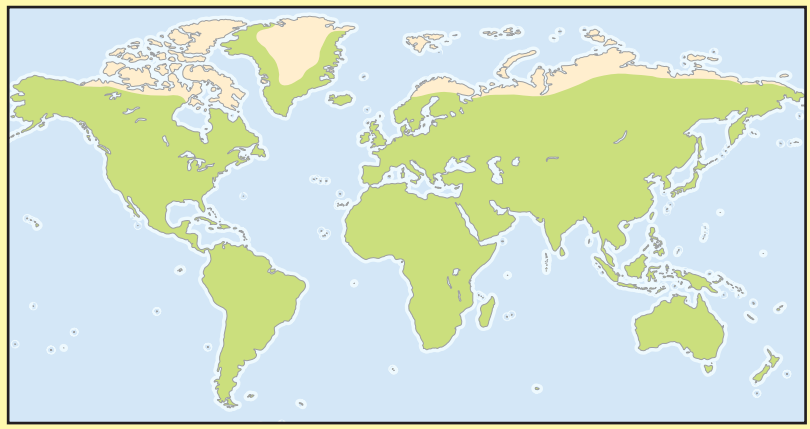
Thumbnail description
Small to very large herbivores; males and often females bear unbranched horns on the head; limb structure is typical of the Artiodactyla, with two main toes terminating in hooves; all have a ruminant digestive system

Size
Length 30–170 in (80–435 cm); shoulder height 24–85 in (60–220 cm); weight 36–2,600 lb (17–1,200 kg)

Number of genera, species
9 genera; 24 species

Habitat
Forest, woodland, savanna, scrub, grassland, alpine meadows, prairie, and steppe

Conservation status
Critically Endangered: 2 species; Endangered: 7 species; Vulnerable: 4 species; Lower Risk/Conservation Dependent: 7 species; Lower Risk/Near Threatened: 3 species



Distribution
Africa, Asia, Europe, and North America

Evolution and systematics

The Bovinae is comprised of 24 extant species in three tribes: Boselaphini, Bovini, and Tragelaphini. Genetic evidence supports the idea that the Bovinae is a monophyletic group and a sister group to the subfamily Antilopinae. The tribe Bovini is also monophyletic and a sister group to the Boselaphini. The Boselaphini, today represented by only two living species, the nilgai (*Boselaphus tragocamelus*) and the chousingha (*Tetracerus quadricornis*), both of India, are probably the most primitive of the Bovinae and closest to the ancestors of this subfamily. The Bovini tribe includes yak (*Bos grunniens*), the various species of wild cattle (*Bos*), the European and American bisons (*Bison*), Asian (water) buffaloes and anoas (*Bubalus*), African buffalo (*Syncerus caffer*), and probably the saola (*Pseudoryx nghetinhensis*). The yak is sometimes placed into the genus *Poephagus*, while *Bison* have been suggested to belong to *Bos*, as has yak. Yaks appear from behavioral and genetic evidence to be intermediate between cattle and bison. The modern members of the tribe Tragelaphini are all African species, which have probably been separated from other Bovinae for 15 million years. Fossils attributed to nyala (*Tragelaphus angasii*) have been found in 6.5-million-year-old deposits. The mountain nyala (*Tragelaphus buxtoni*) is believed to be the precursor of kudu (*Tragelaphus strepsiceros* and *T. imberbis*). Other tragelaphines include the bongo (*Tragelaphus eurycerus*), bushbuck (*T. scriptus*), sitatunga (*T. spekii*), and elands (*Taurotragus*).

Physical characteristics

The smallest species of Bovinae is the chousingha, which weighs 36–45 lb (17–21 kg) and stands around 24 in (60 cm)

Two American bison bulls (*Bison bison*) spar in the National Bison Range, Montana, USA. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Greater kudu (*Tragelaphus strepsiceros*) males sparring in Etosha National Park, Namibia. (Photo by Michael P. Fogden. Bruce Coleman, Inc. Reproduced by permission.)

at the shoulder. However, most species of Bovinae are medium to large ungulates, ranging up to 2,600 lb (1,200 kg), and several stand over 78 in (2 m) at the shoulder.

Males in all but one species of Bovinae have horns. In most of these species, females have smaller horns. This subfamily includes the only living artiodactyl with more than two horns. Male chousingha, also called the four-horned antelope, possess two pairs of short, sharp horns. Horn shape and relative size vary among species. Tragelaphines have long spiral-shaped horns with smooth surfaces, whereas the wild cattle, African buffalo, and smaller Asian (water) buffalo have shorter, smooth, curved, and often stout horns. Water buffalo have very large curved horns that are often ridged towards the base, while the saola's horns are straight and smooth.

Glands are limited in the Bovinae. The chousingha is the only member of this subfamily with pre- or ant-orbital glands in front of the eyes. Other Bovinae also lack pedal glands.

Most species of tragelaphins have a coat with several thin, white, vertical stripes, and some also have white spots. The contrasting white markings of tragelaphins probably act as disruptive patterns that help camouflage the animal by

A bison (*Bison bison*) mother with calf in Yellowstone National Park, Wyoming, USA. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

breaking up the body outline against the bush and forests they inhabit. In contrast, the eland, although a tragelaphin, is not striped and it inhabits open habitats where disruptive pelage would have little adaptive value. The largest members of the subfamily (e.g., American bison, water buffalo, African buffalo, and members of the genus *Bos*) have uniformly dark body pelage, although the lower legs of some species are light colored.

Distribution

Bovinae are native to both the New and Old Worlds and range from the north temperate regions south to the tropics. Africa, North America, Eurasia, India, and southern Asia are the main distribution regions. Bovinae are not native to either South America or Australia. The greatest species diversity of Bovinae is found in Africa and southern Asia, with the least in Europe and North America.

Habitat

Depending upon species, Bovinae inhabit a wide variety of habitats, ranging from open grasslands and savannas, thorn and scrubland, to swamps and dense tropical forests. Bovinae can be found at low elevations or above the tree line on the high mountain plateaus of Asia.

Behavior

For most species, males and females generally live apart for most of the year. Adult males live either alone or in all-male groups. Females form groups of varying size, comprised of their young of one to two years age, other females, and sometimes including subadult males. The degree of social grouping varies within Bovinae and is related partly to habitat and to body size. Most tragelaphines, except elands, live solitarily or in small groups. The largest species inhabiting open habitats are highly social, forming large groups, although group size often declines when they occupy more visually dense habitat where group cohesion is more difficult to maintain. When Europeans first traveled across the North American plains and before their populations were decimated, bison were reported to live in immense herds. These are probably rivaled today only by the migratory herds of wildebeest in the Serengeti of East Africa or of barren-ground caribou in the Arctic tundra of North America. In most species, the adult males form separate all-male groups apart from the females, young, and subadults.

A greater kudu (*Tragelaphus strepsiceros*) cow with nursing calf in Kruger National Park in South Africa. (Photo by Bruce Aiken. Bruce Coleman, Inc. Reproduced by permission.)

Among males, fighting can occur over attendance at cows in heat and involves charging and ramming their horns together. More often, hierarchical disputes are settled by dominance displays that involve swinging the horns and head actively from the side, presumably to enhance their apparent

African buffalo (*Syncerus caffer*) prefer open pasture and swampy areas where they can wallow in the mud. (Photo by David M. Maylen III. Reproduced by permission.)

An American bison (*Bison bison*) rolling in dust in the National Bison Range of Montana, USA. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

African buffalo (*Syncerus caffer*) and cattle egret (*Egretta ibis*). The egret feeds on the insects stirred up by the moving buffalo. (Photo by Fritz Polking. Bruce Coleman, Inc. Reproduced by permission.)

size. The defeated subordinate may act like a juvenile by lowering its head and placing its nose beneath the dominant's belly as if it were to suckle, or it may simple run away.

Feeding ecology and diet

Bovinae include grazers, grazer-browsers (mixed feeders), and browsers. Some such as the bushbuck (*Tragelaphus scriptus*) also eat fruits and seed pods. Tragelaphines are primarily browsers feeding on twigs, leaves, fruits, and new shoots of woody species as well as forbs and sometimes grasses, especially when the latter are newly growing. Larger species such as members of *Bos* and *Bison* rely more heavily on grasses and forbs but will browse when fresh young growth of shrubs is available. In the African buffalo, the smaller forest subspecies relies on browse rather than grasses, while the larger Cape buffalo feeds almost exclusively on grasses in the savanna, open bush, and riverine habitats it occupies.

Reproductive biology

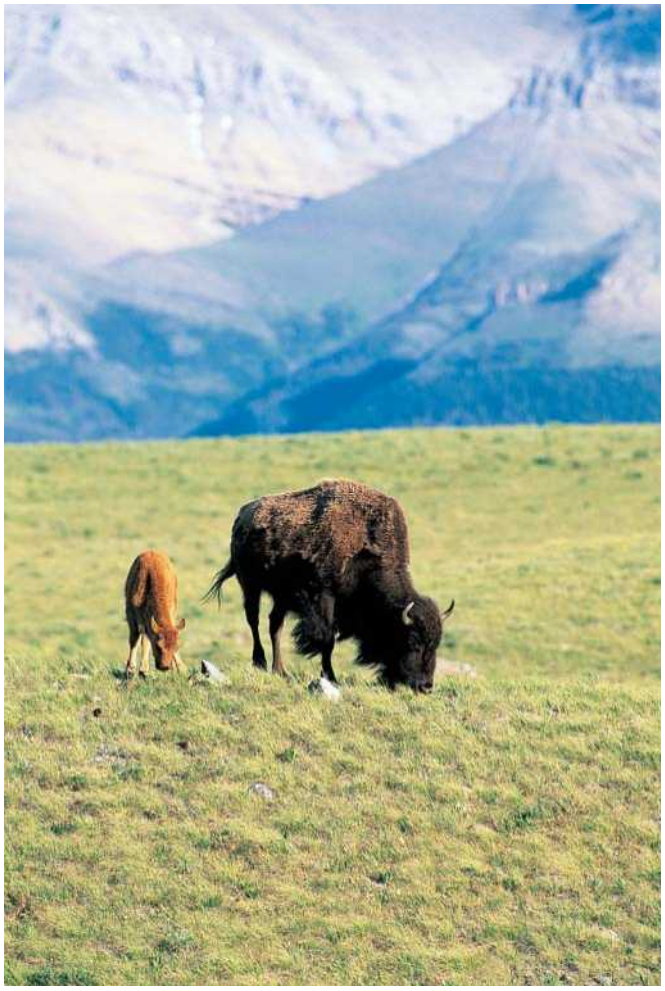
All species are polygynous, with males mating with several females, while females tend to mate with only one male per mating season. Single young are most common, although in some species twins are not uncommon. Among the Bovinae, gestation is shortest (7.5–8 months) in chousingha, longest in the water buffalo (10–11 months), and 8–9 months for most other species. Age at first reproduction is generally in the second year (i.e., mate first when 2.5 years old) for the larger species, but occurs during the first year (i.e., mate first when 1.5 years old) for many of the smaller species.

Conservation status

A total of 22 species are listed in the IUCN Red List of Threatened Species. However, listed as Endangered is the linh duong (*Pseudonovibos spiralis*); this species' existence is questionable as it is suspected of being a hoax. The listings for this subfamily are: Critically Endangered: 2 species; Endangered: 7 species; Vulnerable: 3 species; Lower Risk: 10 species. Excluding the linh duong, 11 of the accepted 21 species, or 52%, are listed in categories of conservation concern.

Most threats to Bovinae come from human activities, including hunting and loss of habitat through the encroachment of agricultural lands and loss of forests for timber harvesting. Increased road access is linked with both the latter activities, which enables hunters to reach previously isolated populations.

Both wisent (*Bison bonasus*) and American bison (*Bison bison*) are examples of the extent to which some Bovinae have been driven to the brink of extinction at the hand of humans. Wisent were all but wiped out, leaving just a few in Poland,



American bison (*Bison bison*) mother and calf grazing in Waterton National Park in Canada. (Photo by Rob Hadlow. Bruce Coleman, Inc. Reproduced by permission.)

while American bison once estimated to number over 60 million at the beginning of the nineteenth century had all but been eradicated through concerted hunting efforts by the end of that century. One of the most important conservation efforts to preserve wisent has been carried out in the Bialowieza Forest in Poland, while for American bison, there have been several centers of bison conservation across the continent.

Significance to humans

All species were hunted, and some such as wisent and bison were especially important for European and North American hunters from Paleolithic to historic times. Today, local peoples still hunt members of the Bovinae for food, and trophy hunters value the species with large horns.

Three species of Bovinae are important domestic species. The most common and widespread is cattle (*Bos taurus*), first domesticated probably some 6,000 years ago. Domestic cattle are represented by numerous breeds around the world and have been bred for meat, milk, hides, as well as draught animals. They are more suited to temperate than tropical regions, although zebu or humped cattle are well adapted to hot climates. Water buffalo is the next most common domestic Bovinae, and, like its wild form, is an animal best suited to tropical regions with high rainfall. Like domestic cattle, water buffalo are kept for their milk, meat, and hides, and provide power primarily for plowing. The yak is of major importance in the high mountain regions of Tibet, Northern India, Nepal, and Afghanistan, where it is well adapted to elevations above 10,000 ft (2,500 m) above sea level. It is also crossed with domestic cattle to create hybrids that are more suitable to lower mountain elevations. Yak and the hybrids are used as beasts of burden to carry loads and plow fields, but also supply milk and sometimes meat. Their hair is valued and is woven into material used for such purposes as making tents.

1. American bison (*Bison bison*); 2. Greater kudu (*Tragelaphus strepsicerus*); 3. African buffalo (*Syncerus caffer*). (Illustration by Joseph E. Trumpey)

1. Yak (*Bos grunniens*); 2. Water buffalo (*Bubalus bubalis*); 3. Chousing ha (*Tetracerus quadricornis*); 4. Female Highland cattle (*Bos taurus*). (Illustration by Joseph E. Trumpey)

Species accounts

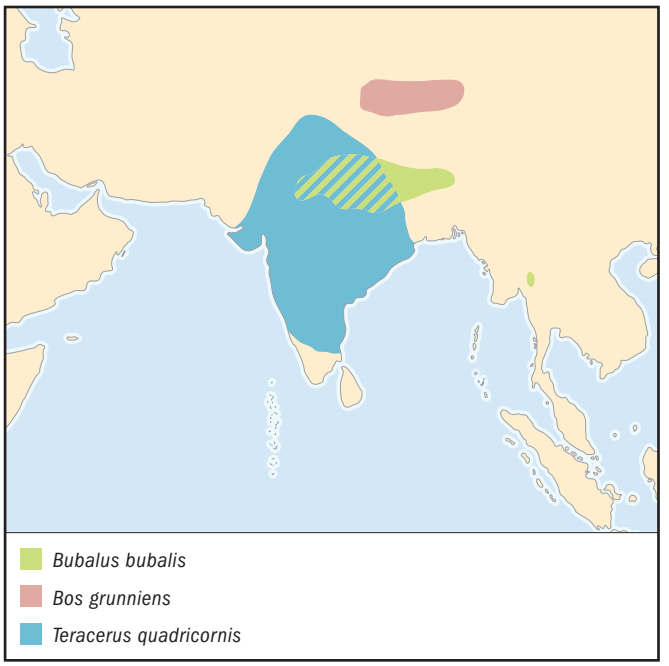
Yak
Bos grunniens

TAXONOMY
Bos grunniens Linnaeus, 1766, boreal Asia.

OTHER COMMON NAMES
French: Yack.

PHYSICAL CHARACTERISTICS
Body length 94.4–127.9 in (240–325 cm); shoulder height 62.9–80.7 in (160–205 cm); tail length 23.6 in (60 cm); weight males 1,100–2,645 lb (500–1,200 kg), females 660–770 lb (300–350 kg). Moderate sexual dimorphism, with females weighing only about 33% of adult males; stocky, ox-like animals with a broad, low-hung head raising steeply to humped shoulders, which are followed by a lower back and rump. Both sexes have long, simple curved, black horns. In adult males, the horns extend up to 37.4 in (95 cm), whereas those of females normally only attain 19.6 in (50 cm). The pelage of wild yak is black with rusty-brown tints and, sometimes, gray hairs on the muzzle. The domesticated yak varies greatly in color from black to light yellow-brown, with many individuals having mottled white patches over parts of their sides and backs. The guard hair is relatively short on the back; on the sides, it can be up to 27.5 in (70 cm) in length, hanging down to form a fringed cape, which extends far enough to the ground to have the legs appear deceptively short. Their long tail is exceptionally bushy throughout.

DISTRIBUTION
The wild yak occurs on the Tibetan Plateau in northern Xizang Province (Tibet) and western Qinghai Province of China. Its historic range included mountains and plateaus of western China, northern India, Nepal, and parts of Mongolia.



Domesticated yak are distributed more broadly across the highlands of central Asia.

HABITAT
A species of the high altitudes, it is found on high elevation alpine steppes devoid of trees and bushes, down to elevations of 6,560–16,400 ft (2,000–5,000 m). In late summer, yaks exploit this alpine-tundra biome foraging on the pockets of natural pasture. As snow begins to accumulate during fall in these high elevations, they migrate to windswept areas of shallow snow or to lower elevations where there are greater amounts of accessible vegetation, such as in valleys and on plateaus.

BEHAVIOR
Yaks form herds, but they are segregated by sex. Female herds comprised of adult females, their calves, and juvenile females and males are typically 6–20 animals, but occasionally more than 100. When males become sexually mature, they leave these female groups and join with older bulls to form all-male herds that are generally 2–5 animals, with some as large as 19. Older bulls are often solitary. When threatened, group members either flee or bunch together and collectively face the predator. In either case, if young are present, they tend to be in the center of the group. During the rut in September, mature bulls join female groups during the four-week breeding season. Males compete for females, and rival males fight by trying to gore each other's flanks.

FEEDING ECOLOGY AND DIET
During summer, yaks consume a variety of growing grasses and forbs such as wildflowers, and supplement their diet with shrubs and lichen. During winter, they consume the dormant grasses and lichens, including some mosses. Yak make altitudinal migrations to exploit seasonal availability of forage.

REPRODUCTIVE BIOLOGY
Polygynous. Reproduction is timed to benefit from the relatively short season of plant growth and less inclement weather; they mate in September, and after a nine-month gestation period, the single calf is born in June. Females give birth every second year.

CONSERVATION STATUS
Classified as Vulnerable, wild yaks face habitat loss and degradation due to livestock grazing on their natural pastures. These alpine/tundra steppes are low in plant productivity and so competition with livestock is exacerbated. Hunting by local people for meat and hides continue to contribute to extirpation of wild yaks. Besides ecological factors, interbreeding between domestic yak and wild yak may pose additional threats to wild populations.

SIGNIFICANCE TO HUMANS
First domesticated over 4,000 years ago, they have supported human life throughout this time in harsh high elevation environments. They are still important to the society and economies of local peoples in many mountain areas in central Asia. Wild yaks are hunted in some areas for meat, wool, and other products. Domestic herds provide milk, cheese, meat, wool, and hides, as well as draft animals and for transporting goods. Their dung is collected for fuel. ◆

African buffalo

Syncerus caffer

TAXONOMY

Syncerus caffer (Sparrmann, 1779), Cape of Good Hope, South Africa.

OTHER COMMON NAMES

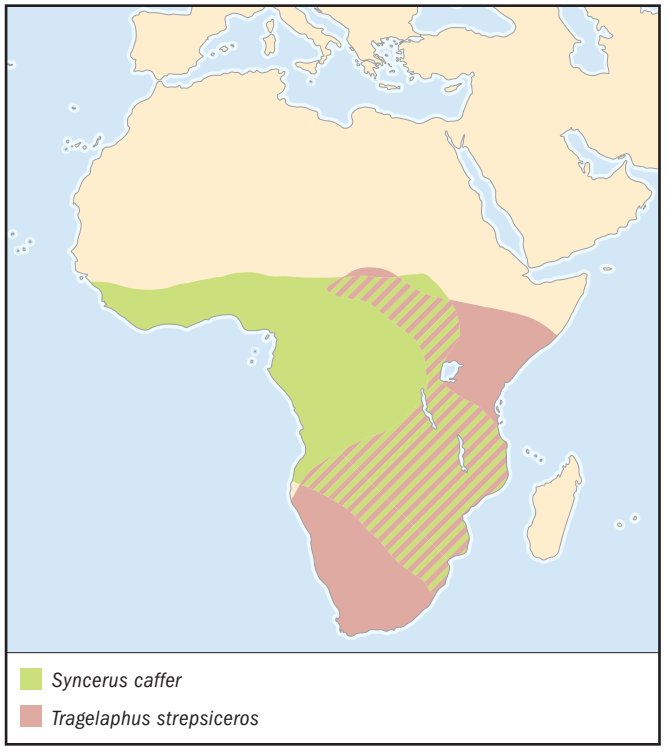
French: Buffle d'Afrique; German: Kaffernbuffel.

PHYSICAL CHARACTERISTICS

Body length 82.6–118 in (210–300 cm); shoulder height 53–70 in (135–179 cm); tail length 29.5–43.3 in (75–110 cm); weight 1,100–1,984 lb (500–900 kg). Minor sexual dimorphism in body size, with adult females weighing about 17% less than adult males; the smallest subspecies from dense forests is half the body weight of the plains form. The most notable feature is its large head and broad muzzle. Males have relatively short (up to 59 in [150 cm]) but stout horns that typically extend sideways, first curving down, then up along the distal half of their length. Females also have horns, but these are smaller and narrower in girth than those of males. On older males, the broad bases of the horns abut, forming an almost solid plate across the forehead. The forest-dwelling subspecies have shorter and less curved horns. The pelage is short across the body and varies from black to reddish brown, depending on subspecies, sex, and age class. The forest subspecies is reddish brown. There is a fringe of long hairs on the ears and a short mane. The tail is long, ending in a prominent black tuft of hairs.

DISTRIBUTION

At a broad level, it is distributed in Africa from Guinea to southern Sudan and then south to Angola and eastern South Africa. Within large portions of this range, its populations are confined to nature reserves. Across its geographic range, it inhabits low to high elevations as long as there are sufficient amounts of suitable habitat. It is particularly abundant in parts of Kenya, Tanzania, Uganda, and Democratic Republic of the Congo.



HABITAT

Most abundant in savannas and riparian complexes (e.g., swamps and river floodplains), but it also occupies forests, grasslands, and shrublands from plains to mountains. In savannas, it requires large areas of dense grass with thickets or trees for resting cover. Populations that are forest dwelling obtain sufficient cover from the trees and bushes, but must meet their food requirements by frequenting small openings among the forest where ground vegetation such as grasses and forbs are abundant. Visit waterholes and muddy areas where they can drink and also wallow.

BEHAVIOR

Form large groups comprised of subgroups complexly structured by sex and age. This structure is in part hierarchically maintained by social dominance. Herd size is mediated by broad habitat factors. In forest-dwelling buffalo, groups are generally between 3–12 individuals comprised of females, their calves, and yearlings; in open habitats, herds are larger, are usually 50–500 animals, but occasionally reach up to 3,000. These largest herds lack the cohesion of the smaller typical groups. Adult females, their young, and males up to three years old form relatively stable subgroups within the herd; males older than three years form their own subgroups, while many males older than 10 years are solitary. Together, these subgroups move about within the larger herd, as it moves throughout its home range. During the dry season, some of the all-male subgroups may leave the herd to exploit feeding opportunities in an increasingly nutritionally challenging environment. In most areas, breeding occurs in the rainy season soon after calves are born. Males test the urine of females to determine if they are in estrus; when ready to mate, the cow will stand and allow the bull to mount and copulate.

FEEDING ECOLOGY AND DIET

Primarily grazers on savannas, consuming vast quantities of grasses. However, the subspecies inhabiting forests include a relatively large amount of shrubs in their diet. Not highly selective feeders, so can acquire the bulk of their forage more easily where there are tall grasses.

REPRODUCTIVE BIOLOGY

Polygynous. Reproduction is tied closely to the rainy season. The gestation period is approximately 11.5 months. Cows first calve when 4.5–5 years old, producing a single young, although occasionally twins are born. Thereafter, mature cows typically reproduce ever two years. Males do not participate in the rut until they are about seven years old.

CONSERVATION STATUS

Classified as Lower Risk/Conservation Dependent. After rinderpest epidemics around the turn of the century, it was greatly reduced across much of its range and extirpated in some regions. Since then, populations have increased and the species has reoccupied much of its former range. However, loss of lower elevation habitat to agriculture has restricted it to nature reserves in many areas.

SIGNIFICANCE TO HUMANS

Hunted by local peoples for meat. As well, it has a reputation for being dangerous and so with its formidable size, this adds to its allure for trophy hunters. Such reputation also makes it undesirable in areas inhabited by humans. ◆

Greater kudu
Tragelaphus strepsiceros

TAXONOMY
Tragelaphus strepsiceros (Pallas, 1766), Cape of Good Hope, South Africa; or Namibia.

OTHER COMMON NAMES
French: Grand koudou; German: Grosskudu.

PHYSICAL CHARACTERISTICS
Body length males 76.7–96.4 in (195–245 cm), females 72.8–92.5 in (185–235 cm); shoulder height males 47.2–59 in (120–150 cm), females 47.2–55.1 in (120–140 cm); tail length males 13.7–21.6 in (35–55 cm), females same; weight males 496–694.6 lb (225–315 kg), females 396.8–473.9 lb (180–215 kg). Sexual dimorphism is moderate, with females being are 5% shorter in length than males and weigh 27% less than males. Males have longest horns in all the Bovinae, extending 66 in (168 cm) or longer in a double spiral; females normally lack horns, but occasionally some individuals have very small ones. The general pelage color is brown and there are several thin, widely spaced vertical stripes along the body from shoulders to rump; the number of stripes depends upon the subspecies. Adult males also have a notably grayish neck. There is a pronounced gray mane hanging from the neck and a band of longer, darker hair running along the spine from the neck to the rump, but most prominently over the shoulders. This ridge of hairs can be erected to form a narrow crest outlining the back. The head has a white strip across the rostrum (nose), just below the eyes. The moderately long tail is white beneath with a black tip.

DISTRIBUTION
Found widely distributed in Africa, occurring in southern Chad, northern areas of the Central African Republic, western and eastern Sudan, northeast Uganda, Ethiopia, and Somalia, and then south and southwest to South Africa, Namibia, Angola, and southeastern Democratic Republic of the Congo. The species has been extirpated in many regions of its former range, and the current main stronghold is South Africa with some major areas of representation in East Africa.

HABITAT
Favors open woodlands with scattered and dense brush, and is found where such vegetation occurs, including plains, rocky hills, and low mountains. It requires brushy thickets for resting cover, and can be found along the wooded banks of dry river courses. Generally, they prefer habitats that provide concealment.

BEHAVIOR
Females form small herds typically of 6–12 individuals, including young, although some form with up to 20 members, consisting of females, their young, and subadult males. Larger groups up 40 will form temporarily. Mature males join these female groups during the mating season, but otherwise live separately for most of the year, either singly or with other males in rather loose groups consisting of up to 10 males.

FEEDING ECOLOGY AND DIET
Primarily browsers, consuming leaves and twigs of a great variety of shrubs and trees, including the seed pods of acacias. They will also periodically consume grasses and forbs.

REPRODUCTIVE BIOLOGY
Polygynous. Reproduction is tied closely to seasonal patterns of rain. Females give birth to a single young after a gestation period that has been estimated to be 7–9 months. Young spend most of the day hidden while their mothers go elsewhere to feed. After about two weeks, young join the herd but continue to hide, mainly at night, for another month.

CONSERVATION STATUS
Classified as Lower Risk/Conservation Dependent. Kudu populations were decimated at the beginning of the twentieth century by Rinderpest epidemics. As a result, the species was greatly reduced across much of its range and extirpated in some regions. Since then, it has reoccupied much of its former range in South Africa. However, in East Africa, loss of habitat at lower elevations has restricted the species to certain areas, including many protected parks and reserves.

SIGNIFICANCE TO HUMANS
Hunted by local peoples for meat. Male greater kudu are much sought-after by trophy hunters because of their large impressive horns. It is also a favorite zoo animal because its impressive size, interesting pelage, and unusual horns appeal to visitors. ◆

Water buffalo
Bubalus bubalis

TAXONOMY
Bubalus bubalis (Linnaeus, 1758), Asia.

OTHER COMMON NAMES
English: Asian buffalo; French: Buffle de l'Inde; German: Wasserbüffel.

PHYSICAL CHARACTERISTICS
Body length 98.4–118.1 in (250–300 cm); shoulder height 59–74.4 in (150–189 cm); tail length 23.6–39.3 in (60–100 cm); weight 1,543–2,645 lb (700–1,200 kg). Females are slightly smaller and weight about 20% less than males. The largest member of the Bovinae, it is a heavy, bulky animal with disproportionately large feet, whose wide hooves help it avoid sinking too deeply in the mud as it moves about wetlands and swamps. Pelage of wild water buffalo, although somewhat sparse, is dark gray to black; domesticated forms can exhibit a range of coat colors. The relatively long tail ends with a bushy tuft of black hairs. Males have massive crescent-shaped pointed horns about 47.2 in (120 cm) long that are almost triangular in cross-section and with heavy ridges on their surface. With the flattened side of the triangular horn facing upward, the horns extend back, almost parallel with the slope of the face. Females also have horns, which after adjusting for their smaller size, are relatively the same size as in males. Domesticated water buffalo have much smaller bodies, almost one-half the size, and also smaller horns than the wild form.

DISTRIBUTION
In the mid-twentieth century, they occurred in two regions. In one region, they were distributed from central peninsular India, north to Nepal, and east to Bhutan. In the second region, they occurred on the Malay Peninsula and north and east to Vietnam, with some on the north portion of the Island of Borneo. This distribution is now severely contracted and fragmented. Currently, wild populations exist in only a few protected areas in India, Nepal, and Bhutan. Another small population occurs in a wildlife reserve in Thailand.

HABITAT
Inhabit tropical and subtropical forests and grassland biomes. Within these biomes, they are closely associated with water and surrounding habitats ranging from lowland swamps to forests, woodlands, and grasslands, and swamps along alluvial plains. These riparian habitats are a mix of tall, dense grasslands interspersed with open forests, side streams, and small lakes surrounded by short grasses. This complex of habitat types provides abundant forage, as well as forest or dense thickets for cover, along with water, not only to drink, but also for creating muddy wallows in which they spend long periods of the day partially submerged.

BEHAVIOR
In early studies made in the Assam region of northwestern India, they formed herds of 10–20 individuals, although up to 100 animals were observed in some groups; these groups were very cohesive. In northern Australia, feral buffalo are abundant and likely exhibit social behavior similar to that expected for wild buffalo in their natural range. Adult females, their young, and sub-adult females form small groups of up to 30 members. Around three years of age, males leave these maternal groups to form all-male groups of up to 10 young bulls. Old males tend to be solitary. Several maternal groups are often loosely organized into a larger herd that together occupy a common home range and may come together nightly. Can frequently be found for long periods during the day immersed in water or lying in muddy wallows.

FEEDING ECOLOGY AND DIET
Primarily grazers, they consume large quantities of grasses, but also eat herbs, aquatic plants, and other vegetation from among the highly productive grasslands and marshes in their home range.

REPRODUCTIVE BIOLOGY
Polygynous. After a gestation of 300–340 days, cows give birth to a reddish brown to yellow-brown calf. Normally, only one calf is born, but occasionally females will give birth to twins. They nurse for 6–9 months. The female typically produces one calf every second year. Females can first mate when 1.5 years old. Males usually do not leave maternal herds until three years old. In some areas, mating and birth show little seasonal periodicity. This can result in calves being found at any time of the year within a herd. In other areas where there are seasonal differences to forage supplies, there can be more distinct mating and birthing periods.

CONSERVATION STATUS
Classified as Endangered. While domesticated water buffalo are very abundant and distributed well beyond their natural historic range, there are probably fewer than 4,000 wild water buffalo left in the world, most of which are in Assam, India. Within the near future, the species faces a high risk of extinction in the wild. Existing populations are very small and restricted to a few nature reserves, most of which are widely separated from each other. The main threats to the species are from hunting and from encroachment by agriculture and livestock. As well, the wild water buffalo is threatened by hybridization with domesticated forms and by diseases transmitted from domestic livestock.

SIGNIFICANCE TO HUMANS
Offer food, hides, and other products to humans. However, their most significant value to humans began 6,000 to 7,000 years ago when they were first domesticated in China near the mouth of the Yangtze River. One of the most important domesticated species in southern and eastern Asia, they are also important in most other subtropical and tropical parts of the world. Large feral populations are established in places such as Australia. Domestic water buffalo continue to provide, in addition to meat, horn, and hides, milk and butter fat. They also provide low cost, accessible sources of power for plowing fields and transportation of people and their crops. ◆

Aurochs
Bos taurus

TAXONOMY
Bos taurus Linnaeus, 1758, Poloniaelig (or Uppsala, Sweden, according to Thomas).

OTHER COMMON NAMES
English: Wild cattle, wild ox; French: Aurochs; German: Ur.

PHYSICAL CHARACTERISTICS
Body length 118 in (300 cm); shoulder height 68.8–72.8 in (175–185 cm); tail length 55 in (140 cm); weight 1,763–2,204 lb (800–1,000 kg). Sexual dimorphism is moderate, with females 20% smaller than males; males had horns, up to 31.5 in (80 cm), that extended sideways and then turned upwards and forwards. Females had notably smaller horns. The legs were somewhat longer than in domestic cattle, and their forequarters were larger than their hindquarters. In northern Europe, the adult males were black-brown with a light streak along the back. This pelage contrasted with a whitish circle around the chin and muzzle. Aurochs were gray-brown in southern Europe and red-brown with a light saddle in Africa.

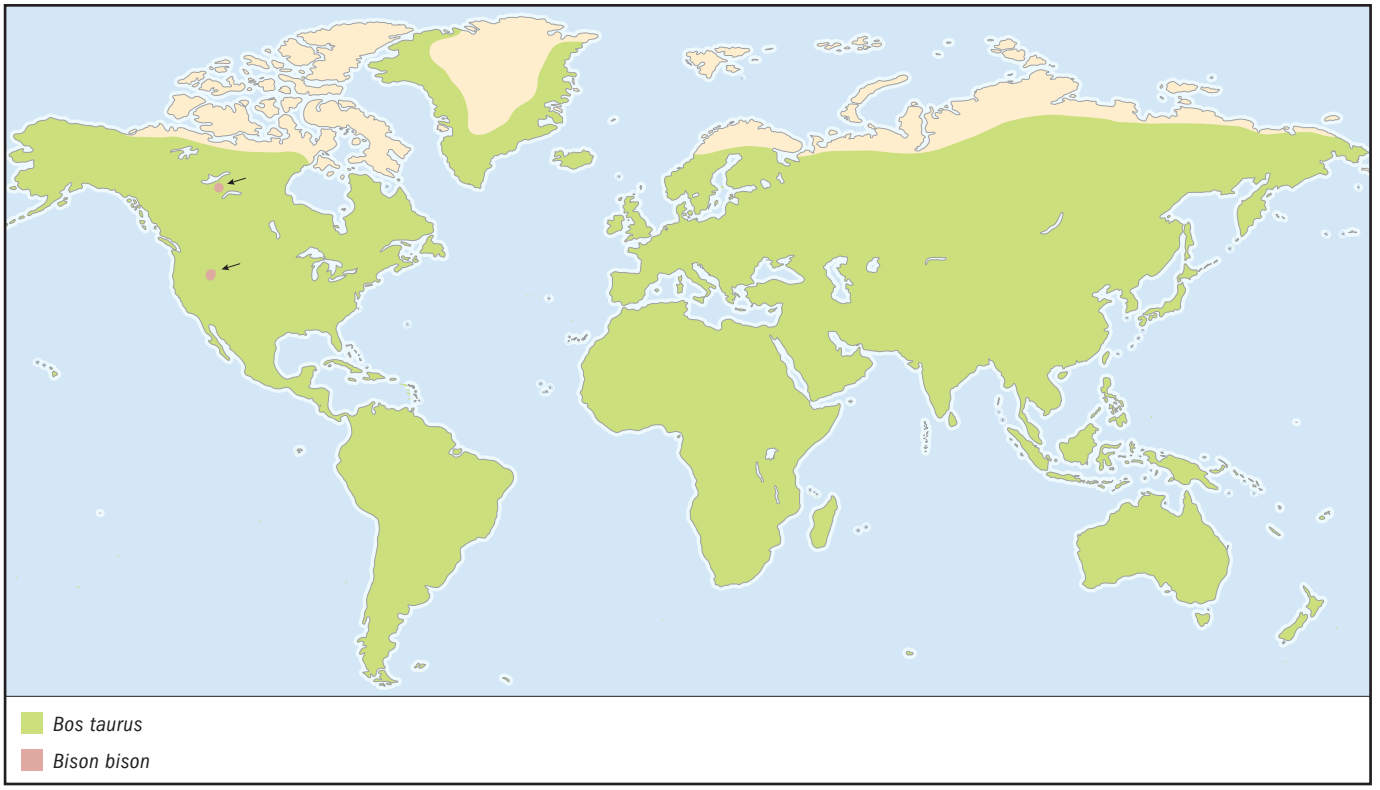
DISTRIBUTION
The original range of wild aurochs was extensive, stretching from Europe to western Russia, and south to the Middle East and northern Africa. Domesticated breeds are now distributed worldwide, except for Antarctica.

HABITAT
Primarily a species of open forests and woodlands with grassy openings. In Europe, such habitat provided abundant forage in the form of grasses, forbs, and browse. These natural pastures included wet meadows and, in the Pyrenees, sub-alpine parklands. In North Africa, they occupied more open steppe habitat.

BEHAVIOR
Groups consisting of adult females with their calves and subadults of both sexes, with adult males living in small all-male groups, except during the mating season.

FEEDING ECOLOGY AND DIET
Beginning in spring and then throughout the summer, aurochs would probably have fed on grasses and forbs, but also browsed on buds and leaves from shrubs and other low vegetation. In fall, they would likely have consumed acorns where available, but still relied primarily on grasses, forbs, and some browse for most of their energy. In winter, they were reported to live on dry leaves in forests. They probably browsed on shrubs and other plants when grasses were unavailable.

REPRODUCTIVE BIOLOGY
Polygynous. Historical accounts indicate calves were born in May and June after a gestation of nine months. Females proba-



bly gave birth first as two-year olds, and males would become fully active in mating by about their fourth or fifth year.

CONSERVATION STATUS
Aurochs is not listed by the IUCN. The last known representatives of the wild form became extinct in Poland in 1627. However, the species in the form of domestic cattle is currently more abundant and widely distributed than ever before.

SIGNIFICANCE TO HUMANS
Aurochs were probably killed for meat and hides by human hunters. However, after domestication, cattle have provided numerous products as well as sources of draft power and transportation. All of these benefits helped facilitate development of human societies and supported agriculture. ◆

American bison
Bison bison

TAXONOMY
Bison bison (Linnaeus, 1758), Canadian River valley, New Mexico, United States.

OTHER COMMON NAMES
French: Bison américain; German: Bison.

PHYSICAL CHARACTERISTICS
Body length males 95.2–125.2 in (242–318 cm), females 68.1–109.4 in (173–278 cm); shoulder height males 65.7–73.2 in (167–186 cm), females 59.8–61.8 in (152–157 cm); tail length males 12.9–35.8 in (33–91 cm), females 11.8–20 in (30–51 cm); weight males 1,199–1,999.5 lb (544–907 kg), females 701–1,201 lb (318–545 kg). High sexual dimorphism, with females 20% shorter in length, but 40% less in weight than males; the largest mammal in North America, it has a broad head that seems to be held low because it is followed by a prominent hump over the shoulders created by elongated spines on the thoracic vertebrae. The hindquarters are much smaller than the forequarters. The legs are short and the tail is medium length, terminating with tuft of black hairs. Pelage is brown to dark brown, with longer hairs on the front and top of the head, along the neck, and onto the shoulders and forequarters, including the forelegs. The hair on the rest of the body is much shorter. The ears are partly hidden among the long fur on the head. Although larger in males, both sexes have a beard of long hairs that extend below the chin. Both sexes also have a fringe of long, dark hair running along the lower margin of the neck as far as the chest to form a noticeable mane. Males have a relatively larger shoulder hump than females and also have longer hair on their heads. Males have short black horns that extend to the side and curve upward, then inward near their sharply pointed tips. Females have horns, but they are more slender, and often shorter and more curved than those of males.

DISTRIBUTION
Historically, they occurred from northwestern Canada to central Canada and then south through much of the United States to northern Mexico. Although there are numerous herds privately managed on ranches and game farms, wild populations are reduced to a few remnant populations and confined to a few parks and reserves in North America.

HABITAT
Inhabited a variety of ecosystems as long as there was sufficient grassland and meadows on which to graze. In northern areas, they inhabited mixed wood forests and parklands as well as ex-

tending into the boreal forests where wet sedge meadows occurred. In more southern regions, they inhabited the long and short grass prairies and parklands across central plains and into the foothills of the Rocky Mountains. Primarily grazers, they relied on grasslands as their primary habitat type, even in northern regions where grasslands and meadows were patchily distributed. Present-day, free-ranging populations occur in areas representative of these primary historic habitats.

BEHAVIOR

Females, calves, and 1–3-year-old males form mixed groups that may contain one or two older males. Additional adult males may join these groups during the rut. Mixed groups tend to be quite cohesive and with strong hierarchies. The three-year-old and older males form small all-male groups of up to 30 animals, although many adult males also occur alone or in pairs. During the rut, these male groups join with female groups. Herds can grow even larger during seasonal migrations. During these migrations bison may travel over 124 mi (200 km) as the animals move to ranges where there is greater forage and shallower snow. Males are polygynous, but an adult male associates with a single female within the larger group. A typical behavior, both sexes wallow; the animals paw a shallow depression in the ground and roll in it.

FEEDING ECOLOGY AND DIET

Bulk feeders, they are typically not highly selective in their food habits. They rely on obtaining large amounts of low-quality forage, rather than small amounts of high-quality forage. Feed almost exclusively on grasses and sedges. Occasionally, they consume forbs and browse, but these food types are minor components of their diet. This dependence on grasses tied bison closely to short and long grass prairies characteristic of the central part of the North American continent.

REPRODUCTIVE BIOLOGY

Mating varies across their geographic range, but mostly takes place during July and August in the southern regions, but extending into September in northern regions. Polygynous. Gestation is on average 285 days, after which they give birth to single calf in spring; twins are very rare. Adult females produce calves usually each year, and generally give birth alone, preferring areas with some taller vegetation for concealment. The calf can run within three hours of birth, and are weaned at 7–12 months. For the first three months of life, they are a reddish brown color that is in marked contrast to the darker pelage of the adults.

CONSERVATION STATUS

Classified as Lower Risk/Conservation Dependent. Historically, they ranged across half of the North American and numbered in the millions. Their range and abundance has been as severely diminished. Wild American bison occur only in several national parks and wildlife reserves in Canada and the United States. However, they also occur on numerous ranches and privately held herds; in fact, there are more bison in private ownership than on public protected areas, thus as a species they are not at risk of extinction. Threats to wild bison come mainly from diseases and parasites transmitted from domestic livestock.

SIGNIFICANCE TO HUMANS

At one time, American bison were the most important game animal for indigenous people across the plains of central and western North America. They provided all manner of uses and products from meat, bones for tools, hides for blankets, leather for garments, and sinews for twine. Skins and horns were also used in ceremonies by Aboriginal peoples. Bison raised on ranches provide a select market for wild game meat and in some places they continue to be desired trophies for hunters. ◆

Chousingha

Tetracerus quadricornis

TAXONOMY

Tetracerus quadricornis (de Blainville, 1816), India.

OTHER COMMON NAMES

English: Four-horned antelope; French: Tetracère; German: Vierhornantiope.

PHYSICAL CHARACTERISTICS

Body length 31.4–43.3 in (80–110 cm); shoulder height 21.6–25.5 in (55–65 cm); tail length 3.9–5.9 in (10–15 cm); weight 33–55 lb (15–25 kg). Unique among Bovinae because the males have two pairs of horns longer pair is 1.9–4.7 in (5–12 cm), smooth, and black, positioned at the top of the head just anterior to the ears; second pair is much smaller, between 0.7–1.5 in (2–4 cm) long, and located on the forehead well between the orbits. Females are hornless, and they exhibit little sexual dimorphism. Pelage is brown to reddish brown on the back, getting lighter on the sides and changing to white along the abdomen and insides of the legs. The anterior surface of each leg is dark brown. The rostrum and forehead is dark brown to blackish. The outer surfaces of the ears are colored similarly and they have an almost-black rim. The upper lip along the sides is white as is beneath the jaw. This changes to a brown neck that is lighter than the back and sides.

DISTRIBUTION

Occur in thickets and wooded areas across most of India and into Nepal; absent from northeast India and the southern quarter of the Indian Peninsula. Occur in many parks and nature reserves, but are increasingly absent from lands outside these protected areas.

HABITAT

Occupy a variety of habitats such as dry deciduous, dry deciduous scrub, and southern tropical moist mixed deciduous forest types. Many of these forests occur in hilly terrain, but have some flatter areas providing small grassy openings. They frequent these meadows and other small openings, but never stray far from dense thickets of bushes or bamboo where they quickly retreat when disturbed. These landscapes are generally dissected with streams and small rivers, and they are frequently seen near water.

BEHAVIOR

Normally found as solitary or in groups of two. During the rut, males are aggressive towards other males. Individuals seem to occupy the same home range year-round.

FEEDING ECOLOGY AND DIET

Eat a variety of plants and plant parts. As they travel their diverse habitats, they consume leaves of shrubs, shoots, fruit, and grasses.

REPRODUCTIVE BIOLOGY

Mating occurs over a somewhat protracted breeding season from June through September and coincides with monsoon rainy season. Polygynous. Gestation is 7.5–8 months; most young are born February through March. Adult females give birth to between one to three young.

CONSERVATION STATUS

Classified as Vulnerable. Although they are still widely distributed in their historical range, local populations face threats from hunting for meat and loss of habitat to deforestation as well as degradation of habitat due to grazing by livestock. Other conservation concerns are that the areas occupied by chousingha are increasingly becoming isolated as habitat fragmentation proceeds through agricultural practices.

SIGNIFICANCE TO HUMANS

The species has little significance to humans other than its unique curiosity as the only mammal with four horns. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
European bison *Bison bonasus* Spanish: Bisonte europeo	Short hair in neck area, pelage is same color as relatives. Horns are well-developed. Average female weight 662–1,190 lb (300–540 kg), male 882–2,028 lb (400–920 kg).	Temperate coniferous forest like Bialowieza. For feeding, prefer areas of vegetation at least 20 years old. Remain in large groups during winter and break into male-oriented groups during calving season. Most of life is spent feeding and resting.	Extinct except where reintroduced — eastern Poland, western Russia, and Caucasus Mountains.	Grasses, mosses, trees, and shrubs.	Endangered
Gaur *Bos frontalis* French: Gaur	Coat is short, dense, and dark brown. Lower legs white to tan, dewlap under shin extends between front legs. Shoulder hump pronounced in adult males. Horns found on both sexes. Bulging gray-tan ridge connects horns on forehead. Head and body length 98–130 in (250–330 cm), shoulder height 67–87 in (170–220 cm), tail length 27–39 in (70–100 cm), weight 1,543–2,205 lb (700–1,000 kg).	Tropical woodlands, but have been largely disturbed. Diurnal, live in groups led by a single male.	India; Nepal; Myanmar; Thailand; south Tibet and Yunnan, China; southern Vietnam; Cambodia; and Peninsular Malaysia.	Grasses, shoots, and fruit.	Vulnerable
Banteng *Bos javanicus* French: Banteng	Males are dark chestnut brown, cows and juveniles are reddish brown. Both sexes carry horns. Considered the most beautiful of all wild cattle. Adult male weight 1,400–1,760 lb (635–798 kg), females 1,320–1,500 lb (600–680 kg). Average life in wild is 11 years.	Open, dry, deciduous forests. Generally occur in groups of 10–30 individuals.	Myanmar, Thailand, and Indochina south to northern Peninsular Malaysia; Java; Borneo; introduced to Australia, Bali Island, Sangihe and Enggano Islands; and domesticated in Southeast Asia.	Grasses, bamboo, leaves, fruit, and young branches of woody shrubs.	Endangered
Kouprey *Bos sauveli* French: Boeuf gris cambodgien; Spanish: Kouprey, toro cuprey	Dark brown or black. Body is massive, legs are long, backs are humped.	Prefer open deciduous forests, grasslands, wooded grasslands, and patches of closed monsoon forest. Nocturnal.	Cambodia, southeast Thailand, southern Laos, and western Vietnam.	Primarily grazers, but will also consume fruit.	Critically Endangered
Nilgai *Boselaphus tragocamelus*	Large body with short, smooth horns in males. Gray to brownish gray in males, females and young are brown to orangish. Patches of white on face and below chin. White "beard" or tufts of hair present. Stands 46–60 in (119–150 cm) at the s houlder. Weight 240–275 lb (109–306 kg).	Ranges from level ground and thin brush with scattered trees, to cultivated plains. Usually herd in small groups of 10 individuals.	Eastern Pakistan and northern India south to Bombay and Mysore; and introduced into Texas, United States.	Mixed feeders, preferring browse, short grass, and agricultural crops.	Lower Risk/ Conservation Dependent
Anoa *Bubalus depressicornis* French: Anoa des plaines; Spanish: Anoa de ilanura	Young have thick, yellowish brown, woolly hair. Adults have thick, black skin with white or yellowish white stockings on each foreleg. Sometimes there are blotches of white on throat or nape. Horns are triangular and wrinkled. Weight 198–662 lb (90–300 kg).	Lowland forests including secondary formations and swampy areas, along coasts, and also at high elevations in mountainous areas. Aggressive toward humans. Can live up to 30 years.	Sulawesi.	Grasses, ferns, saplings, palm, ginger, and fallen fruit.	Endangered
Bushbuck *Tragelaphus scriptus*	Males have horns that spiral once and are parallel to one another. Both sexes have white spots and stripes, patterns vary geographically. Weight ranges from 88 to 176 lb (40–80 kg), males being larger than females.	Forest edges or brushy covers near rivers or streams. Aggressive, nocturnal, good swimmers. Generally solitary, but have been seen in small groups.	Southern Mauritania to Ethiopia and southern Somalia, and south to northern Namibia and South Africa.	Herbs, leaves, twigs, and flowers.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Greater kudu *Tragelaphus strepsiceros*	Tallest antelopes, shoulder heights range from 39 to 60 in (100–150 cm). Large horns, body coloration varies from reddish brown to blue-gray, with darkest individuals in southern populations. Six to ten stripes along backs, tails tipped with white undersides. Males have beards. Average weight 265–695 lb (120–315 kg).	Areas where adequate cover is provided, including bushes and thickets. Live in temporary groups of one to three individuals.	Southern Chad, northern Central African Republic, western and eastern Sudan, north-east Uganda, Ethiopia and Somalia south and southwest to South Africa, Namibia, Angola and southeast Democratic Republic of the Congo (Zaire).	Herbs, fruits, vines, flowers, and some new grass.	Lower Risk/ Conservation Dependent
Mountain nyala *Tragelaphus buxtoni*	Coat is grayish chestnut or sandy gray-brown. Males are larger than females and have spiral-shaped horns. Head and body length 75–102 in (190–260 cm), tail length 7–10 in (20–25cm), adult weight 330–660 lb (150–300 kg).	High-altitude woodland, bush, heath, moorland, and valley-bottom grassland. Travels in small groups of two to 13 animals.	Ethiopia, east of Rift Valley.	Herbs, shrubs, grasses, ferns, and lichens.	Threatened

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Bovids II
Hartebeests, wildebeests, gemsboks, oryx, and reedbucks
(Hippotraginae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subfamily Hippotraginae

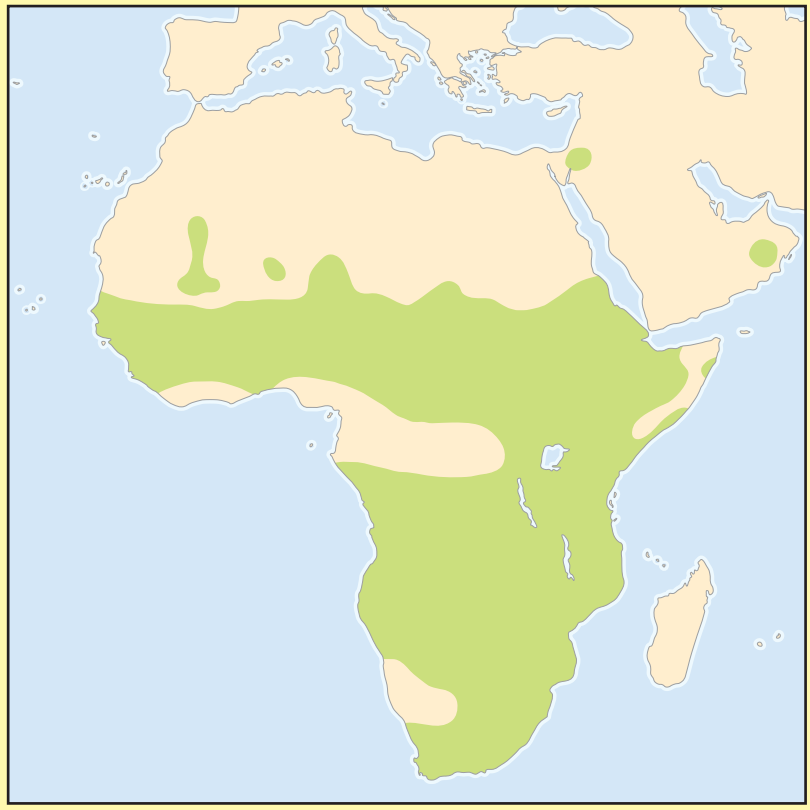
Thumbnail description
Medium to large grazing antelopes, slender to heavily built; male horned (also female in some species); color white, gray, brown, red-brown, or black; some with prominent facial markings

Size
Body length 3.5–8.8 ft (105–265 cm); shoulder height 2.1–5.3 ft (65–160 cm); tail 4 in to 3.3 ft (10–100 cm); 42–680 lb (19–309 kg); horns 6 in to 5.5 ft (15–165 cm)

Number of genera, species
7 genera; 23 extant species, 1 recently extinct

Habitat
Dry to wet grasslands, wetlands, light woodland, savanna, and deserts up to 16,400 ft (5,000 m)

Conservation status
Recently Extinct: 1 species; Extinct in the Wild: 1 species; Critically Endangered: 2 species; Endangered: 1 species; Lower Risk/Near Threatened: 1 species; Lower Risk/Conservation Dependent: 18 species



Distribution
Africa and Arabia

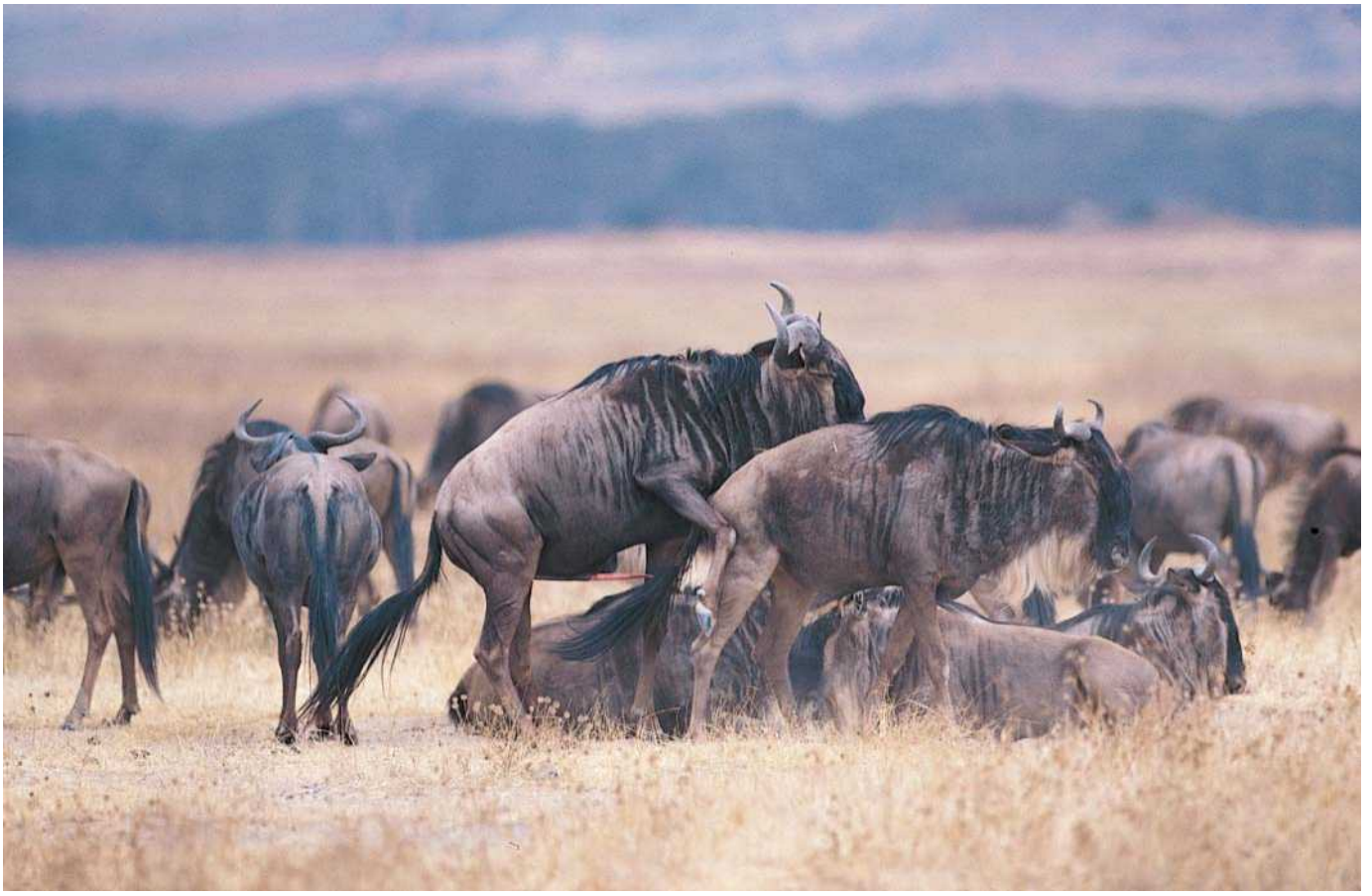
Evolution and systematics

The subfamily Hippotraginae, the grazing antelopes, includes 24 species in 11 genera. Fossil bovids first appear in early Miocene deposits; the earliest African material being from Libya about 20 million years ago. Analysis of mitochondrial DNA suggests there was a rapid radiation of the family in that period, perhaps in association with the emergence of savanna habitat in Africa, and that all living lineages had arisen by 16–17 million years ago (mya).

The subfamily classification used recognizes three tribes. The Reduncini includes nine species in three genera: *Redunca* (reedbucks) comprises the southern reedbuck (*R. arundinum*), bohor reedbuck (*R. redunca*), and mountain reedbuck (*R. fulvorufula*). *Kobus* contains the waterbuck (*K. ellipsiprymnus*), the lechwe (*K. leche*) and Nile lechwe (*K. megaceros*), the kob (*K. kob*), and the puku (*K. vardonii*). The gray rhebok (*Pelea capreolus*) is also included, although its classification is controversial and it is sometimes placed in its own subfamily (Peleinae), or even with the dwarf antelopes (Antilopinae; Neotragini) or goats (Caprinae).

The Alcelaphini, with eight species in five genera, includes the black wildebeest (*Connochaetes gnou*), the blue wildebeest (*C. taurinus*), the sassabies, and the hartebeests. The sassabies comprise three species: Hunter's hartebeest (*D. hunteri*), the blesbok and bontebok (*D. pygargus*), and the topi (*D. lunatus*), while the hartebeests include the hartebeest (*Alcelaphus buselaphus*) and Lichtenstein's hartebeest (*A. lichtensteini*). The impala (*Aepyceros melampus*) is sometimes placed in the Antilopinae, or in its own subfamily (Aepycerotinae), but it is now thought to be an early offshoot of the Alcelaphini.

The horse-like antelopes (Hippotragini) have seven species in three genera. *Hippotragus* contains the extinct bluebuck (*H. leucophaeus*), the roan (*H. equinus*), and the sable (*H. niger*), plus three oryx species, the scimitar-horned oryx



Wildebeest (*Commachaetes taurinus*) mating, Ngorongoro Crater, Tanzania. (Photo by Animals Animals ©A. & M. Shah. Reproduced by permission.)

(*Oryx dammah*), the Arabian oryx (*O. leucoryx*), and the gemsbok (*O. gazella*). The addax (*Addax nasomaculatus*) is also included.

Some authorities elevate these tribes to subfamily status (Reduncinae, Alcelaphinae, and Hippotraginae).

Alcelaphines appeared first in the fossil record about five mya and appear to be almost wholly African in their evolution. Early Pleistocene remains of *Pelea* are known, while *Hippotragus* species and the southern reedbuck first appear in the middle and upper Pleistocene. Earlier *Redunca* species appeared in the late Pliocene or lower Pleistocene, at which time the first *Kobus* fossils are recorded. Fossil Aepycerotine over three million years old are known from East Africa.

Physical characteristics

The Reduncini is an assemblage of medium to large species, the males having strongly ridged horns that are short and curve forward at the tips in reedbucks, but long and lyre-shaped in most *Kobus* species. The reedbucks are pale brown in color, with short hair. *Kobus* species have a long, rough coat. Color varies from yellowish brown to mid-brown or bright chestnut, males being darker, some almost black. The underparts are white, and there is also white on the rump and often on the face. Lechwes are higher at the hindquarters than at the shoulders, and have long pointed hooves and large pseudo-claws, an adaptation to their semi-aquatic existence. The smallest species, the gray rhebok, is lightly built with short, almost vertical horns and a grayish woolly coat.

With the exception of the impala, the Alcelaphini are medium to large, with horns in both sexes, either smooth and initially curving downward (*Connochaetes*) or upright, ridged basally and twisted (other genera). They have long heads, elevated shoulders, and thin legs. Color varies from gray to reddish brown or almost black. Wildebeests have a mane, a beard, and a very long, tufted tail; the black wildebeest also has a tuft of stiff hairs on the face. The impala is medium sized, slender and gazelle-like, with long, lyrate horns only in the male.

The Hippotragini are large and horse-like, with a long, tufted tail. Both sexes have long, ridged horns that may be straight, backwardly curved, or spirally twisted. All species except the addax have a mane. Colors range from white, cream, or gray (desert species) to chestnut; sable bulls are black. There is often a conspicuous head pattern. Desert species have large, widely splayed hooves for traveling in sand. The extinct blue antelope was a smaller, lightly built species, standing only 3.3–3.9 ft (100–120 cm) high at the shoulder, with a blue-gray coat and curved, swept-back horns.

Blue wildebeest (*Connochaetes taurinus*) at a waterhole in Etosha National Park, Namibia. (Photo by Animals Animals ©Ana Laura Gonzalez. Reproduced by permission.)

Distribution

The Hippotraginae are confined to Africa and Arabia. The members of the tribe Reduncini are grassland and wetland antelopes, the bohor and southern reedbuck occupying northern and southern lowland savannas, respectively, while the mountain reedbuck occurs in three widely separated relict populations in Cameroon, East Africa, and southeast Africa. The waterbuck is widespread in sub-Saharan savannas, the *ellipsiprymnus* group of subspecies ranging from East Africa to southern Africa, almost entirely east of the Great Rift Valley, and the *defassa* group occurring west of the rift. The lechwes are confined to wetlands of central-southern Africa and Sudan/Ethiopia, while the kob and the puku occur in the northern and southern savanna zones, respectively. The gray rhebok is confined to upland areas of South Africa, Lesotho, and Swaziland.

In the Hippotragini, the roan antelope ranges from Senegal east to Ethiopia and south to South Africa, while the sable antelope is largely confined to eastern Africa. The other members of this tribe are dry-country species: the addax and the scimitar-horned oryx occur in the Sahel and Sahara zones, the Arabian oryx in the Arabian peninsula, and the gemsbok in East Africa and southwestern Africa.

Restricted-range species within the Alcelaphini include the blesbok/bontebok of South Africa and Hunter's hartebeest of Kenya and Somalia. The topi has a fragmented distribution in savannas from Senegal east to Ethiopia and south to South Africa. Lichtenstein's hartebeest occurs in savanna from East Africa to southern Africa, while the red hartebeest ranges from Senegal to Somalia and south to Tanzania, and from southern Angola to Zimbabwe and South Africa. The blue wildebeest occurs in grasslands from Kenya and Angola to South Africa, but the black wildebeest only in South Africa. The impala is widespread in savanna woodland from Kenya to Angola and South Africa.

Habitat

The Hippotraginae have colonized all African grassland habitats from permanently inundated swamps to montane grasslands, the dry Sahel region, and the Sahara and Namib deserts.

Oryx species and the addax frequent the most arid areas. Addax are true desert antelopes, while gemsbok occur in grassland, dry steppe, light open woodland, brush savannas, and stony plains, as well as semi-desert and desert. Scimitar-horned oryx favored semi-desert and grassy steppes, while Arabian oryx occupied similar habitat in the Arabian and Sinai peninsulas. The other two members of the Hippotragini, the roan and sable antelopes, inhabit moist grasslands and open woodlands.

The Alcelaphini occupy the fertile grasslands and woodlands of the moist northern and southern savannas. The topi specializes on the grass of valley bottoms and intermediate vegetation zones. Red hartebeest favor the margins of woods, scrub, and grassland, while Lichtenstein's hartebeest prefers mixed open woodland and floodplain grassland. Blesbok, bontebok, and black wildebeest occur in South African grasslands, while the blue wildebeest ranges over open grasslands and

Gemsbok (*Oryx gazella*) live in arid areas of Africa and can survive days without drinking water. (Photo by David M. Maylen III. Reproduced by permission.)

Hartebeest (*Alcelaphus buselaphus*) grazing in Etosha National Park, Namibia. (Photo by Animals Animals ©Peter Weimann. Reproduced by permission.)

woodlands of the southern savannas, being particularly common where grass is short after fire or grazing by other species. The impala inhabits the open woodlands in central and southern Africa.

Wetlands and montane grasslands are the home of the Reduncini. The southern and bohor reedbucks inhabit lowland floodplains and inundated grasslands of the southern and northern savannas, respectively, while the waterbuck lives in savanna and woodland adjacent to wetlands. Lechwe occur at floodplains and seasonally inundated swamps, while the puku and the kob inhabit moist savannas, floodplains, and the margins of adjacent light woodland. The mountain reedbuck and gray rhebok inhabit upland grasslands, the rhebok often in more exposed and rocky situations.

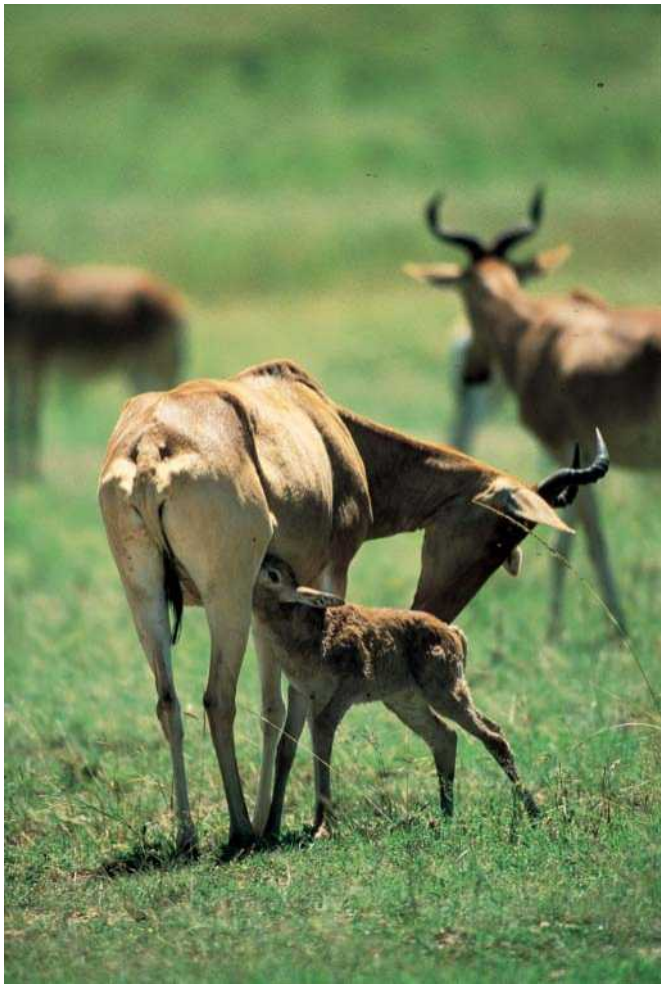
Behavior

Most species are most active in the early morning and late afternoon. Some such as the roan antelope and the desert oryx species are also active at night. The southern reedbuck is largely nocturnal when food and water are plentiful, but becomes more active during the day in the dry season. Desert oryx species and the addax excavate scrapes with their front legs in the shade of bushes or rocks, in which they rest during the heat of the day.

Socialization is poorly developed in the reedbucks and the gray rhebok, which live singly or in pairs, or in small groups of females and young that either live within the territories of single males or range over a few male territories. The other species in the subfamily are more social and occur in larger groups. In most species, adult males hold territories (often year-round), females and young form herds, often with a distinct hierarchy and led by a dominant female, and non-territorial adult males form bachelor herds. During the rutting season, territorial males mate with females from herds entering their territories.

Lechwe occur in large aggregations, while kob and topi also sometimes occur at a high density. In such situations, these species usually maintain territorial breeding grounds (leks) during the rut. When population density is not high, kob and topi do not lek, but individual males hold small territories.

Addax and oryx have a tight social structure, with a smallish herd centered on one or more adult bulls and with a hierarchy of adults of both sexes.



Coke's hartebeest (*Alcelaphus buselaphus cokii*) mother and calf. (Photo by David Madison. Bruce Coleman, Inc. Reproduced by permission.)

Several different methods are used to mark territories. Reduncines lack functional pedal and pre-orbital glands and do not physically mark the habitat; reedbuck advertise the territory by whistling. Rhebok mark the territory with urine and preputial gland secretions. The Alcelaphini use pedal glands and dung middens, while facial or pre-orbital gland secretions are mainly used to mark the body. Sable use visual marks (vegetation damage), feces, pedal scent, and display.

Elaborate dominance displays and appeasement behavior often replace or reduce aggression, and it is uncommon for serious injury to result from fighting. However, gray rhebok sometimes have serious fights in which individuals are killed. Sable, roan, and the Alcelaphini are unusual in that males fight in a kneeling position. The demands of a hierarchical society have given rise to unique ritualized oryx tournaments, in which herd members run around in circles with sudden spurts of galloping and ritualized pacing interspersed with brief horn clashes.

Courtship displays include approaching in an erect or a low stretch posture, prancing with nose-lifting, male walking behind female (mating march), foreleg-lifting, and urine testing (in gray rhebok, impala, the Hippotragini, and the wildebeests).

Many species wander in response to the availability of food. Lechwe follow the rising and falling waters of their floodplain habitats, feeding on exposed grasses. Scimitar-horned oryx migrate seasonally in search of grazing areas. Blue wildebeest may be sedentary, nomadic, or migratory, depending on the local distribution of rain and green grass; the regular and spectacular migrations of the herds in the Serengeti of Tanzania are famous.

Feeding ecology and diet

The Hippotraginae are primarily grazers, although several species also browse during the dry season, while desert and semidesert species supplement a basic diet of grass with food such as acacia seed pods, wild melons, cucumbers, tubers, and bulbs.

The addax is adapted to coarse food and the absence of water in its desert habitat. It can apparently sense patches of

Gemsbok (*Oryx gazella*) mating interaction. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Gemsbok (*Oryx gazella*) running on the Etosha Plain, Etosha, Namibia. (Photo by J & D Bartlett. Bruce Coleman, Inc. Reproduced by permission.)

vegetation at long distance and obtains sufficient water from its food. The scimitar-horned oryx eats a variety of grasses and forbs, utilizing plants with relatively high water and protein content. Because of its ability to locate these plants, and to physiologically conserve water, it is capable of going for long periods without drinking. The gemsbok can go without water for several days, but drinks at streams and waterholes when water is available. Oryx are experts at finding water and often dig into dried riverbeds to access ground water. Roan and sable are mainly grazers, but will also browse, particularly during the dry season.

The mountain reedbuck is adapted to a coarse, fibrous diet and can go for long periods without water. The other reedbuck species, and the waterbuck, predominantly graze on grasses and reed shoots. Lechwe eat mainly grasses, but also eat sedges and other semi-aquatic plants, and often graze in water up to shoulder height. Pukus also predominantly eat grasses. The gray rhebok predominantly browses on shrubs and forbs.

Wildebeest eat grass, but the black wildebeest will browse during the winter. Blue wildebeest prefer areas of short grass, especially that sprouting on burnt areas or after rain. The sassabies are almost exclusively grazers, while the impala is an intermediate mixed feeder, largely grazing in the rains, but often browsing extensively in the dry season.

Reproductive biology

Reproductive cycles are often closely linked to the annual rainfall pattern so that, in regions with distinct rainy and dry seasons, births often peak in or near the rains. However, several species show no marked seasonal peak in breeding, for example, the Arabian oryx and the beisa oryx produce calves in any month, while roan produce a calf about every 10.5 months.

All Hippotraginae species bear single offspring, although waterbuck occasionally have twins. Estrus lasts for a day in territorial species and several days or more in non-territorial species. Gestation is 8–9 months in larger species and 6.5–8 months in the smaller species, but the gray rhebok has a nine-month gestation period.

In most species, the female leaves the herd or family group to give birth. Most species produce relatively helpless young that lie hidden for a period varying from only 1–2 days (impala) to two months or more (reedbucks). However, female wildebeest bear calves within the herd and the young can run a few minutes after birth. Young tsessebe (*Damaliscus l. lunatus*) are also able to keep up with the herd from shortly after birth.

Females return to hidden calves to suckle them. In herding species, calves associate together when they rejoin the herd, returning to the mother for nursing and in emergen-

A common reedbuck (*Redunca arundinum*). (Photo by © Image Ideas, Inc./PictureQuest. Reproduced by permission.)

cies. In most species, weaning takes place at 6–8 months, but blesbok, topi (*Damaliscus lunatus jimela*), and black wildebeest are weaned at four months. Addax and scimitar-horned oryx, which live in very arid environments where water is at a premium, wean their young at only 3.5 months. In contrast, young Lichtenstein's hartebeest are not weaned until they are 12 months old.

In most species, females begin breeding when 1–2 years old. Males may be sexually mature at 18 months to 2 years, but often have to wait for several more years before they can occupy a territory; they do not breed until 4–6 years of age. Longevity varies with species, being about 10 years in some (e.g., reedbuck) and reaching 20 years in the black wildebeest, scimitar-horned oryx, and Lichtenstein's hartebeest.

Conservation status

Populations of all species have suffered declines in recent years, and their ranges have been reduced, largely as a result of habitat loss (especially due to agriculture and competition from domestic stock), human disturbance, hunting, and poaching. Droughts and disease have also seriously affected some species. Wetland-dependent species have been affected by damming and draining; for example, after the damming of the Kafue River for a hydroelectric scheme in 1978, the population of the Kafue lechwe (*Kobus leche kafuensis*), originally about 94,000, was halved. As a result of these factors, the survival of all species is of concern.

The bluebuck is the first historically recorded African mammal to become extinct. It may have been declining from natural causes since the Pleistocene and its grazing habitat may have been adversely affected by the introduction of domestic sheep from about A.D. 400. In the eighteenth century, the first European settlers found it relatively uncommon, occurring only in a small coastal area of the southwestern Cape. It was quickly driven to extinction by hunting and settlement pressure, and was last recorded in 1799–1800.

Two races of living species have also become extinct recently. Roberts' lechwe (*Kobus leche robertsi*) occurred in northwestern Zambia, while the bubal hartebeest (*Alcelaphus b. buselaphus*) was formerly widespread in North Africa, but died out in the late 1920s.

The scimitar-horned oryx once ranged through much of the Sahelian grassland and scrubland on the northern and southern fringes of the Sahara. There have been no sightings in the wild since the late 1980s, and it is listed as Extinct in the Wild. It is a victim of habitat loss from overgrazing, droughts, warfare, hunting, and competition with domestic cattle. Worldwide, at least 1,250 are kept in zoos and private facilities, and more than 2,000 are on ranches in Texas. It is the second most common antelope in captivity. Since 1985, reintroductions have been made to national parks in Tunisia, Morocco, and Senegal.

Two species and one race are Critically Endangered. The addax is now reduced to about 250 individuals in the wild. Hunter's hartebeest had declined to about 300 individuals in 1995; apparently, only one exists in captivity. Competition with domestic cattle played a large role in its decline, although severe drought and poaching are also factors. The giant sable (*Hippotragus niger variani*) of northern Angola has an uncertain future.

The Endangered Arabian oryx has been saved from extinction by captive breeding in zoos. The red hartebeest, formerly abundant and widespread throughout much of Africa, has suffered a great reduction in range and numbers from hunting, habitat modification, and competition from cattle. The subspecies *swaynei* and *tora*, formerly occurring

Gemsbok (*Oryx gazella*) males in territorial dispute. (Photo by K & K Ammann. Bruce Coleman, Inc. Reproduced by permission.)

Gemsbok (*Oryx gazella*) grazing in South Africa. (Photo by Dr. Eckart Pott. Bruce Coleman, Inc. Reproduced by permission.)

from Egypt to Somalia, are Endangered. Much of their remaining range in Sudan and Ethiopia was devastated by drought in the 1980s and few are thought to survive. Also Endangered is the western mountain reedbuck (*Redunca fulvorufula adamauae*), confined to Cameroon and Nigeria.

The five Vulnerable races include the bontebok, the black-faced impala, and the korrigum (*Damaliscus lunatus korrigum*), found from Senegal to Cameroon. Two races of the lechwe are Vulnerable: the black lechwe (*K. l. smithemani*) of north-eastern Zambia and the Kafue lechwe (*K. l. kafuensis*) of the Kafue Flats in southern Zambia.

In addition, 18 species are classed as Lower Risk/Conservation Dependent, and the Nile lechwe as Lower Risk/Near Threatened.

Significance to humans

The Arabian oryx was one of the earliest semi-domesticated animals. Herds were kept in ancient Egypt, and oryx meat was apparently a regular food item of Solomon's household. The species also appears in Roman mosaics and Juvenal records that gourmets approved its meat. Oryx horns have had a phallic significance for many cultures and are sought after as charms. The legendary unicorn was possibly based on the Arabian oryx.

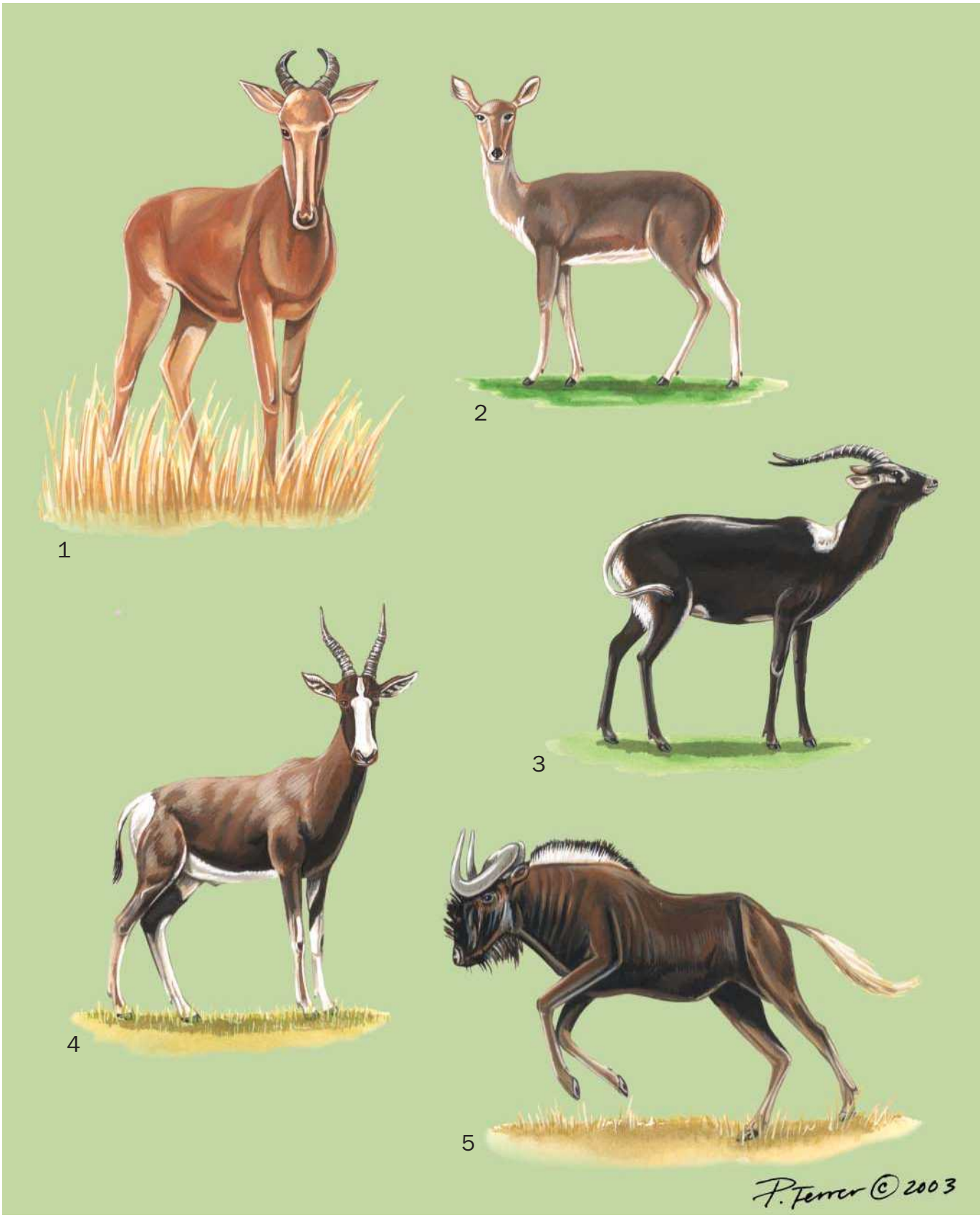
Addax were also kept in large numbers in ancient Egypt. They were stabled, fed from troughs, led on a bridle, and were probably slaughtered for ceremonies. The ancient Egyptians are also said to have domesticated hartebeest, but probably not particularly successfully, as in captivity this animal is difficult to breed and is aggressive.

In some parts of Masailand, East Africa, blue wildebeest were formerly captured as calves and run with cattle, while lactating females were used to feed cattle calves and thus save cows' milk for human consumption. In East Africa, young bohor reedbuck are sometimes reared in captivity and herded with goats.

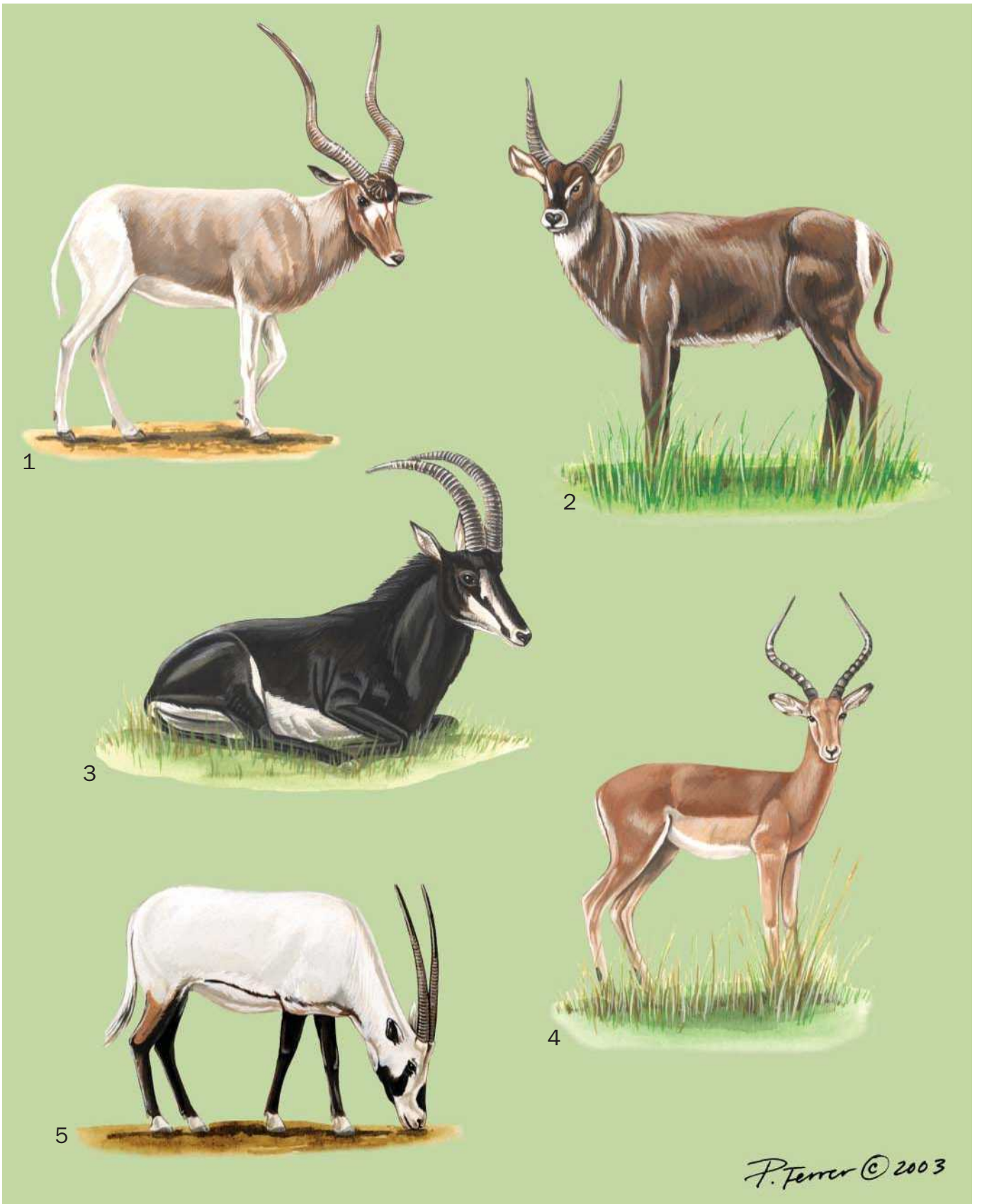
Hippotraginae species have always been hunted for their meat, hides, and horn by the indigenous peoples of Africa and Arabia. The more recent history of these antelopes has been one of increasing persecution and elimination, not only by subsistence hunting, but also for sport and trophies, and because they potentially compete with expanding agriculture and human settlement for habitat.

The diet of the Alcelaphini and of cattle is broadly similar so that these antelope have come to be regarded as competitors for grazing land, and populations have thus been persecuted and often largely exterminated as a result of livestock expansion. Large populations of kob and other reduncines are unlikely to survive unless their potential for sustained yield cropping is realized. The kob is especially suited to this, while the topi can coexist with cattle after the carrying capacity for livestock has been reached and thus has potential for multiple land-use. Impala, which are numerous on many cattle ranches, are commonly cropped for their meat and hides.

Hippotragine antelopes are very popular in zoos and on farms and ranches, and such institutions have played a great part in maintaining captive populations of several endangered species and in building up stocks for reintroductions.



1. Lichtenstein's hartebeest (*Sigmoceros lichtensteinii*); 2. Southern reedbuck (*Redunca arundinum*); 3. Nile lechwe (*Kobus megaceros*); 4. Blesbok/bontebok (*Damaliscus pygargus*); 5. Black wildebeest (*Connochaetes gnou*). (Illustration by Patricia Ferrer)



1. Addax (*Addax nasomaculatus*); 2. Waterbuck (*Kobus ellipisprymnus*); 3. Sable antelope (*Hippotragus niger*); 4. Impala (*Aepyceros melampus*); 5. Arabian oryx (*Oryx leucoryx*). (Illustration by Patricia Ferrer)

Species accounts

Southern reedbuck
Redunca arundinum

TAXONOMY
Antilope arundinum (Boddaert, 1785), Cape of Good Hope, South Africa. Two subspecies.

OTHER COMMON NAMES
English: Common reedbuck; French: Cobe des roseaux; German: Grossriedbock; Spanish: Redunca comun.

PHYSICAL CHARACTERISTICS
Body length 4–5.3 ft (120–160 cm); shoulder height 2.1–3.5 ft (65–105 cm); tail length 7.2–12 in (18–30 cm); 86–209 lb (39–95 kg); female smaller than male. Horns 10–18.4 in (25–46 cm). Light brown to gray brown with whitish rings around eyes. Bushy tail is white underneath.

DISTRIBUTION
Subspecies *R. a. occidentalis*: southern Gabon to Democratic Republic of the Congo, northern Angola and Tanzania, Zambia, and probably northern Malawi and Mozambique; subspecies *R. a. arundinum*: northeastern Namibia, Botswana, Zimbabwe, Mozambique, and eastern South Africa.

HABITAT
Valley and upland grasslands. Requires tall grass, reedbeds, or herbaceous cover, and water.

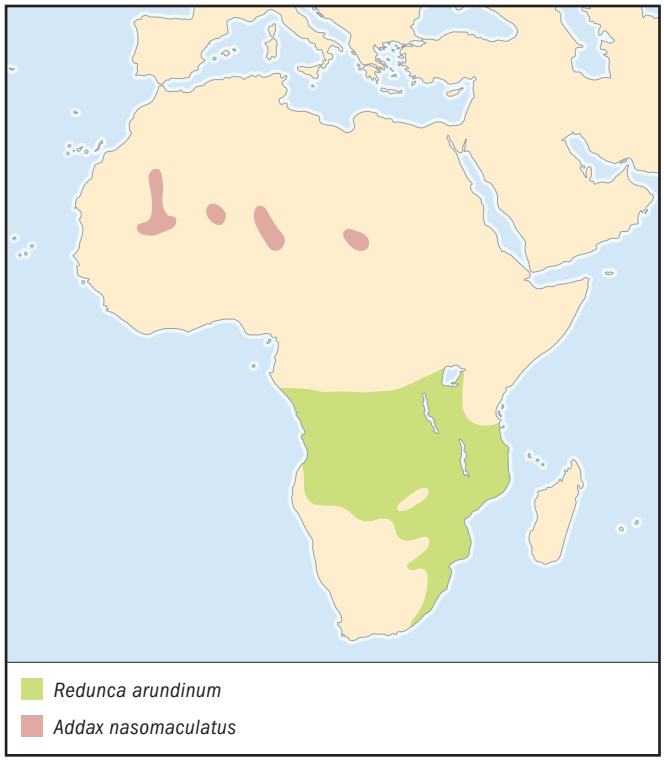
BEHAVIOR
Old bucks hold permanent territories, usually with an attendant female; other individuals solitary, or in loose herds of up to 20 animals in the dry season. Runs with an odd rocking-horse motion; characteristic call is a shrill whistle.

FEEDING ECOLOGY AND DIET
Eats grasses and reed shoots; may browse during dry season.

REPRODUCTIVE BIOLOGY
Polygynous. Gestation period 7.5 months. Births occur all year, but peak December–May. Weaning age unknown; sexually mature at 1.5 years. Lifespan 10 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Range and numbers reduced significantly in some areas due to habitat loss and hunting; in Malawi, now largely confined to reserves.

SIGNIFICANCE TO HUMANS
Hunted for sport and for food. ◆



Waterbuck
Kobus ellipsiprymnus

TAXONOMY
Antilope ellipsiprymnus (Ogilby, 1833), Molopo River, Lataku, Namibia.

OTHER COMMON NAMES
English: Common waterbuck, defassa waterbuck; French: Cobe à croissant, cobe defassa; German: Ellipsenwasserbock, Defassa Wasserbock; Spanish: Antilope aquatico.

PHYSICAL CHARACTERISTICS
Body length 6–7.3 ft (180–220 cm); shoulder height 3.3–4.3 ft (100–130 cm);tail 8.8–18 in (22–45 cm); males 470–680 lb (217–308 kg), females 350–400 lb (158–181 kg). Horns 1.6–3.3 ft (55–100 cm). Long, shaggy brown-gray coat with conspicuous white ring encircling rump.

DISTRIBUTION
The *ellipsiprymnus* group (white ring on rump): eastern Africa from southern Somalia south through Kenya, Tanzania, Malawi, eastern and southern Zambia, and Zimbabwe, to extreme southeast Namibia (Caprivi), southern Botswana, central Mozambique, and extreme northeastern South Africa (Zululand); *defassa* group: Senegal east to Ethiopia and south to Angola, east and southeast Democratic Republic of the Congo, and most of Zambia; hybrids with *ellipsiprymnus* group occur in areas of overlap.

HABITAT
Always associated with water; principally in grassland habitats, especially floodplains, small drainage systems, and valleys; also rocky hills, savanna, scrub, and woodland.

BEHAVIOR
Groups of up to 30 females and young wander over a home range of 494–1,483 acres (200–600 ha), which encompasses several male territories. At 5–7 years, males become territorial, staking out areas of 150–625 acres (61–253 ha). About 5–10% of mature males are territorial.

FEEDING ECOLOGY AND DIET
A grazer, eating protein-rich medium and short grasses; sometimes feeds in water. Also eats foliage, reeds, and herbs when green grass is unavailable. Requires permanent access to water.

REPRODUCTIVE BIOLOGY
Polygynous. Breeds throughout the year. Gestation period 8.5–9 months; weaned at 6–7 months; females sexually mature at 12–14 months, males at 14–18 months. Lifespan 18 years.

CONSERVATION STATUS
Both races are Lower Risk/Conservation Dependent. Populations are apparently decreasing due to poaching and human encroachment along riverine habitat, and protected areas are important for the species' survival.

SIGNIFICANCE TO HUMANS
Hunted for sport, creating a strong motive to provide effective protection and management. Waterbuck have a high exhibit value in zoo collections. ◆

Nile lechwe
Kobus megaceros

TAXONOMY
Antilope megaceros (Fitzinger, 1855), Sobat River, Bahr-el-Ghazal, Sudan. Monotypic.

OTHER COMMON NAMES
English: Mrs. Gray's lechwe; French: Cobe leche du Nil; German: Nile litschi; Spanish: Lechwe de Nilo.

PHYSICAL CHARACTERISTICS
Body length 4.5–5.5 ft (135–165 cm); shoulder height 2.6–3.5 ft (80–105 cm); tail 18–20 in (45–50 cm); 132–264 lb (60–120 kg); horns 18–35 in (45–87 cm) long. Males have chocolate brown coat with white shoulder patches; females' coat is uniformly rufous in color.

DISTRIBUTION
Most wild populations occur in the Sudd ecosystem of southern Sudan. Smaller populations in the Machar marshes of the upper Nile near Ethiopia and in Ethiopia (Gambella National Park).

HABITAT
Almost entirely in floodplains, freshwater marshes, and swamps.

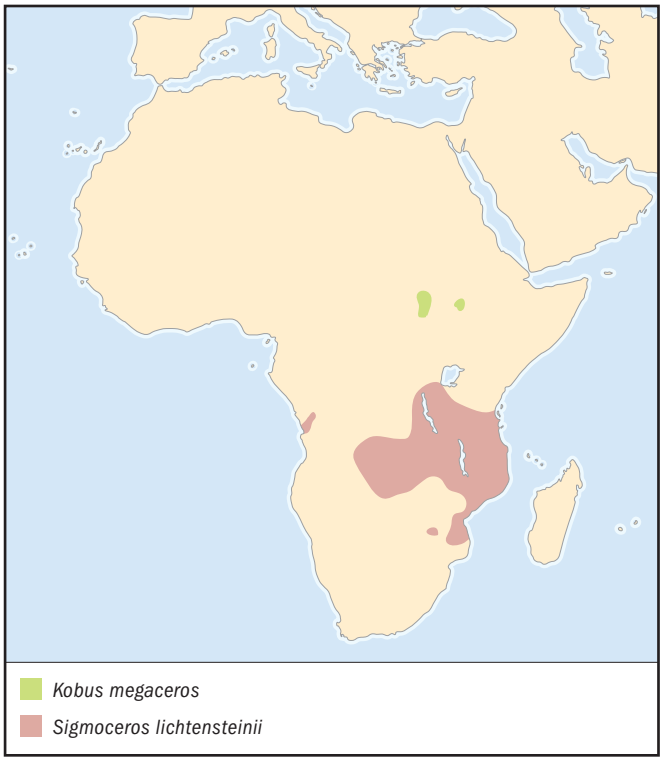
BEHAVIOR
Expert waders and swimmers, they move in leaps through water too shallow to swim through. One male may control a harem herd of 50 or more females. Males may utter squeaky grunts when fighting, which they often do in water. Females give toad-like croaks when on the move.

FEEDING ECOLOGY AND DIET
Eats grasses and water plants.

REPRODUCTIVE BIOLOGY
Polygynous. Gestation period 7–8 months; young weaned after four months. Females sexually mature 1.5 years, males at 2.5 years. Lifespan at least 10 years.

CONSERVATION STATUS
Lower Risk/Near Threatened. The wild population is estimated at 30,000–40,000 animals (almost 95% of these in the Sudd), and is potentially jeopardized by water development projects that reduce their habitat. The remoteness of the Sudd protects them from most forms of commercial or trophy hunting.

SIGNIFICANCE TO HUMANS
Hunted where populations are accessible to people. ◆



Black wildebeest
Connochaetes gnou

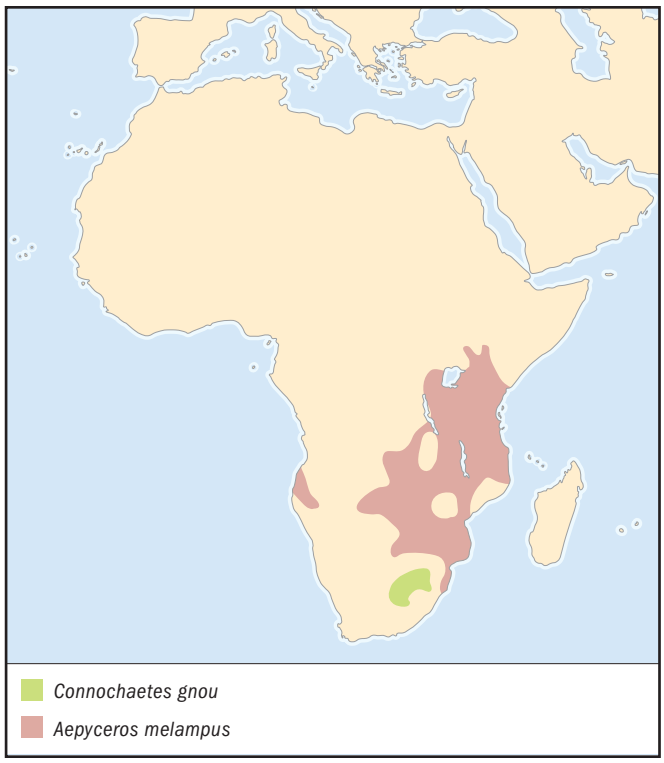
TAXONOMY
Antilope gnou (Zimmerman, 1780), Cape Province, South Africa. Monotypic.

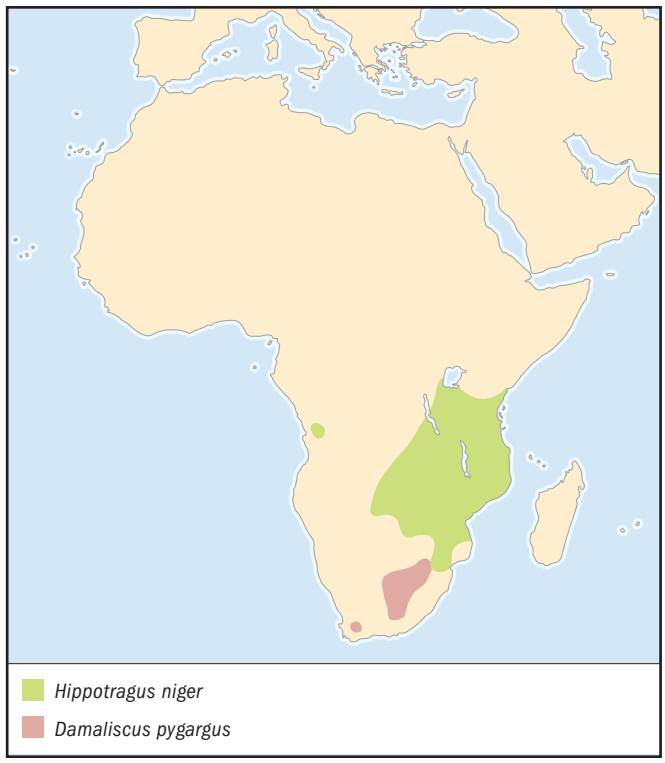
OTHER COMMON NAMES
English: White-tailed gnu; French: Gnou à queue blanche; German: Weißschwanzgnu; Spanish: Nu negro.

PHYSICAL CHARACTERISTICS
Body length 5.6–7.3 ft (170–220 cm); shoulder height 3–4 ft (90–120 cm); tail 2.6–3.3 ft (80–100 cm); 242–396 lb (110–180 kg), female smaller than male. Horns 18–31 in (45–78 cm). Dark brown to black, males darker than females. Both have lighter coats in summer and heavier coats in winter. Bristly mane stands up on neck and is cream to white, with black tips. Beard is black.

DISTRIBUTION
East-central South Africa, mainly eastern northern Cape and Free State: formerly central Cape Province to Natal and southern Transvaal.

HABITAT
Open plains, formerly in Karoo (arid shrublands) and grassland.





BEHAVIOR
Females and young form closely knit herds with a distinct hierarchy; males form bachelor groups. Territorial conflicts involve ritualized posturing and horn wrestling, accompanied by a blaring "ge-nu" call. Possibly originally had extensive movements or migrations, now restricted by fencing.

FEEDING ECOLOGY AND DIET
Primarily a grazer, preferring short grasses; in winter, also browses on karroid bushes.

REPRODUCTIVE BIOLOGY
Polygynous. The primary mating season is February–April. Gestation period 8–8.5 months; calves are born in November–January. Young weaned after four months. Females sexually mature at 1.5–2.5 years, males at three years. Lifespan up to 20 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. No truly wild animals remain, all being descended from captive individuals.

SIGNIFICANCE TO HUMANS
These animals were almost exterminated by white settlers, who viewed them as pests, and also valued their tails, which they used as fly swats. ◆

Blesbok/Bontebok

Damaliscus pygargus

TAXONOMY
Antilope pygargus (Pallas, 1767), Cape Province, South Africa. Two subspecies.

OTHER COMMON NAMES
French: Blesbok, bontebok, Damalisque à front blanc; German: Blessbok, Buntbok; Spanish: Blesbok.

PHYSICAL CHARACTERISTICS
Body length 4.6–5.3 ft (140–160 cm); shoulder height 2.8–3.3 ft (85–100 cm); tail 12–18 in (30–45 cm); 121–220 lb (55–100 kg). Horns 14–20 in (35–50 cm). Dark brown coat, white belly and inside legs. White face patch, ears.

DISTRIBUTION
D. p. phillipsi east-central South Africa; *D. p. dorcas* small area of southwestern Cape.

HABITAT
Grasslands of the highveld and coastal plains.

BEHAVIOR
Male bontebok hold permanent territories of 10–69 acres (4–28 ha). Blesbok males defend territories of 22–101 acres (9–41 ha) only during the rut; in the dry season, both sexes and all ages may congregate in large herds.

FEEDING ECOLOGY AND DIET
Predominantly grazers, although blesbok browse occasionally.

REPRODUCTIVE BIOLOGY
Rutting in March–May (blesbok) and January–March (bontebok). Polygynous. Gestation 238–254 days. Female stays with herd when giving birth to young in November–January (blesbok) and September–November (bontebok). Weaned after four months; sexually mature at 2.5 years. Longevity 17 years.

CONSERVATION STATUS
The blesbok is Lower Risk/Conservation Dependent. Its distribution is largely artificial and it occurs in protected herds on fenced reserves and farms. The bontebok is Vulnerable. It was hunted almost to extinction in the nineteenth century, but was

saved by protection from a few enlightened farmers. After the establishment of the Bontebok National Park in 1931, numbers increased and stocks were introduced to other farms and reserves.

SIGNIFICANCE TO HUMANS
Both races were formerly hunted extensively. ◆

Lichtenstein's hartebeest
Sigmoceros lichtensteinii

TAXONOMY
Bubalis lichtensteinii (Peters, 1849), Tete, Mozambique. Monotypic.

OTHER COMMON NAMES
French: Bubale de Lichtenstein; German: Lichtensteins Kuhantilope, Konzi; Spanish: Bubalo de Lichtenstein.

PHYSICAL CHARACTERISTICS
Body length 5.3–5.7 ft (160–200 cm); shoulder height 4–5 ft (120–135 cm); tail 16–20 in (40–50 cm); 275–440 lb (125–200 kg). Horns 16–24 in (40–60 cm). Sandy yellow with reddish "saddle." Tail is black.

DISTRIBUTION
Tanzania, southeast Democratic Republic of the Congo, northeast Angola, Zambia, Malawi, southeast Zimbabwe, and northern Mozambique.

HABITAT
Savanna, associated with ecotones of open woodland, vleis, and floodplains.

BEHAVIOR
Gregarious, usually in harem herds of up to 10 (rarely 15) females and young led by an adult male, who defends a permanent territory of about 1 mi^2 (2.5 km^2) year-round.

FEEDING ECOLOGY AND DIET
Almost exclusively a grazer, taking a wide variety of grasses; occasionally eats tree leaves and fruit. Dependent on surface water.

REPRODUCTIVE BIOLOGY
Polygynous. Rutting in November–February; gestation period 240 days; young born July–September. Weaned at 12 months; sexual maturity probably at two years. Lifespan 20 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Range has contracted, at least in extreme south, due to hunting, habitat loss, and human encroachment.

SIGNIFICANCE TO HUMANS
Hunted for food. ◆

Addax
Addax nasomaculatus

TAXONOMY
Cerophorus nasomaculatus (Blainville, 1816), probably Senegambia. Monotypic.

OTHER COMMON NAMES
French: Addax; German: Mendesantilope; Spanish: Addax.

PHYSICAL CHARACTERISTICS
Body length 3.6–4.3 ft (110–130 cm); shoulder height 3.1–3.8 ft (95–115 cm); tail 10–14 in (25–35 cm); 132–275 lb (60–125 kg). Horns 2–3.6 ft (60–109 cm) in male, 1.8–2.6 ft (55–80 cm) in female.

DISTRIBUTION
Historically ranged over entire Sahara Desert; now restricted to isolated populations in south Algeria, Mauritania, Mali, Niger, and Chad. Probably extinct in western Sudan.

HABITAT
Desert and semidesert, with sand dunes, hard-packed terrain, and scant vegetation.

BEHAVIOR
Formerly probably lived in family groups of 5–20 individuals led by dominant male, with social hierarchy based probably on age; now found only in groups of 2–4. Nomadic, following rains.

FEEDING ECOLOGY AND DIET
Eats desert grasses, succulents, herbs, and tender young shoots of shrubs and trees. Obtains all water from food.

REPRODUCTIVE BIOLOGY
Gestation period 257–264 days (8.5 months). Young born primarily in winter and spring; weaning at 3.5 months; females sexually mature at 1.5 years, males at three years. Lifespan up to 20 years in managed environments.

CONSERVATION STATUS
Critically Endangered; CITES I. Fewer than 250 remain in the wild. Competition with goats, disturbance from people, prolonged droughts, wars, and harassment by tourists in vehicles are all problems. Over 1,000 are registered in zoological collections worldwide, and in the United States, 2,000 are owned by private individuals. Reintroductions were initiated in Tunisia in 1985–1988 and in Morocco in 1994–1997.

SIGNIFICANCE TO HUMANS
Addax have been hunted extensively for their horns, meat and skin. ◆

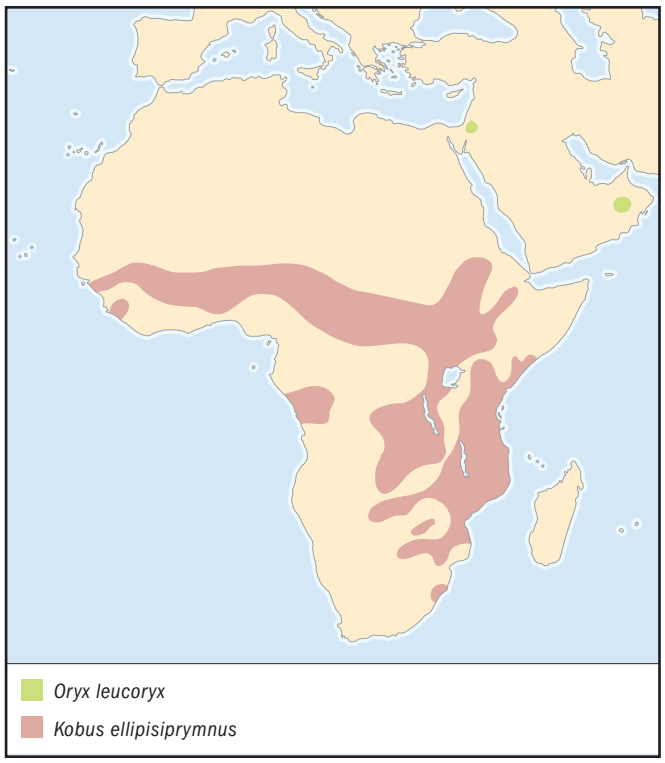
Arabian oryx
Oryx leucoryx

TAXONOMY
Antilope oryx (Pallas, 1777), Arabia. Monotypic.

OTHER COMMON NAMES
French: Oryx d'Arabie; German: Arabischer spiessbock; Spanish: Orix de Arabia.

PHYSICAL CHARACTERISTICS
Body length 5.3 ft (160 cm); shoulder height 2.7–3.4 ft (81–102 cm); tail 1.5–2 ft (45–60 cm); 143–165 lb (65–75 kg). Horns 1.6–2.2 ft (50–68 cm). Sandy pelage.

DISTRIBUTION
Formerly, found in most of Arabian Peninsula, Sinai Peninsula, Israel, Jordan, and Iraq. Reintroduced to Oman, Saudi Arabia, Jordan, and Israel.



HABITAT
Barren steppes, semideserts, and deserts; prefers gravel plains and fringes of sand desert.

BEHAVIOR
Lives in groups of 2–15, led by adult bull. Bulls establish territories when conditions permit; bachelor males are solitary. Moves toward rain, sometimes for hundreds of miles (kilometers), to find food.

FEEDING ECOLOGY AND DIET
Eats primarily grasses; also herbs, buds, leaves, fruit, and roots. Can exist for weeks without water.

REPRODUCTIVE BIOLOGY
Polygynous. Gestation period 8.5–9 months; young born at any time of year. Weaning after 3.5 months; attains sexual maturity at 1.5–2 years. Lifespan up to 20 years.

CONSERVATION STATUS
Endangered; CITES I. Saved from extinction by captive breeding in zoos. The last wild individuals were probably killed in 1972. In the 1950s, efforts were made to establish captive herds in Arabia. In 1962, several were exported to the United States to be placed in a breeding facility in the Phoenix Zoo, Arizona. Successful reintroductions began in Oman in 1982 and there are more than 3,000 animals in captivity in North America. Recently, poaching has become a serious problem and, in 1996, Oman's reintroduced population was reduced to about 130 animals. The demand for captive animals in the region is a major conservation problem.

SIGNIFICANCE TO HUMANS
Hunted to the brink of extinction for its meat, hide, and exquisite horns. ◆

Sable antelope
Hippotragus niger

TAXONOMY
Aigocerus niger (Harris, 1838), near Pretoria, South Africa.

OTHER COMMON NAMES
French: Hippotrague noir; German: Rappenantilope; Spanish: Antilope sable.

PHYSICAL CHARACTERISTICS
Body length 6.3–8.5 ft (190–255 cm); shoulder height 3.9–4.7 ft (117–143 cm); tail 1.3–2.5 ft (40–75 cm); 420–660 lb (190–300 kg), female smaller than male. Horns 2.6–5.5 ft (80–165 cm) in males, 2–3.3 ft (60–100 cm) in females.

DISTRIBUTION
H. n. roosevelti: extreme southeastern Kenya through Tanzania; *H. n. kirkii*: Zambia, presumably eastern Angola and southeastern Democratic Republic of the Congo, also probably Malawi and Mozambique; *H. n. niger*: southwestern Zambia, north and northeast Botswana, Zimbabwe, and extreme northeastern South Africa, limits not clear; *H. n. variani* (giant sable): Angola, between Cuanza and Loando rivers.

HABITAT
Dry open woodlands and medium-tall grass savannas.

BEHAVIOR
Herds of up to 30 females and young have home range 59–198 acres (24–80 ha). Herds of 200–300 recorded in dry season. Bulls hold territories of 62–99 acres (25–40 ha).

FEEDING ECOLOGY AND DIET
Eats grasses; during the dry season will also browse on herbs, bushes, and trees. Drinks at least once a day.

REPRODUCTIVE BIOLOGY
Polygynous. Breeding seasonal, births occurring during rains. Gestation period about nine months; weaning at eight months; sexually mature at 2–3 years. Lifespan 17 years.

CONSERVATION STATUS
Race *variani* is Critically Endangered: only about 1,000 remain, and their future is unpredictable; none are held in captivity. The other races are Lower Risk/Conservation Dependent. The wild population was believed stable at around 54,000 individuals in 1998, 75% of these in protected natural habitat.

SIGNIFICANCE TO HUMANS
Valued as a trophy species, also hunted for meat. ◆

Impala
Aepyceros melampus

TAXONOMY
Antilope melampus (Lichtenstein, 1812), Cape Province, South Africa. Six subspecies.

OTHER COMMON NAMES
French: Impala; German: Impala; Spanish: Impala.

PHYSICAL CHARACTERISTICS
Body length 4–5.3 ft (120–160 cm); shoulder height 2.5–3.1 ft (75–95 cm); tail 12–18 in (30–45 cm); 88–176 lb (40–80 kg); male larger than female. Horns 18–37 in (45–92 cm). Red brown coat with white chin, belly, tail. Black stripes down forehead, ear tips, thighs, and tail.

DISTRIBUTION
A. m. melampus: northeast South Africa to southeast Angola and south Malawi; *A. m. johnstoni*: north Mozambique, Malawi, eastern Zambia; *A. m. katangae*: southeast Democratic Republic of the Congo; *A. m. petersi*: southwest Angola, extreme northwestern Namibia; *A. m. rendilis*: Kenya, Uganda; *A. m. suara*: Tanzania, Rwanda.

HABITAT
Light open woodland and savanna. Prefers ecotones between open grassland and woodland; requires cover and surface water.

BEHAVIOR
During the dry season, may congregate in hundreds. In the rains, females and young form herds of 10–100 individuals, males form groups of up to 60 bachelors. About 30% of males hold a territory of 0.07–0.3 mi^2 (0.2–0.9 km^2). During the breeding season, males make hoarse grunts ("roaring").

Predator avoidance techniques include making jumps up to 8 ft (2.5 m) high in any direction, often over bushes or even other impala, and fleeing into dense vegetation.

FEEDING ECOLOGY AND DIET
Feeds mostly on grass during and after the rains, but browses and eats some fruit and seeds during the dry season. Drinks at least once a day in the dry season.

REPRODUCTIVE BIOLOGY
Polygynous. Births occur throughout the year in equatorial Africa, peaking in wet seasons elsewhere. Estrous cycle 12–29 days, lasting 24–48 hours. Gestation 194–200 days. Weaning at 4.5–7 months. Females conceive at two years. Lifespan 15 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Introduced widely into areas outside their normal range in southern Africa, and reintroduced to privately-owned land and reserves. The race *petersi* (black-faced impala) is Vulnerable as a result of habitat loss and degradation.

SIGNIFICANCE TO HUMANS
Hunted mainly for meat. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Roan antelope *Hippotragus equinus* French: Antilope chevaline	Pelage is grayish brown with a hint of red. Legs are darker than rest of body, head is dark brown or black, white around mouth and nose, large white patches in front of eyes and pale patches behind them. Mane of short, stiff hair. Tail has a brush of black on the tip. Weight 495–660 lb (225–300 kg).	Lightly wooded savanna with medium to tall grass and access to water. Mostly active during cooler parts of day. Groups can consist of up to 35 individuals.	Senegal to western Ethiopia; south to northern South Africa, northern Botswana, and Namibia.	Leaves and shoots.	Lower Risk/ Conservation Dependent
Bluebuck *Hippotragus leucophaeus* German: Blauwbok	Long, tall, parallel horns. Gray to bluish pelage. Sleek body with long, slender legs. Weight rarely over 355 lb (160 kg).	Grassy plains with adequate water sources. Group sizes consisted of up to 20 individuals.	Southern Cape Province, South Africa.	Grazers, eating mostly grasses and leaves.	Extinct
Scimitar-horned oryx *Oryx dammah* French: Oryx de Libye; Spanish: Orix de cimitarra	Coat is white on neck and bright russet on chest. Light wash of russet over flanks and thighs. Facial mask of vertical russet stripes through eyes and wide reddish nose strip. Long, tufted, dark brown tail. Two sickle-shaped horns found on both sexes. Head and body length 63–69 in (160–175 cm), shoulder height 43–50 in (110–125 cm), weight 395–440 lb (180–200 kg).	Grassy steppes, semi-deserts, and deserts in a narrow strip of central northern Africa. In Sahara during wet season. Generally solitary, herds gather in wet season. Mixed herds of up to 70 individuals.	Formerly western Sahara and Tunisia to Egypt; Mauritania to Sudan; now survives only as a naturalized population in Chad.	Grasses, fruits, and leaves.	Extinct in the Wild
Gemsbok *Oryx gazella*	Dramatic facial masks with halter-like facial markings paired with white patches, black striping along sides near underbelly. Short mane runs from head to shoulders, ears are large and broad. Body is buffy tan to brown. Long horns, ringed on lower half. Weight 395–440 lb (180–225 kg).	Arid areas, including dry steppe, brush, and tree savannas in flat and hilly areas, as well as semi-desert and desert. No particular breeding season. Groups consists of 30–40 individuals.	Northeastern Ethiopia and southeastern Sudan to Somalia, northeastern Uganda and northern Tanzania; southwestern Angola, Botswana, and western Zimbabwe to northern South Africa.	Grasses and herbs, juicy roots, fruits, melons, leaves, buds, and bulbs.	Lower Risk/ Conservation Dependent

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Kob *Kobus kob* German: Kobantilopen	Smooth, shiny coat varying from golden brown to chestnut above, underparts are bright white. White facial markings: eye rings, inside of ears, and throat. Bushy tails, S-shaped horns on males. Shoulder height 27–41 in (70–105cm), tail length 7.8–15.8 in (20–40 cm), weight 110–265 lb (50–120 kg).	Well-watered areas (like floodplains) across central Africa. Males are territorial. Groups consist of maternal and bachelor groups of one to 40 individuals.	Senegal to western Ethiopia and Sudan; south to northern Democratic Republic of the Congo (Zaire), Uganda, western Kenya, and northwestern Tanzania. Now extinct in Tanzania.	Mainly grasses.	Lower Risk/ Conservation Dependent
Lechwe *Kobus leche* French: Cobe lechwe; German: Der Litschi; Spanish: Coco de lechwe	Medium-sized antelopes, chestnut in color, underparts are white. White throat and facial markings. Dark leg and body markings, which vary from black to red. Thin horns are 17.7–36.2 in (45–92 cm) in length, weight 135–282 lb (61–128 kg).	Areas of the flood plains that border swamps because they are close to water and food. May take refuge in forested areas. Spend most of time in groups consisting of bachelors or mothers and calves. Males may be territorial.	Northern Botswana, northeastern Namibia, southeastern Angola, southeastern Democratic Republic of the Congo, and Zambia.	Nutritious grasses that are found in flooded meadows.	Lower Risk/ Conservation Dependent
Hunter's hartebeest *Damaliscus hunteri* English: Hirola	Coat is light sandy brown, turning more gray in adult males. Two white lines form a chevron between the eyes, circles around eyes. Long, thick, white tail. White ears with black tips. Lyrate horns with heavy ridges. Head and body length 47–79 in (120–200 cm), shoulder height 39–49 in (100–125 cm), tail length 11.8 –17.7 in (30–45 cm), weight 175–260 lb (80–118 kg).	Arid, grassy plains bound by semi-desert inland and coastal forests on the south-eastern coast of Kenya. Groups consists of females and their young and range from five to 40 individuals. Fairly sedentary.	Southern Somalia to northern Kenya.	Mainly grasses.	Critically Endangered
Topi *Damaliscus lunatus* French: Damalisque; German: Leierantilope	Body is short, glossy, tan in color with purple spots underneath. Markings are either white or dark in color. Long, narrow muzzles. Horns are S-shaped and ringed, range in length from 11.8 to 15.8 in (30–40 cm). Height 41–46 in (104–118 cm), weight 198–325 lb (90–147 kg).	Prefers grassland habitats, including large treeless plains to areas with little bush and tree savannas. May sometimes be found in uplands, but usually found in the lowlands. Social organization varies regionally. Generally breed once a year.	Formerly Mauritania and Senegal east to western Ethiopia and southern Somalia, and south to Tanzania; also Zambia to South Africa.	Consists almost entirely of grasses.	Lower Risk/ Conservation Dependent
Hartebeest *Alcelaphus buselaphus* German: Somali-Kuhantilope	Varies from pale brown to brownish gray. Large ungulate, steeply sloping back, long legs, tufted tail, and long, narrow rostrum. Head and body length 59–96 in (150–245 cm), weight 165–440 lb (75–200 kg).	Savannas and grasslands of Africa, as well as scrublands. Social animals, herds may consists of up to 300 individuals. Males are territorial. Sedentary.	Senegal to Ethiopia, south to eastern Democratic Republic of the Congo, Uganda, Kenya and northern Tanzania; southern Angola, western Zimbabwe, Botswana, Namibia, and South Africa. Extinct in northern Africa, Somalia, and much of its former South African range.	Consists almost entirely of grasses.	Lower Risk/ Conservation Dependent
Blue wildebeest *Connochaetes taurinus* English: Blue and white-bearded wildebeest; German: Streifengnu	Adults may vary from deep slate or bluish gray to light gray or brown-gray. Underparts are darker. Dark brawn, vertical bands on neck and forequarters. Slight hump above shoulders, slight slope toward rear. Long tail, black mane, flowing beard in both sexes. Head and body length 67–95 in (170–240 cm), shoulder height 45–57 in (115–145 cm), weight 308–640 lb (140–290 kg).	Open and brush-covered savanna in south and east Africa. Groups consist of females and their young, ten to 1,000 individuals. Females give birth to one young per year. Males are territorial.	Southern Kenya, Tanzania, and Zambia south to Angola, Namibia, Botswana, and northeastern South Africa. Extinct in Malawi.	Grasses.	Lower Risk/ Conservation Dependent

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Organizations

IUCN Species Survival Commission, Antelope Specialist Group, Dr. Richard D. Estes, Chair. 5 Granite Street, Peterborough, NH 03458 USA. Phone: (603) 924-9804. Fax: (603) 924-9804. E-mail: richard.estes2@verizon.net Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Barry Taylor, PhD

△

Bovids III
Gazelles, springboks, and saiga antelopes
(Antilopinae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subfamily Antilopinae

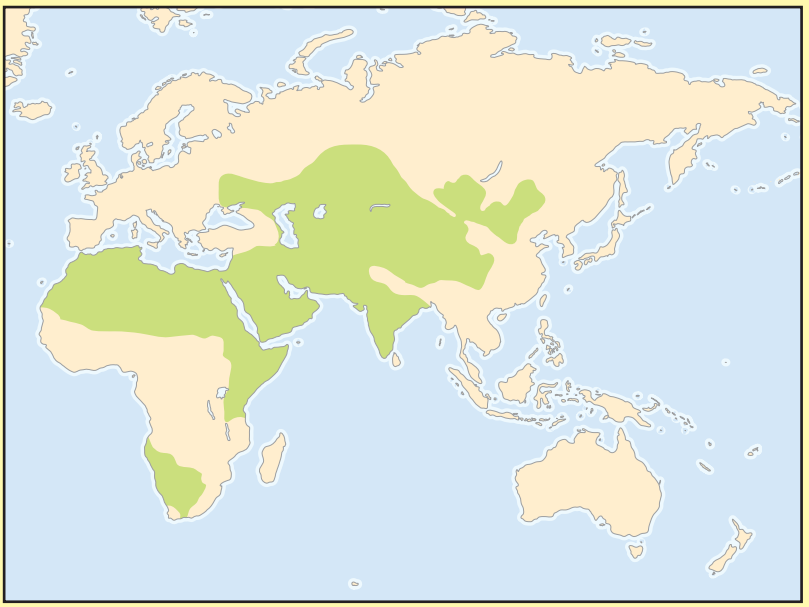
Thumbnail description
Small- to medium-sized, slender-limbed and thin-necked herbivores characterized by a back that is straight or slightly higher at the croup, a pair of horns always present in males and sometimes present in females, narrow crowns of the molars, a hairy muzzle, many skin glands throughout the body, a four-chambered stomach, and a similar body color in the two sexes

Size
Head and body length of 2.8–5.6 ft (85–170 cm), tail length of 2.4–13.8 in (6–35 cm), shoulder height of 1.8–2.8 ft (54–84 cm), horn length (when present) of 3–19 in (8–48 cm), and weight of 26–128 lb (12–58 kg)

Number of genera, species
7 genera; 20 species

Habitat
Woodlands, plains, steppes, deserts, and other similar areas

Conservation status
Critically Endangered: 2 species; Endangered: 3 species; Vulnerable: 6 species; Lower Risk/Conservation Dependent: 6 species; Lower Risk/Near Threatened: 3 species



Distribution
Africa and Asia

Evolution and systematics

Antilopinae evolved from its family Bovidae, which is recognized to have a geological range of early Miocene (24 million to 5 million years ago [mya]) to Recent in Europe and Africa, middle Miocene to Recent in Asia, and Pleistocene to Recent in North America. A rapid diversification of the family into genus and species occurred possibly due to the formation of savannah habitat in Africa. The Antilopinae lineage was present by about 16–17 mya based on molecular genetic evidence. They were forced from the northern parts of Europe and Asia in the Pleistocene (which started about 1.6 mya) to their present locations in Africa and Asia, but did not cross over to North America except for the saiga antelope (*Saiga tatarica*), which did not survive in North America.

Physical characteristics

Antilopinae are long-legged, slender, and graceful animals with fawn-colored to reddish brown upper parts and pale undersides. Stripes can often occur at various locations around the body. Their tail is short or medium in length. Pits are present in the forehead of the skull, with narrow crowns on the molar teeth. On the rather small face, they have glands below their rather large eyes, with other skin glands throughout the body and a narrow, hairy muzzle. The indented preorbital glands are well developed. All males and many females grow short- to medium-sized horns (they are shorter and thinner in females when present) that vary greatly in size and shape (often lyre-shaped, or like a "U," but sometimes spiral-shaped, or like a "S") but the basic structure is always one of being: compressed at the base; attached to the frontal bones of the skull; single bony protrusions without branches; covered in a sheath of keratin; never shed; and ringed for part or most of their length. They are very fast on their feet and some species have been clocked at maximum speeds of nearly 60 mph (100 kph). Two-toed lateral hooves are at the ends of their very slender legs. They all have a four-chambered stomach, which allows most of them to digest foods that are too low in nutrients for many other animals, notably grasses.

Thomson's gazelles (*Gazella thomsonii*) grooming young. (Photo by Animals Animals ©A. & M. Shah. Reproduced by permission.)

Distribution

Antilopinae range throughout Africa and across the Middle East and into Asia.

Habitat

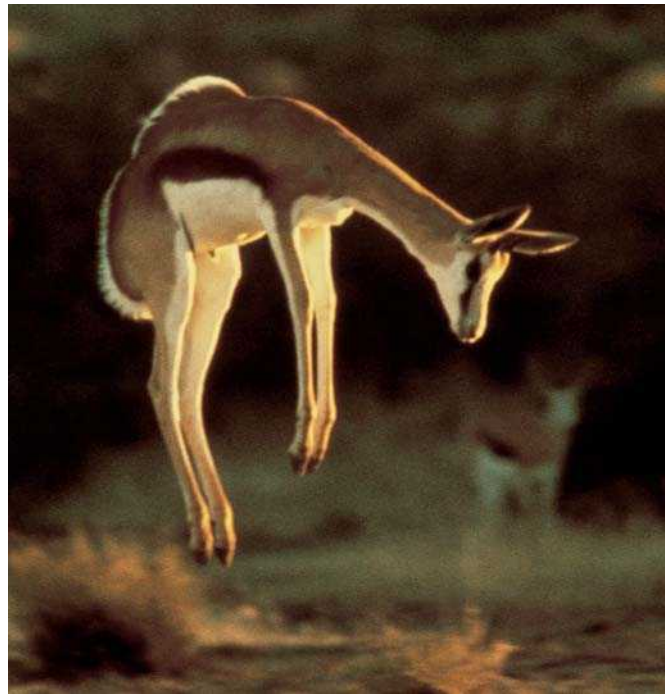
Antilopinae live in a variety of habitats from open woodlands and grassy plains to short grass steppes and steppes with trees and dense bush to barren high-altitude steppes, semi-deserts, and deserts.

Behavior

Antilopinae are generally gregarious animals but normally keep a certain distance apart from each other, and under certain circumstances will seek temporary isolation. In most cases, they form groups ranging from two to hundreds (and sometimes even thousands) of individuals. The differences in herd size depend on the environment, population density, season, and species. Herds generally are open, where members come and go freely. Most herds are classified as all-female, all-male (sometimes all-bachelor), or mixed (female/male). Only adult males become territorial, but not all of the adult males become territorial: only those who are successful with the mating of females. They are not territorial throughout their lives, alternating between non-territorial and territorial periods. Owners of territories, in some species, exclude other males from their territories, or at least dominate them within the territorial boundaries. Such owners also mark their territories with

Two male gerenuk (*Litocranius walleri*) fighting. (Photo by Kennneth W. Fink. Bruce Coleman, Inc. Reproduced by permission.)

Mother and newborn springboks (*Antidorcas marsupialis*). (Photo by Jen & Des Bartlett. Bruce Coleman, Inc. Reproduced by permission.)



Pronking springbok (*Antidorcas marsupialis*) in Kalahari Gemsbok Park. Photo by Animals Animals ©J & B Photographers. Reproduced by permission.)

The mhorr gazelle (*Gazella dama mhorr*) is Endangered. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

Gerenuk (*Litocranius walleri*) have pre-orbital glands in front of the eyes that emit a tarlike, scent-bearing substance they deposit on branches and bushes to mark their territory. (Photo by David M. Maylen III. Reproduced by permission.)

Springboks (*Antidorcas marsupialis*) battle in Kalahari Gemsbok Park. (Photo by Animals Animals ©J & B Photographers. Reproduced by permission.)

secretions from the preorbital gland and with urine and feces. Females will periodically visit the males in their territories.

Feeding ecology and diet

Antilopinae are herbivorous, but a few will take a small amount of meat if it is available. Their diet consists of grasses, herbs, leaves, buds, and shoots. Water is acquired from moisture within and on their food, although most will drink when water is available.

Reproductive biology

Males and females are usually polygamous, and territorial males and females remain as separate and independent social units. When there are many neighboring territories, a male may guard an all-female herd while in his territory, but will change guardianship as different female herds enter and exit. Females normally give birth to one young at a time, but may give birth to more under ideal conditions. Births occur generally in tandem with the rainy season, when food is plentiful, and can occur throughout the year. Females isolate themselves from the herd before giving birth and remain solitary with her young immediately after the birth. Males have little or no parental activity toward the young.

Conservation status

According to the 2002 IUCN Red List of Threatened Species, *Procapra przewalskii* and *Saiga tatarica* are Critically Endangered; *Gazella cuvieri*, *Gazella dama*, and *Gazella leptoceros* are Endangered; *Antilope cervicapra*, *Ammodorcas clarkei*, *Gazella dorcas*, *Gazella rufifrons*, *Gazella soemmerringii*, and *Gazella spekei are* Vulnerable; *Gazella bennettii*, *Gazella gazella*, *Gazella granti*, *Gazella thomsonii*, *Litocranius walleri*, and *Antidorcas marsupialis* are Lower Risk/Conservation Dependent; and *Gazella subgutturosa*, *Procapra gutturosa*, and *Procapra picticaudata* are Lower Risk/Near Threatened.

These animals are threatened by overhunting, as well as by habitat loss and degradation from human activities.

Significance to humans

Antilopinae are hunted for their meat, skin, and sport.

1. Gerenuk (*Litocranius walleri*); 2. Dorcas gazelle (*Gazella dorcas*); 3. Mountain gazelle (*Gazella gazella*); 4. Thomson's gazelle (*Eudorcas thomsonii*); 5. Mongolian gazelle (*Procapra gutturosa*); 6. Saiga antelope (*Saiga tatarica*); 7. Springbok (*Antidorcas marsupialis*). (Illustration by Joseph E. Trumpey)

Species accounts

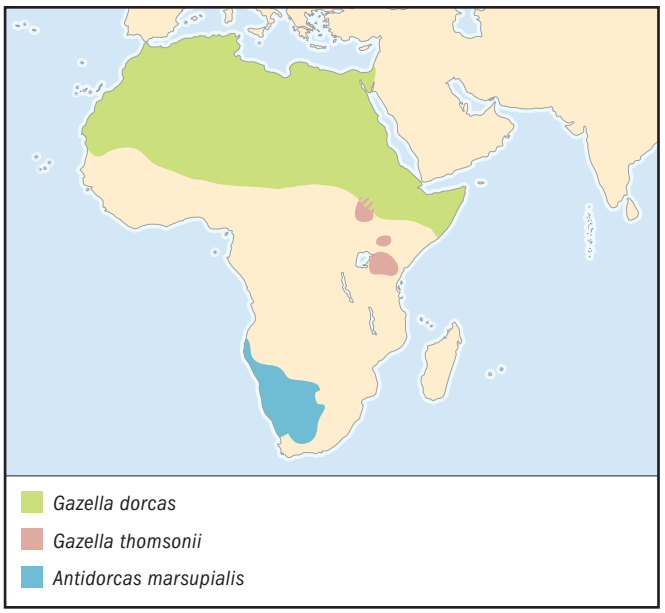
Dorcas gazelle
Gazella dorcas

TAXONOMY
Capra dorcas (Linnaeus, 1758), lower Egypt.

OTHER COMMON NAMES
French: Gazelle dorcas.

PHYSICAL CHARACTERISTICS
Dorcas gazelles have a head and body length of 3.0–3.6 ft (90–110 cm), tail length of 6–8 in (15–20 cm), shoulder height of 1.8–2.1 ft (55–65 cm), and weight of 27–44 lb (12–20 kg). They are considered one of the smallest of the gazelles, but proportionately are the longest limbed. Their slender limbs contain splayed hooves. They can reach running speeds of 60 mph (95 kph) and can maintain steady speeds of 30 mph (48 kph). Dorcas gazelles have long ears. Across their nose is a fold of skin that can be inflated and vibrated when they feel threatened, thus generating a sound like the quacking of a duck. The upper coat is colored pale beige or sandy-red, while the undersides and rump are white. A wide, sometimes indistinct, rufous stripe runs along the lower flank between the front and rear legs; the stripe separates the white belly from the upper coat. Another similarly colored strip is located on the upper hind legs, creating a border for the white rump. The head is the same beige color as the body. There is a white ring around each eye, and a pair of white and dark brown streaks running from each eye to the corners of the mouth. The forehead and bridge of the nose are generally light reddish tan in color.

Strongly ridged, lyre-shaped (pointed outward and then coming in at the tips) horns are found in both sexes, but those of the females are smaller and more slender. They may have up to 25 annular rings on their horns. In males they are bent sharply backwards, and curve upwards at the tips, growing 10.0–15.2 in (25–38 cm) long. The horns of the females are much thinner and straighter, with fewer ridges, and a length of 6–10 in (15–25 cm).



DISTRIBUTION
Morocco south to Mauritania (and formerly to Senegal) east to southern Israel and Egypt and from there south to Sudan, northeastern Ethiopia, and northern Somalia.

HABITAT
They live in savannas, dry hills, sub-deserts, and true deserts; but prefer stony deserts to rocky deserts and avoid steep terrain. They live primarily on the perimeter of the Sahara, but it is not uncommon for them to venture further into the desert.

BEHAVIOR
Dorcas gazelles are well suited to desert climates. They may go their entire lives without drinking water, obtaining necessary moisture from plants that they eat. Being well adapted to dry climates, they produce very concentrated urine during dry weather. They are usually active, especially during hot weather, only at dawn, dusk, and throughout the night. However, they can withstand very hot temperatures, if necessary. Animals will migrate and run in herds over large areas in search for food. Herds tend to consist either of single-sex animals with up to 40 animals or mixed herds of up to 100. When not foraging for food, groups usually only reach about 12 in number, with one adult male. In order to defend against predators, groups of 2–5 males sometimes form. They tend to congregate in areas where recent rainfall has stimulated plant growth, and may also associate with other gazelles and camels.

Adult males are territorial, establishing piles of dung throughout their range in a conspicuous display in which the male will first paw at the ground, then stretch over the scraped area and urinate, and finally crouch with his anus just above the ground, at which time he deposits his dung. Males defend small territories during the breeding season or, sometimes when times are good, for the entire year. The preorbital glands, although functional, are not used for marking. Its call of alarm when sensing danger, which sounds like a duck's quack, is made through the nose, which inflates during the process.

FEEDING ECOLOGY AND DIET
Dorcas gazelles eat grasses, shoots, leaves (especially the pods of acacia trees), blossoms, and succulents. They also browse the green leaves of some bushes and dig up bulbs of perennial plants. Often they will stand on their hind legs to reach leaves high off the ground. They will occasionally eat invertebrates.

REPRODUCTIVE BIOLOGY
Polygamous. Mating season is December to November in the wild. In areas where agriculture (or nature) has led to below normal amounts of available water, they may breed at other times of the year. Female gestation period is 164–174 days, with usually one baby born (on rare occasions two are born). Newborns weigh 2.2–4.0 lb (1.0–1.8 kg). After birthing, mothers will hide their young for 2–6 weeks. Mothers will induce defecation in nursing young and ingest the feces (which is thought to be a water conservation adaptation). They are weaned after 2–3

months; become sexually mature at 9–12 months for females and at 18 months for males; and have a life span of up to 12.5 years in the wild and up to 17 years in captivity.

CONSERVATION STATUS
Vulnerable. According to IUCN, their population trends are drastically declining primarily due to overhunting. Predators include the common jackal, cheetah, lion, leopard, serval cat, desert lynx, wolf, striped hyena, vulture, and eagle. Smaller cats, honey badgers, jackals, and foxes eat fawns. They are particularly vulnerable when they migrate in large numbers.

SIGNIFICANCE TO HUMANS
They are hunted for their meat and skins. They help to keep vegetation from becoming overgrown. ◆

Thomson's gazelle
Gazella thomsonii

TAXONOMY
Gazella thomsonii Günther, 1884, Kilimanjaro, Kenya.

OTHER COMMON NAMES
English: Tommies.

PHYSICAL CHARACTERISTICS
Thomson's gazelles have a head and body length of 3–4 ft (91–122 cm), tail length of 6–8 in (15–20 cm), and weight of 29–66 lb (13–30 kg). Males have a shoulder height of 23–28 in (58–70 cm), and a weight of 37– 66 lb (17–30 kg), while females have a shoulder height of 23–35 in (58–64 cm), and a weight of 29–53 lb (13–24 kg). They have a light reddish brown coat on top, a white belly, a fawn colored stripe underneath, a distinctive black stripe running from the foreleg to the hindquarters, and a white rump patch that extends to the entirely black tail. The uniquely dark side stripes may serve as visual signals to keep the herd together. They have pronounced facial markings. The eyes are rimmed with a white line, which then extends to the nose along the muzzle and above black cheek stripes. A dark finger-like pattern occurs on the inside of the ears. Their sight and sense of hearing are well developed, which lets them scout out a large area. Their dark parallel horns are long and only slightly curved. Males have robust, curved horns with large ridges (rings) encircling them. They can reach 11.5–12.0 in (29.2–30.5 cm) in length and are used exclusively for intra-species fighting. Female horns are shorter and more slender; and are used in order to defend their feeding area, especially when food resources are limited. Because of this excess use of their horns, females often end up with broken or deformed horns, or without horns. They have facial and leg glands for territorial marking and species recognition. This species is the least drought tolerant of all the gazelles.

DISTRIBUTION
Southern and central Kenya, southwestern Ethiopia, northern Tanzania, and southeast Sudan.

HABITAT
They stay primarily in the short grassy plains and savannas where food is most abundant and where the landscape is open enough to allow for the gathering of large herds. They feed and reproduce on the short-grass plains during the rainy season and in the taller grasslands in the drier season.

BEHAVIOR
Thomson's gazelles are both nocturnal and diurnal, but are most active early and late in the day, preferring to rest during the hottest part of the day. They are primarily silent animals. Their primary defense against predators is to run, which they can do very effectively at speeds of 40–50 mph (65–80 kph). They can gracefully leap 10 ft (3 m) into the air, jump 30 ft (9 m) in a single leap, and make turns much faster than can a cheetah, one of its main predators. Thomson's gazelles engage in gaits called "stotting" or "pronking" when playing or alarmed. This action entails bouncing stiff-legged so that all four legs land on the ground together. It is believed that this activity helps them to communicate alarm to each other, to give them a better view of approaching predators, and even to confuse or intimidate predators. They have elongated foot bones and anklebones that gives them their speed. They live in herds up to 200 members but normally associate in groups of 2–20. These groups are loosely based, and can change by the hour. They often migrate in groups numbering in the thousands. Multiple groups are often seen interacting with each other. Territories can range from 6 to 495 acres (2–200 ha) but normally are 25–75 acres (10–30 ha). They are very water-dependent but can become water-independent when necessary. During dry periods, they need to be near a water source, sometimes travelling as much as 100 mi (160 km) to find one. During the breeding season males establish territories in order to secure mating rights with females. Males mark their territories with urine and dung piles, and also with secretions from their pre-orbital glands. Territorial males will tolerate familiar subordinate males in their territories as long as they remain subordinate and do not approach the females. Nonbreeding males form bachelor herds.

FEEDING ECOLOGY AND DIET
Thomson's gazelles graze on short grasses, alfalfa hay, and leaves. They avoid tall grass areas. Almost all of their diet consists of grasses. They get most of the water they need from the grasses they eat.

REPRODUCTIVE BIOLOGY
Polygamous. Thomson's gazelles generally breeds twice a year in parallel with the coming rainy season in late December/early February (short rains) and late June/July (long rains), but reproduction is also dependent on the health of the female and environmental conditions. Females give birth to one baby after a gestation period of 5–6 months. The young coat is mottled darker than the mother's coat, but lightens within 1–2 weeks. Females isolate themselves during the birth of their young in order to strength the fawn, and will remain separated from the herd for the first few weeks of life. Once the offspring can run well enough (within 3–4 weeks), mother and fawn will rejoin the group. The weaning period lasts about four months. Females can become impregnated 2–4 weeks after giving birth. Lifespan in the wild is 10–20 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Predation on this small gazelle is always high; they are preyed upon primarily by cheetahs, but also by lions, hyenas, wild dogs, jackals, honey badgers, crocodiles, and leopards. Smaller predators such as pythons, serval cats, baboons, and birds of prey (such as eagles) will also eat the young. Despite the large numbers and types of predators, Thomson's gazelles can be found in numbers of up to 500,000 in Africa, the most common of the gazelles in east Africa.

SIGNIFICANCE TO HUMANS
They are hunted for food and skins. ◆

Springbok
Antidorcas marsupialis

TAXONOMY
Antilope marsupialus (Zimmermann, 1780), Cape of Good Hope, South Africa.

OTHER COMMON NAMES
English: Springbuck.

PHYSICAL CHARACTERISTICS
Springboks have a head and body length of 4.0–4.6 ft (120–140 cm), tail length of 7.5–10.8 in (19.0–27.5 cm), shoulder height of 2.4–2.9 ft (73–87 cm), and weight of 70–100 lb (32–45 kg). A dark reddish brown horizontal band along its flanks divides the cinnamon-fawn upper parts from the white underside, back of the thighs, inside of the legs, and the tail. Their hindquarters also appear to be slightly higher than the shoulders. They have white coloration on their face and muzzle, with a dark reddish brown stripe running through the eyes down to the corner of the mouth. The stripes turn to a darker shade and eventually to white on the lower third of the body. Their backside is white. Both sexes have medium-long, lyre-shaped, curved, black horns with bulges across them, although mature males have distinctly thicker and longer ones, growing as much as 14–19 in (36–48 cm) long. They are generally distinct from other gazelle species with respect to their teeth. Springboks have five pairs of grinding teeth in their lower jaws, two premolars, and three molars, while other gazelles have six pairs of grinding teeth in all. Another species difference is the fold of skin extending along the middle of the back to the base of the tail. This fold is covered with hair, much lighter in color than the rest of the back. When alarmed by possible predators, they open and raise this fold so that white hair is conspicuously displayed as a crest along the back. While showing this fold, white hairs on the rump are erected and the animal frequently leaps high.

DISTRIBUTION
Originally found in Namibia, southwestern Angola, Botswana, and South Africa, but range has been drastically reduced.

HABITAT
Springboks prefer open, arid plains, savannas, and grasslands that occur in the arid western areas of the southern African subregion.

BEHAVIOR
Springboks are highly gregarious, being active during the cooler times of the day and partially active at night. When springboks sense danger they repeatedly "spring" up (hence their name) to 9.8–11.5 ft (3.0–3.5 m) into the air with their front and hind legs close together and stiff; hooves bunched; backs arched and showing off their broad, white crests; and their heads straight, in a display called "pronking." They then hit the ground and rebound with apparently little effort. This action often results in other springboks responding with the same efforts. The leaps are used primarily to distract predators. Also when in fear for their safety, springboks will let out a high-pitched alarm. They normally congregate in small mixed or ram (male) herds, but can occasionally be seen in herds of several thousands when moving to new feeding grounds. During drier months they divide into smaller groups of up to 100 females and young, each associated with a number of adult males. Non-territorial solitary males form bachelor herds of up to 50 individuals. They are territorial, especially when they gather up female groups during the rutting season. They do not, however, remain in their territories throughout the year.

FEEDING ECOLOGY AND DIET
They graze and browse both on grass and flowers/shrubs (especially karroo shrubs), often switching from one to the other depending on the season. They are fairly independent of the water supply, being able to switch to flowers (which have double the mean water content from that of grasses) when less water is available. They can survive long periods of time without drinking water, but will drink it when available, because they obtain sufficient water from the succulent leaves they select. They will also dig up succulent roots.

REPRODUCTIVE BIOLOGY
Polygamous. Males that are younger, older, or injured (or with other problems) wander together in search of mates, but are of lower status with regards to reproduction. Dominant males and females with their earlier offspring remain in herds during the mating season. Springboks generally mate during the dry season and lactate during the hot, wet season when resources are most abundant. Births usually occur from October to December, at the start of the wet season. Gestation period is 4–6 months (averaging 171 days), and females generally reproduce every two years, starting between the ages of 1–2. Each female gives birth to a single young. Weaning usually occurs from 6–12 months. Parental contribution is primarily by the mother. They have a lifespan of about 7–10 years.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Natural disasters and ongoing drought, along with pathogens and parasites, continue to threaten the animals.

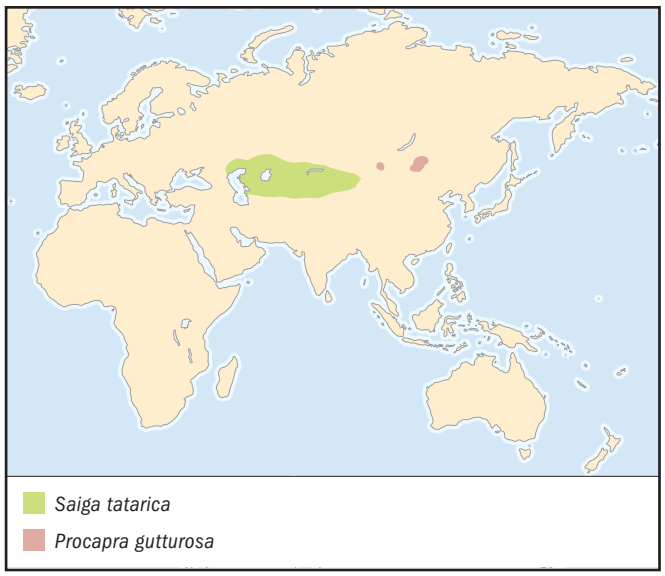
SIGNIFICANCE TO HUMANS
Springboks are hunted for their meat. They can inflict enormous damage onto cultivated crops when their large-numbered groups migrate. ◆

Saiga antelope
Saiga tatarica

TAXONOMY
Capra tatarica (Linnaeus, 1766), "Ural Steppes," western Kazakhstan.

OTHER COMMON NAMES
English: Saiga; French: Saïga.

PHYSICAL CHARACTERISTICS
Saiga antelopes have a head and body length of 3.3–5.6 ft (100–170 cm), tail length of 2.4–5.2 in (6–13 cm), shoulder height of 2.0–2.6 ft (60–80 cm), and weight of 66–152 lb (30–69 kg). Their most distinctive feature is a large head with a bulging shape and with a huge, inflatable humped nose that hangs over its mouth and with downward-pointing nostrils. This fleshy nose has a unique internal structure, with convoluted bones, mucous-secreting glands, and many hairs. The large nose is believed to filter out airborne dust during summer migrations and to heat the cold air before getting to the lungs during winters. The eyes appear to stand out on small, bony protrusions when viewed straight on. Their senses of hearing and smell are poorly developed, but their eyesight is acute, and they are able see danger up to 0.6 mi (1 km) away. Males possess a pair of long, semi-translucent, waxy colored horns with ring-like ridges along their lower two-thirds of length, which grow 8–10 in (20–25 cm)



long. Except for their unusually large snout and horns, they resemble small sheep. They have long, spindly legs that support a slightly robust body. The hooves are slightly broader at the rear. During summer months, they have a cinnamon-buff to yellowish red back and neck with a paler underside. The summer coat is short and almost smooth. In the winter, the coat becomes denser and longer, and it turns a muted gray to almost a white color on the back and neck and a light brownish gray shade on the underside. The winter coat, looking wool-like, may be up to twice as long and 70% thicker than the summer coat. A course set of bristly hairs protects them from the harsh weather. They have a very short tail that is always light in color. There is a small mane on the underside of the neck.

DISTRIBUTION
Northern Caucasus, Kazakhstan, northern Uzbekistan, southwestern Mongolia, and Singkiang, China.

HABITAT
Dry steppes and semideserts. Herds are found primarily on flat, open areas (such as plains) covered with low growing vegetation (such as grasses) that do not contain rugged terrain and hills. They generally do not move more than about 2–4 mi (3–6 km) per hour while grazing. But, may move 75–125 mi (120–200 km) within two days when severe frost cuts off their food supplies.

BEHAVIOR
Saiga antelopes are a very timid and easily startled species, which can cause immediate flights for safety. They are a polygamous species. During the breeding season they congregate into groups consisting of 5–10 females and one male. Males are very protective of their harem of females, with violent fights often breaking out (and sometimes leading to death) between males. Because males do not feed during the mating season, rather they spend most of their time defending their harem; they grow very weak near the end of the breeding season. As a consequence, male mortality often reaches 80–90%. At the end of breeding season, herds will form consisting of 30–40 individuals, but will form again at the beginning of next year's breeding season. They are a nomadic herding species, migrating as a group for food, and in order to escape such weather as snowstorms and droughts. Seasonal migrations move north in the spring to the summer grazing grounds, and return southward in the fall. Spring migrations may include 200,000 individuals in a herd, while summer groups have only 30–40 members. They have no fixed home range, and usually walk 48–72 mi (80–120 km) in a day. When they march, their heads are often kept low to the ground. They tend to avoid areas of broken terrain or dense cover because such ground is not conducive to fast running. They are very good runners, and are able to reach speeds up to 48 mph (80 kph). During the day, they graze and visit watering holes, but may rest during midday. Before night they dig a small round depression in the ground that serves as their bed.

FEEDING ECOLOGY AND DIET
Saiga antelopes are herbivores, grazing on over 100 different plant species; however, the most important are grasses, herbs, prostrate summer cypress, saltworts, fobs, sagebrush, steppe lichens, and other plants containing salt. They will often eat plants that contain poisonous substances, which are not eaten by other animals. They will visit watering holes about twice a day when moist plants are not available.

REPRODUCTIVE BIOLOGY
Polygamous. They have a high rate of reproduction where in a favorable season they may grow in population up to 60% in a single year. The rutting season begins in the wintering grounds, when males become territorial in an attempt to gain a harem of usually 5–25 females. During the mating season, which only lasts 6–7 days, males will only eat snow, using most of its time to defend its harem from lurking males. Females reach sexual maturity at 7–8 months, while males reach sexual maturity at 20–24 months. The breeding period lasts from late November to late December, with births occurring from the end of March to May. The gestation period is about 140–150 days, and usually gives birth to two, sometimes three, young after the first year (in which only one is normally born). Mothers usually drop their calves within a few days of each other. Newborns will lie concealed and immobile for the first three days, and then will begin to graze at 4–8 days old on bits of green food. The lactation period lasts for about four months, and the weaning period is 3–4 months. Very few animals live beyond 3.5 years of age, but known lifespan in the wild is 6–12 years, with males especially susceptible to death after fasting during the mating season, just before the cold winter season.

CONSERVATION STATUS
Critically Endangered. They are threatened from increased habitat loss and degradation primarily from human disturbances, along with the continuing presence of illegal hunting for meat and male horns (for medicinal properties). Their most dangerous predators are wolves, foxes, and birds of prey.

SIGNIFICANCE TO HUMANS
They are hunted for their fur, meat, and horns. The horns are considered as their most valuable feature. Horns are ground up and used in Chinese medicines to reduce fevers. They occasionally destroy agricultural plants and feed on crops. ◆

Mongolian gazelle
Procapra gutturosa

TAXONOMY
Procapra gutturosa (Pallas, 1777), southeastern Transbaikalia, Russia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Mongolian gazelles have a head and body length of 3.3–5.0 ft (100–150 cm), tail length of 3.2–4.8 in (8–12 cm), shoulder height of 1.8–2.8 ft (54–84 cm), and weight of 44–86 lb (20–39 kg). They seldom make a sound, but occasionally will make loud bellows during the rutting season. Their coat is colored a light brown or buff that has orange-buff tones with pinkish cinnamon sides in the summer; the hairs become longer, each hair going up to 2 in (5 cm) in length, and paler in winter. The darker upper coat gradually converts into the white under parts, while the heart-shaped patch of white hair on the rump is very distinctive. The muzzle, chin, and jowls are white, while the bridge of the nose may be slightly darker than the body color. During the breeding season, males develop a swollen throat, and may also get a "bulbous" muzzle. Their eyes are small, but they protrude noticeably from the head. Only males possess horns that are dark gray and lyre-shaped horns, curling backward from the forehead and then running parallel to the back. Slightly ridged along most of their length, the horns grow 10–16 in (26–40 cm) long and diverge along their length, such that the tips are 6–10 times farther apart than at the base.

DISTRIBUTION
Eastern Mongolia and Inner Mongolia, China.

HABITAT
Grassy steppes and sub-deserts.

BEHAVIOR
Mongolian gazelles are active during the daylight hours of fall and winter, mostly grazing in the mornings and late afternoons. They will excavate a depression bed within bushes in order to shelter themselves from winds and harsh weather. Being very fast animals, they are able to run up to 40 mph (65 kph), sustain this speed for 7–9 mi (12–15 km), and can leap up to 6.6 ft (2 m) into the air. They also are good swimmers, and can easily cross wide rivers. Large-scale migrations are regularly taken by this species. Herds of 6,000–8,000 animals of both sexes gather in the spring where they begin their northerly migrations for food and to drop young, often covering 120–180 mi (200–300 km) in a day. When reaching summer pastures in June, the sexes will isolate themselves and females prepare to give birth. Herds generally use several hundred square miles (kilometers) as their summer home range, regularly shifting areas in the search for food. During the winter, herds normally number no more than 120 animals. Sometimes single-sex herds of 20–30 animals will gather.

FEEDING ECOLOGY AND DIET
They eat grasses and herbs.

REPRODUCTIVE BIOLOGY
Polygamous. The mating season is from November to January, with resulting births from May to July. Mating occurs within the herds, and males actively collect harems. Female gestation period is about 185 days, with usually 1–2 births per pregnancy (twins are common), although three births sometimes occur. Mothers will hide her young for their first days of life, but will later join the herds after 4–8 days. Herds tend to be small during this time. Young are weaned after about five months, sexual maturity occurs at 1.5–2.0 years, and life span is around seven years.

CONSERVATION STATUS
Lower Risk/Near Threatened. Humans primarily threaten them from habitat loss and degradation, and ongoing hunting. Their primary enemy is the wolf, but lynxes and dogs also prey on them. Foxes, cats, and eagles may take the young.

SIGNIFICANCE TO HUMANS
They are hunted for their meat and skin. ◆

Mountain gazelle
Gazella gazella

SUBFAMILY
Antilopinae

TAXONOMY
Gazella gazella (Pallas, 1766), Syria.

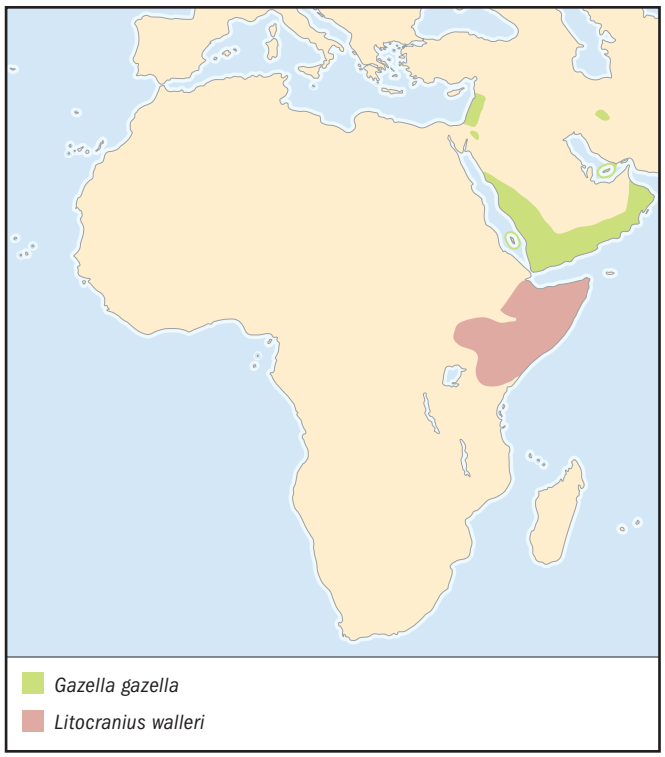
OTHER COMMON NAMES
French: Edmi.

PHYSICAL CHARACTERISTICS
Mountain gazelles have a head and body length of 3.1–3.4 ft (95–105 cm), shoulder height of 2.0–2.6 ft (60–80 cm), tail length of 5.9–7.9 in (15–20 cm), and weight of 33–77 lb (15–35 kg). Males have a weight of 38–77 lb (17–35 kg), while females have a weight of 33–55 lb (15–25 kg). They have a slender build with proportional looking long necks and legs and exceptionally long hind legs. The coat is a dark brown in color, with white on the under parts and the backs of the legs. The coat is short and sleek during the summer months (in order to reflect the sun's rays) and is longer, thicker, and rainproof during the winter months (in order to protect it from the heavy rains). A narrow, dark flank band separates the dark dorsal tones from the white belly. A white line begins on the thigh and ends at the lower leg joint. The base of the hairs from the underside is buff colored, while the black tail is short and bushy. Both males and females have two elliptical (in cross-section) horns that are arched backwards, generally S-shaped, and separated by about 1 in (25 mm). Horns are used primarily for defense against predators (for example, butting small enemies). Male horns are 9–12 in (22–29 cm) long, thick and ringed, of different lengths depending on the habitat, and bowed out from the base with the tips almost always pointing in. Female horns are 3–6 in (8–15 cm) long, curved slightly forward, slender, and not ringed. Facial markings include numerous shades of brown throughout the face and two white stripes beginning from the eyes and ending near the nostrils. They have well-developed vision, along with good hearing and smell. Vision is the primary sense used for predator detection, whereas smell is used mainly for finding food. They have a large snout and tooth rows are nearly straight. The ears are relatively short.

DISTRIBUTION
Arabian Peninsula, Egypt, Iran, Israel, Jordan, Lebanon, Oman, Saudi Arabia, Syrian Arab Republic, Yemen, and the United Arab Emirates.

HABITAT
They are found in a wide variety of habitats in hilly and mountainous terrain, including light forests (especially oak and pine), fields, grasslands, and stony desert plateaus.

BEHAVIOR
Mountain gazelles are diurnal and highly territorial. Their territories are widely spaced apart. They generally gather in three groups: maternity herds, bachelor male herds, and territorial solitary males. Fights occur more frequently as males mature,



however fights between neighboring males are ritualized and less violent than when males fight over females. Immature bachelor males make more numerous contacts with their horn when fighting than do adult or territorial males. They regularly migrate over 75 mi (120 km) for food. Normally they will spend days resting and sleeping in hilly areas, and later will descend to valleys in order to feed at nights or in early mornings. They can run at high speeds for several hundred feet (meters), reaching speeds up to 50 mph (80 kph).

FEEDING ECOLOGY AND DIET

They are browsers and grazers, eating herbs and shrubs in the summer and green grasses in the winter. They are well adapted to living in harsh desert climates, being able to go without water for long periods of time. They utilize water from plants as well as dew, but also will visit waterholes on a frequent basis.

REPRODUCTIVE BIOLOGY

Polygymous. Males attend to one or more females and their young generally in groups of 3–8. Estrous occurs every 18 days and lasts 12–24 hours, repeating until the female becomes pregnant. Males and females reproduce with various partners. Females usually give birth to one baby per season (and, on average, 11 in her lifetime). The usual mating season is in early winter (October to November), although mating also occurs in the spring (April to mid-May) and at other times when food is plentiful. The gestation period is about 180 days. Newborns generally weigh about 11–12% of the mother's weight. Mothers give birth away from the herd. The newborn can stand shortly after birth, and spends the first few weeks nursing. They begin to take solid food when they are 3–6 weeks old, but suckling may last up to three months. Males do not contribute to the care of the young. At this time, mother and young will join a maternity herd. Female young will remain with the mother, but male young will leave the mother at about six months, joining a herd of young males. Females reach sexual maturity (and their adult weight) at about 18 months, while males reach this stage at about 3 years. They rarely live longer than eight years in the wild, but in captivity can live 12–15 years.

CONSERVATION STATUS

Lower Risk/Conservation Dependent. They are regularly threatened with human-induced habitat loss and degradation from increased amounts of pastureland for livestock and deforestation for agriculture and home building, along with invasive alien species and ongoing hunting by humans. Their primary predators are the cheetah and human, but are also sought after by the desert lynx, feral dog, hyena, jackal, leopard, red fox, and wolf. Predators do not (normally) affect their populations, except in the case of humans.

SIGNIFICANCE TO HUMANS

They are hunted for skins, meat, and as trophies and often eat the cultivated crops within their habitat. ◆

Gerenuk

Litocranius walleri

SUBFAMILY

Antilopinae

TAXONOMY

Gazella walleri (Brooke, 1879), Somalia.

OTHER COMMON NAMES

English: Giraffe gazelle, gugufto, nanjaat, Waller's gazelle.

PHYSICAL CHARACTERISTICS

Gerenuks have a head and body length of 4.6–5.2 ft (140–160 cm), tail length of 8.7–13.8 in (22–35 cm), shoulder height of 3.0–3.3 ft (90–100 cm), and weight of 64–128 lb (29–58 kg). Males and females possess a similar shape, but males are more muscular so weigh more than females. They have long necks and long, slender legs, both which are their most defining features. The giraffe-like neck is only 7–10 in (180–255 mm) in circumference. Their coat contains short, fine, glossy hair that is evenly distributed throughout the body, and is colored a pale tawny brown with white along the breast, underbelly, and inner legs. There are small, dark patches of fur on the knees of the forelegs and at the end of the tail. The long, narrow head contains medium-sized ears, with reduced cheek teeth and chewing (masseter) muscle. There is a narrow muzzle with very flexible lips; the long upper lip and long tongue both help to pluck high-reaching leaves off of trees. The dark patch around the eyes becomes paler as it goes outward until it forms a white rim. Only males have horns, which are scimitar shaped; relatively massive; curved backward, upward, and hooked forward near the ends; and of length 9.8–17.3 in (25–44 cm).

DISTRIBUTION

Eastern Ethiopia, Somalia, Kenya, northeastern Tanzania.

HABITAT

Their habitat varies from treeless plains (in southern portions of the range) to dry high deserts (in northern portions). They are well adaptable and do well in a variety of habitats as long as there is an ample supply of succulent plants.

BEHAVIOR

Gerenuks are primarily active during the day. Males are solitary and very territorial, only associating with females during the mating season or when they are young. Dominant males

establish territories by marking shrubs and trees with their preorbital gland. A male inside his own territory will not force off other dominant males, but will show aggression to young males who enter his domain. Male territories are 300–850 acres (120–345 ha) and can support several individuals. Females form small bands of up to about ten individuals, usually consisting of related female adults with young and roaming freely throughout male territories. Young males will often form bachelor herds that roam nomadically until they become mature enough to develop their own territories and to breed. They travel singly, in pairs, or in groups of 6–7 females led by a single male. Gerenuks will stand motionless, hiding behind bushes or trees, when predators approach, and then look over or around their cover by means of their long neck. When frightened, they leave in a stealthy, crouched trot with neck and tail carried horizontally. They are not fast animals, as compared to the other genera.

FEEDING ECOLOGY AND DIET

They are well adapted to foraging in arid habitats, usually alone. Their long necks and legs, and their ability to stand (even walk to a certain extent) on their hind legs, allow them to obtain tree leaves that are high off the ground and out of the reach of most other animals. It usually leans with its front legs against a tree trunk or a branch. They consume a select number of herbaceous plants, often numbering as many as 80 different plant species, including grasses, foliage, acacia leaves, and succulent plant parts. They do not drink standing water, but take in moisture within succulent plants that they eat.

REPRODUCTIVE BIOLOGY

The mating ritual of gerenuks is complicated. Females will raise their nose into the air when seeing a potential male mate, and then pull her ears close to the head as a defensive sign. At the same time, males will display his horns and neck in a sideways pose. If the male sees that the female is receptive, he will mark the female on the thigh with the contents of his preorbital gland and then follow her around in a stance of guarding her. He will repeatedly kick the female in her thigh region. When she attempts to urinate the male will perform (what is called) the "flehmen test" or "lip curl test" where he smells her urine. When the female comes into estrous the male will notice the difference in the urine and will begin mating. The polygamous males will perform this routine on several females. The gestation period is about 165 days. Females breed every 1–2 years, depending on the sex of their previous year's offspring, and will give birth to one young, rarely two. Reproduction occurs throughout the year, often depending on the quality and quantity of available food. Newborns begin to walk almost immediately after being born, and are able to eat tender leaflets. Young gerenuks will remain motionless in bushes and tall grasses while mothers are feeding to help hide from predators. The weaning period is 12–18 months. Male young sexually mature later than female young, with an average maturity period of 1–2 years. The average life span in the wild is 10–12 years, with females slightly outliving males.

CONSERVATION STATUS

Lower Risk/Conservation Dependent. A wide range of predators, especially Cape hunting dogs, hyenas, leopards, lions, and cheetahs, preys upon gerenuks. Young are often preyed upon by desert lynxs, large eagles, honey badgers, and servals (African wild cats).

SIGNIFICANCE TO HUMANS

They are hunted for their meat and as trophies. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Dibatag *Ammodorcas clarkei* English: Clarke's gazelle	Upperparts are grayish fawn, rump and undersides are white, white stripes run from above eye to muzzle. Line of chestnut across nose. Body is thin, legs and neck are long and thin. Head and body length 59.8–66.1 in (152–168 cm), tail length 9.8–13.8 in (25–35 cm), weight 49–77 lb (22–35 kg).	Sandy areas with scattered thorn scrub and grasses to arid, low-lying, scrub-covered plains. Births occur in October and November. Diurnal, motile, solitary, territorial, and social.	Eastern Pakistan (extinct but reintroduced); India from Punjab south to Madras and east to Bihar (formerly up to Assam); extinct in Bangladesh and now localized in India; introduced to Nepal, Texas, United States, and Argentina.	Leaves and shoots.	Vulnerable
Blackbuck *Antilope cervicapra* English: Sasin; French: Antilope cervicapre; Spanish: Cervicapra	Females and young upper coats are yellowish fawn; after two years, males gradually darken from tan to deep brown or black. Both sexes have white underparts and short tails. Only males have spiral, ridged horns, 14–29 in (35–73 cm). Head and body length 39.6–60 in (100–150 cm); shoulder height 24–33.6 in (60–85 cm); tail length 4–6.8 in (10–17 cm); weight 55–77 lb (25–35 kg).	Dry woodland and clearings. Diurnal during the cooler season, graze in the open in the early morning and late afternoon during warmer weather. Alert females, and then the entire herd of animals, leap into the air upon recognizing a potential threat. Males are territorial during the breeding season.	Eastern Pakistan (extinct but reintroduced); India from Punjab south to Madras and east to Bihar; introduced to Nepal; Texas, United States; and Argentina.	Grasses, leaves, buds, and field fruits.	Vulnerable

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Dama gazelle *Gazella dama* French: Gazelle dama	Large body, reddish brown coat. Face, bottom, and rump are white. White patch on throat. Thin legs and skinny neck. Horns are S-shaped. Head and body length 55.2–66 in (140–168 cm), shoulder height 36–48 in (91–122 cm), weight 88–187 lb (40–85 kg).	Arid areas with sparse vegetation, including pastures of the Sahara Desert in the rainy season and semi-deserts and open bushlands in the dry season. Diurnal species. Occur singly or in small groups of 15 to 20 individuals.	Formerly from Morocco, western Sahara, Mauritania, and Senegal east to Egypt and Sudan. Now extinct in Mauritania, Senegal, Morocco, Algeria, and Egypt; survives at least in Mali, Niger, Chad, Burkina Faso, and Sudan.	Herbs, shrubs, and coarse desert grasses.	Endangered
Grant's gazelle *Gazella granti*	Upperparts are fawn colored; underparts are white. Some populations have a dark stripe along the mid-body. Both sexes have horns; males' are longer, up to 19.2–31.2 in (50–80 cm), thicker, and more strongly ringed. Males weigh 121–176 lb (55–80 kg); females weigh 77–110 lb (35–50 kg).	Semi-desert and open savannas. Can obtain sufficient water from vegetation during drought. Form mixed-sex groups; males are territorial during the breeding season.	Southeastern Sudan, northeastern Uganda and southern Ethiopia south to southern Somalia, Kenya, and northern Tanzania.	Grasses, leaves, and fruits.	Lower Risk/ Conservation Dependent
Red-fronted gazelle *Gazella rufifrons*	Upper coat is short and tan; underparts are white. Red forehead with faint red and cream lines from the eyes to the nose. Tail has a black tuft. Both sexes have thick, ridged horns; female length 6–10 in (15–25 cm); male length 8.8–14 in (22–35 cm). Head and body length 42–48 in (105–120 cm); shoulder height 25.6–35.2 in (65–92 cm); tail length 6–10 in (15–25 cm); weight 44–77 lb (20–35 kg).	Open savanna and vegetation-covered dunes of the Sahel. Obtains water from vegetation, but more water-dependent than other species of gazelle. Migrate seasonally. Live in small mixed herds of 2–6 animals, rarely up to 15; breeding males defend territories.	Senegal to northeastern Ethiopia, south to northern Togo and northern Central African Republic.	Grasses and leaves.	Vulnerable
Slender-horned gazelle *Gazella leptoceros* English: Loder's gazelle, rhim, sand gazelle; French: Rhim, gazelle deptocère gazelle à cornes fines	Upper coat is buffy brown with faint stripes on the face and flanks; underparts are white. Both sexes have horns, males' are longer and ridged. Head and body length 39.6–43.2 ft (100–110 cm); shoulder height 25.2–28.8 ft (65–72 cm); tail length 6–8 in (15–20 cm); weight 44–66 lb (20–30 kg).	Live in the desert, in small, mixed groups of 3–10 individuals, sometimes up to 20. Males are territorial during the breeding season.	Algeria, Tunisia, Libya, western Egypt, Niger, and northern Chad.	Grasses, succulents, herbs, and foliage of shrubs. They obtain sufficient water from their food, but drink water when it's available.	Endangered
Persian gazelle *Gazella subgutturosa* English: Goitered gazelle	Body light brown, darker toward belly; white underparts; black tail. Only males have black, S-shaped horns, 10–17.2 in (25–43 cm) long. During the breeding season, the males' larynx bulges outwards, resembling a goiter. Head and body length 36–45.6 in (90–115 cm); shoulder height 24–1.2 in (60–80 cm); tail length 6–8 in (15–20 cm); weight 40–73 lb (18–33 kg).	Live in deserts, semi-deserts, hilly plains, and plateaus in southern and central Asia. In summer, found in small family groups of 2–5 animals; in winter, large herds with dozens or even hundreds of individuals. Males are territorial during the breeding season.	Israel; Jordan, central Arabia and eastern Caucasus through Iran; Afghanistan; west-central Pakistan; Kazakhstan; Turmenistan; Uzbekistan; Mongolia; and western China.	Grasses, leaves, and shoots.	Lower Risk/Near Threatened
Tibetan gazelle *Procapra picticaudata* English: Goa	Coat is orange-buff above in summer, with pinkish cinnamon sides, and paler in the winter; underparts are white. Only males have horns, 7.9–9.8 in (20–25 cm) long. Head and body length 37.4–58.3 in (95–148 cm); tail length 0.8–4.7 in (2–12 cm); shoulder height 21.3–33.1 in (54–84 cm); weight 44–88 lb (20–40 kg).	Dry grassland up to 18,860 ft (5,750 m). Northward migration in spring, at which time herds of 6,000–8,000 individuals form.	Szechuan, Tsinghai, and Tibet, China; and adjacent Indian Himalayas.	Vegetation.	Lower Risk/Near Threatened

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William Arthur Atkins

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Bovids IV
Dikdiks, beiras, grysboks, and steenboks
(Neotraginae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subfamily Neotraginae

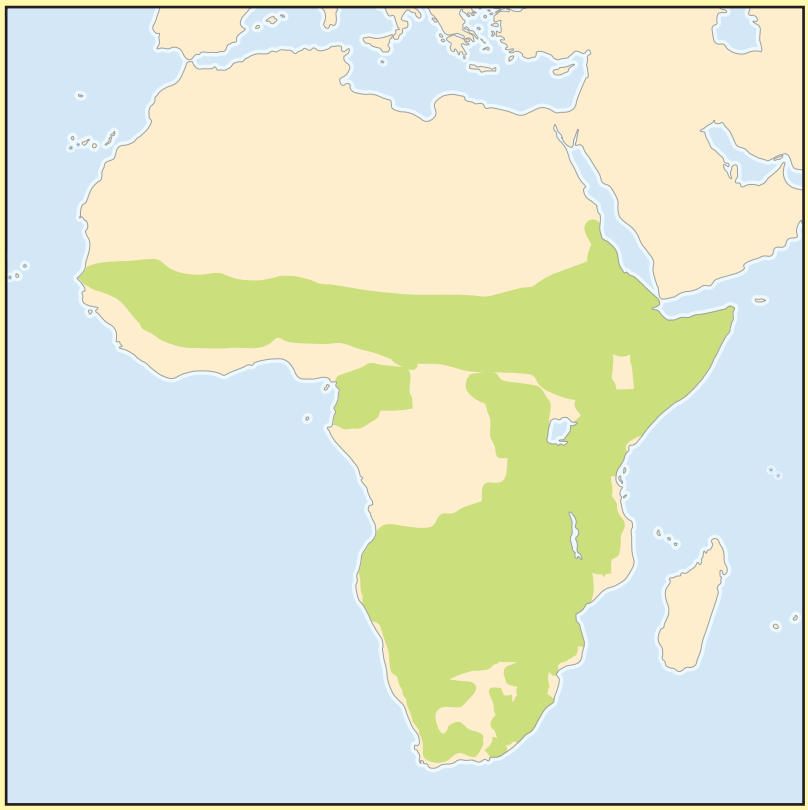
Thumbnail description
Small graceful antelopes, females typically larger than males; simple spike horns in males only; well-developed scent glands for olfactory communication; primarily selective browsers

Size
Body length 16–42 in (40–112 cm); shoulder height 10–26 in (25–67 cm); 3.9–48 lb (1.8–22 kg)

Number of genera, species
6 genera; 13 species

Habitat
Forest, woodland, mixed woodland, savanna, scrub, sub-desert, reed beds, hilltops, and flood plains

Conservation status
Vulnerable: 2 species; Lower Risk/Near Threatened: 2 species; Lower Risk/Conservation Dependent: 5 species; Lower Risk/Least Concern: 4 species



Distribution
Sub-Saharan Africa

Evolution and systematics

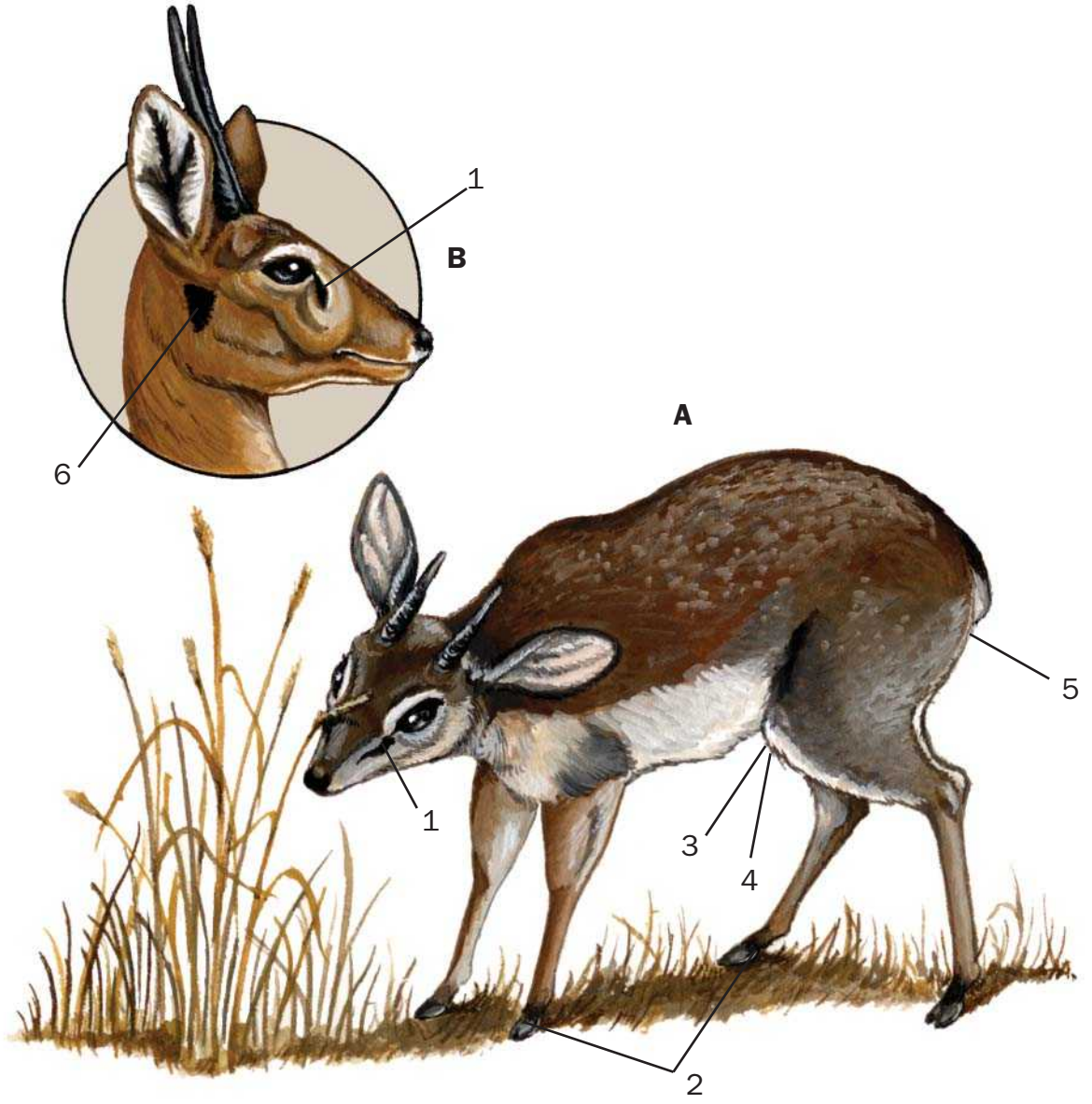
The Neotragines, or dwarf antelopes, are placed beside the Antilopini, both belonging to the subfamily Antilopinae. This sister group Antilopini includes the larger gazelles that serve as popular icons of Africa's savanna ecosystems. The neotragines are a polyphyletic group, and more recent molecular-based phylogenies suggest that some members may belong to the Antilopini or even Reduncini. The neotragines are considered to have originated in Eurasia and represent, with the Bovinae, one of the oldest subfamilies of the Bovidae. Fossil evidence suggests that the first neotragines appeared 5–12 million years ago and very closely resembled the animals observed today. The modern Neotraginae is represented by 13 species from six genera.

Physical characteristics

The neotragines are the smallest of the antelope. They range in body shape from crouched and hare-like, to compact and stocky, and to lean and graceful. They weigh 3.9–48 lb (1.8–22 kg) and range in height from 10 to 26 in (25–67 cm). Females are 5–15% larger than males, but this sexual dimorphism does not extend to coloration. Body color varies from pale gray to dark reddish brown to sandy, and the belly is white or cream. Ears are medium to large and often have distinctive markings in their white lining that allows individual identification of animals. Tails are medium to short. Only males possess horns and these are dagger-like, straight, and sharp. Hooves, horns, and eyes are black. The dwarf antelope is characterized by a prevalence of scent glands, most notably the pre-orbital gland, but also pedal, inguinal, and others.

Distribution

The Neotraginae occur widely across Africa and nowhere else. At least one member of this group can be found in every African country south of the Sahara Desert. Areas of highest density include the Horn of Africa and the equatorial forests, but large populations occur across a diverse array of regions



A. Suni (Neotragus moschatus) scent-marking grass with its pre-orbital glands (1). Other sources of scent are (2) pedal glands, (3) urine, (4) inguinal (genital) glands, and (5) feces. B. Oribi (Ourebia ourebi) head, showing swollen preorbital gland (1) and the post-auricular gland (6), peculiar to oribis. (Illustration by Gillian Harris)

and biotic zones. The historic, or Paleolithic, distribution of this subfamily includes North Africa and perhaps beyond, but today no natural population occurs further north than Mauritania.

Habitat

The neotragines have adapted to a broad range of habitats. For example, the dikdiks (*Madoqua* sp.) primarily occur in dry scrub or thorn-brush habitats, while the tiny royal and dwarf antelopes (*Neotragus pygmeus* and *N. batesi*) occupy lush undergrowth in equatorial forests. Several species are desert-adapted and require little or no water. Even a single, widely distributed species like the oribi (*Ourebia ourebi*) thrives in more than nine distinct habitat types, from sub-desert scrub to lush coastal savanna and forest clearings. With regard to habitat selection, the klipspringer (*Oreotragus oreotragus*) is unique among the Neotraginae in that it has adapted to life on rocky hilltops and mountain slopes. In all of these habitats, animals require access to some form of cover for both hiding from predators and avoiding the often brutal midday sun.

Behavior

Most neotragines are solitary, but some are found more often in pairs or small groups of three to five animals (up to

12). All are nonmigratory and nearly all are territorial or defend exclusive home ranges. Defense of a territory often, but not always, involves scent marking with feces and urine placed on conspicuous dung middens, as well as the careful placement of secretions of the preorbital and other glands. Scent marking can occupy more time than feeding in the life of many neotragines and some species mark as many as 45 times per hour. Males commonly engage in battles over territory ownership, dominance, and females, but these fights only rarely involve contact between the combatants and instead are built around threats. Threats are signaled through postures, vocalizations, and also with aggression towards inanimate objects such as bushes. Fights that escalate to contact between males commonly result in the wounding of one or both combatants.

The neotragines are best known for their reliance on olfactory communication, but they also display a range of vocalizations. The most commonly encountered of these is the alarm whistle. This shrill whistle varies in structure and tone but some form of it is used by most species in this group to alert conspecifics (those of the same species) to the presence of a potential threat. Other vocalizations include barks, bleats,

Kirk's dikdiks (*Madoqua kirkii*) are skittish, and flee in a zig-zag pattern. (Photo by Ann & Steve Toon Wildlife Photography. Reproduced by permission.)

A female steenbok (*Raphicerus campestris*). (Photo by © Lynda Richardson/Corbis. Reproduced by permission.)

Kirk's dikdik (*Madoqua kirki*) watches for predators. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)

mews, and at least two species have been observed to emit a strangely human-sounding scream on being captured.

Daily activity patterns are linked closely to environmental conditions. In hot, dry climates or during the dry season in variable environments, animals are crepuscular and nocturnal. Avoiding the midday heat is essential to maintaining water balance, and animals in extreme environments will seek out cooler, shaded areas and remain inactive for hours. In more temperate areas, animals are active at various times both day and night.

Feeding ecology and diet

Nearly all neotragines browse selectively on high-protein, low-fiber portions of a huge range of bushes, herbs, and trees. This includes, but is not limited to, fresh shoots, leaves, roots, flowers, seeds, fungi, and fruits. Frequent consumption of grasses is rarely seen in this group except in the oribi for which green grasses comprise 60–95% of the diet. Several species have been observed to eat soil and chew on bones, presumably to ingest minerals that are otherwise in short supply. Animals also are known to occasionally eat nestlings or other sources of animal protein when encountered opportunistically.

Foraging occurs at any time of day or night, depending on weather conditions and proximity of potential threats. Species in this group also spend a great deal of their time lying down and ruminating. Most species are extremely efficient at maintaining water balance and require little or no access to open water.

Reproductive biology

Several members of this group are monogamous while others are polygamous. Monagamy has been confirmed in some of these species using molecular techniques. At least one species, the oribi, displays polygyandry in parts of its range. These polygyandrous associations are rare among bovids and are characterized in oribi by the cooperative defense of a harem and territory by two to four adult males.

The dew and moisture from the vegetation that it eats provides Kirk's dikdik (*Madoqua kirkii*) with sufficient water. (Photo by Ann & Steve Toon Wildlife Photography. Reproduced by permission.)

Kirk's dikdik (*Madoqua kirkii*) sniffing a scent marker in Etosha National Park, Namibia, Africa. (Photo by Martin W. Grosnick. Bruce Coleman, Inc. Reproduced by permission.)

Courtship in the neotragines typically begins when a female approaches or reaches estrus at which time the male begins to guard her closely. The male conveys his desire to mount through bleats and mews and with repeated pats on the female's hind legs ("laufschlag"). Mounting lasts a short time (5–20 seconds) and is repeated several times during estrous. One young is born after a gestation of five to seven months, after which it is hidden in tall grass or thicket for two to 16 weeks. Breeding typically coincides with rainy seasons, when lactating mothers and developing young will have greatest access to food of high quality. Males do not participate in parental care beyond whistling to alert group members to danger or, very rarely, butting potential predators of young such as hawks and eagles.

Conservation status

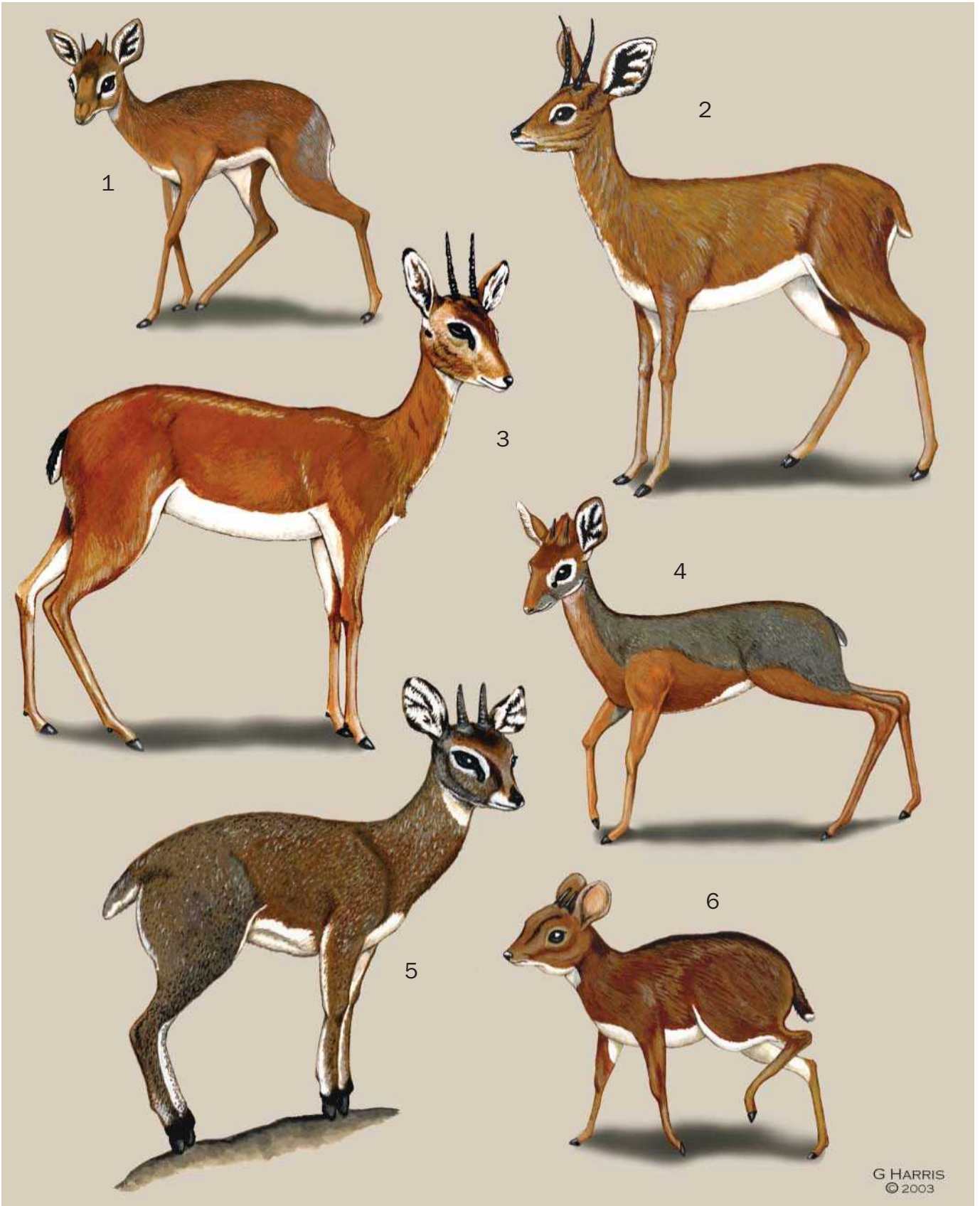
Overall, the Neotraginae are a widespread and common group. Members of this group such as the Kirk's dikdik (*Madoqua kirkii*) occur at densities beyond that of any other antelope. Contrary to expectation, some species have increased locally as a result of human alterations of the habitat such as forest clearing and livestock grazing. However, all members of this group are heavily hunted and decline in areas where human densities are high. The healthiest populations and thus, species, are those that occur in protected areas or where human densities are low. The small and shrinking distribution of the beira (*Dorcatragus megalotis*), silver dikdik (*Madoqua piacentinii*), Cape grysbok (*Raphicerus melanotis*), and the royal and dwarf antelopes make these species the greatest concerns for conservation among the Neotraginae.

Total population estimates range from the tens of thousand for five species to the high hundreds of thousands for the Kirk's dikdik. Of the 13 species in this group, populations of only two are estimated to be stable. Primary causes for decline across all species in this group are overhunting and habitat loss or degradation resulting from agriculture and overgrazing of livestock. Together, these factors are rapidly reducing the once contiguous distributions of many of these species into a collection of fragments.

A male steenbok (*Raphicerus campestris*) eats leaves from the mopane tree in Etosha National Park in Namibia (Photo by Jen & Des Bartlett. Bruce Coleman, Inc. Reproduced by permission.)

Significance to humans

The neotragines are widely represented in traditional and modern African folklore and literature. Many of the species in this group represent the only wild mammals seen routinely by Africans near areas of human settlements. As such, they have great cultural significance by representing a tangible link to nature. These species are relied upon for food and combined they account for a substantial proportion of the trade in bush meat. They are used in traditional ceremonies and for clothing, musical instruments, and other craftwork. Some species represent a minor pest to agriculture, but in most cases the economic benefits of their presence far outweighs the costs.



1. Kirk's dik-dik (*Madoqua kirkii*); 2. Steenbok (*Raphicerus campestris*); 3. Oribi (*Ourebia ourebi*); 4. Salt's dik-dik (*Madoqua saltiana*); 5. Klipspringer (*Oreotragus oreotragus*); 6. Dwarf antelope (*Neotragus batesi*). (Illustration by Gillian Harris)

Species accounts

Oribi
Ourebia ourebi

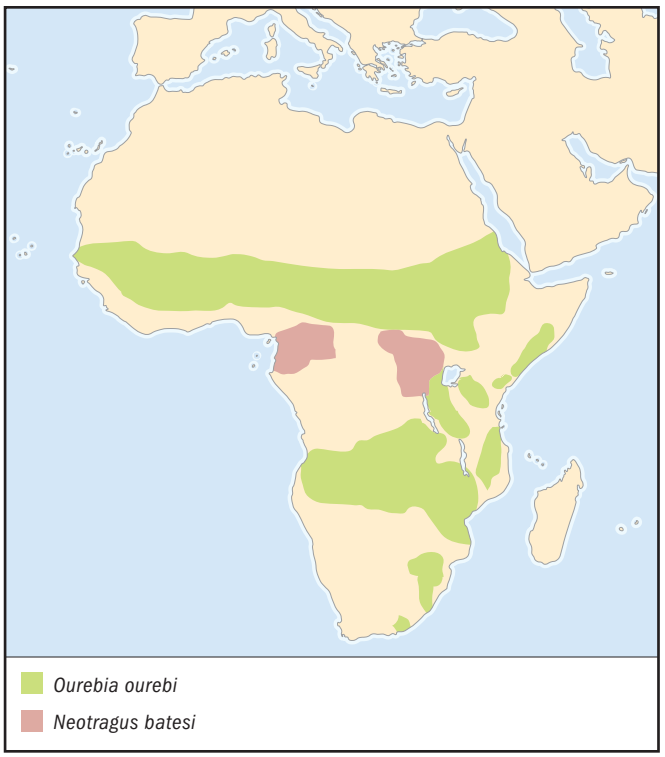
TAXONOMY
Antilope ourebi (Zimmermann, 1783), Cape of Good Hope, South Africa. Thirteen proposed subspecies.

OTHER COMMON NAMES
French: Ourébie; German: Bleichbockchen; Spanish: Oribi.

PHYSICAL CHARACTERISTICS
Slender, small antelope; males have distinctively large glands beneath the eyes. Length 37–44 in (93–111 cm); height 24–27 in (60–69 cm); weight 33–46 lb (15–21 kg). Pelage sandy to rufous with white undersides, throat, chin, mouth, eyebrows, and ear linings. Eyes large and black. Tail often darker than body with white underside. Horns on males straight, sharp, and annulated, grow to 7.5 in (19 cm) and angle slightly to the anterior.

DISTRIBUTION
Most widespread member of the Neotraginae, it is found throughout sub-Saharan Africa on fire-climax grasslands and mixed savannas.

HABITAT
Highly variable, but this species generally occurs in open habitats ranging from guinea savanna, moist savannas, woodland mosaics, flood plains, to montane and coastal grasslands. Densities in optimal habitat recorded at up to 91 per mi^2 (35 per km^2), but more typically 1–10 per mi^2 (0.5–4 per km^2) in suitable habitats.



BEHAVIOR
Behaviorally flexible, this antelope is adapted to a range of environmental conditions and behavior is linked to local conditions. Males defend females and territories cooperatively in some areas and simply follow a single female throughout her home range in other areas. Scent marking with urine, feces, and glandular secretions is used to demarcate territory borders where territories are defended. Primary vocalization is a shrill whistle used to alert group members to approaching danger. Other vocalizations include bleats, mews, and, upon capture, human-like screams.

FEEDING ECOLOGY AND DIET
The only predominately grazing member of the Neotraginae. Selective grazer of fresh green grasses; forbs, legumes, and tree foliage are eaten when fresh grass is unavailable. Fungi, flowers, and fruit are often eaten, as is soil, for their nutrient content. Feed actively at day and night, but generally avoid heat of midday and are most active during cool hours of early morning and late afternoon. Survive in some areas with little access to open water.

REPRODUCTIVE BIOLOGY
Polygamous. Group size is highly variable and ranges from solitary animals to groups of up to 12 adults. Territories range in size from 0.25–148 ac (0.1–60 ha). Pair bonds may last years. One young is born after a gestation period of 6.5–7 months. Young hide in tall vegetation for up to three months before joining group. Birth peaks coincide with the arrival of rainy seasons.

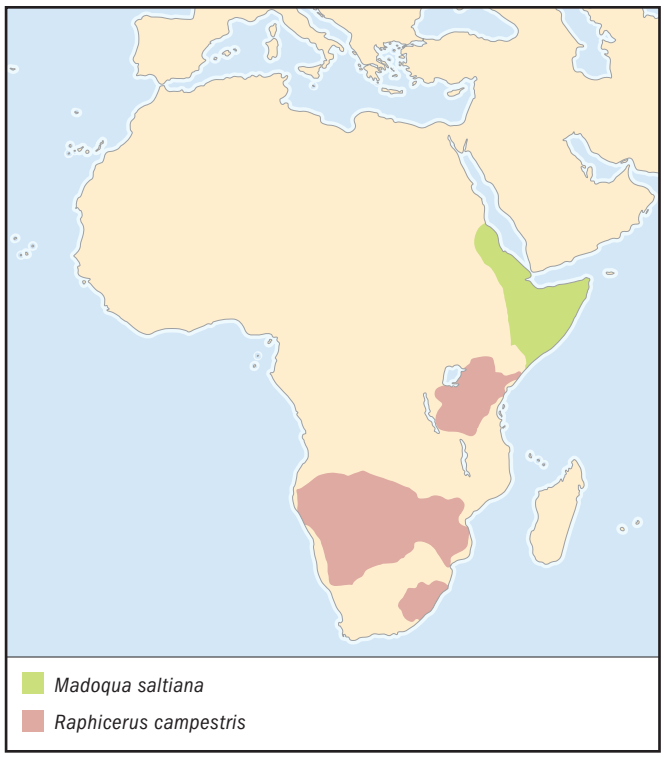
CONSERVATION STATUS
Lower Risk/Conservation Dependent. Two putative subspecies, *O. o. haggardi*, of coastal Kenya and Somalia, and *O. o. keniae*, of the Mount Kenya region are classified as Vulnerable and Extinct, respectively. Total population of this species is estimated in the hundreds of thousands. It is shot, snared, and trapped throughout its distribution and hunting is the primary reason for dramatic population declines in human-dominated areas. Like other neotragines, oribi have poor stamina and are easily run down by domestic dogs.

SIGNIFICANCE TO HUMANS
This animal is prized for its meat in many regions and provides subsistence and income for hunters in much of sub-Saharan Africa. The skin is used for drums and other traditional craftwork. ◆

Steenbok
Raphicerus campestris

TAXONOMY
Raphicerus campestris campestris (Thunberg, 1811), Cape of Good Hope, South Africa. Seven proposed subspecies.

OTHER COMMON NAMES
English: Steenbuck, steinbuck, steinbok; French: Steenbok; German: Steinbockchen; Spanish: Steenbok.



PHYSICAL CHARACTERISTICS
Slender, graceful antelope, third largest of the neotragines but still only 18–24 in (45–60 cm) tall, 28–35 in length (70–90 cm), and weighing 18–33 lb (8–15 kg). Body color ranges from light beige to reddish brown; belly, chest, chin, and ear-linings are white to off-white. Large ears and short tail; horns are sharp, thin, and upright in males, up to 6 in (15 cm) in length.

DISTRIBUTION
Displays two distinct distributions, with the first in East Africa in southern Kenya and northern Tanzania, and the second in southern Africa from Angola and Zambia south to the Cape of South Africa. The largest populations today occur in Namibia and Botswana.

HABITAT
Varies from desert scrub habitats near the Kalahari to moist mountain forests in Kenya. Generally occurs in bushy or scrubby areas of open habitats such as dry mixed savannas and grassland plains. Areas cleared by fire, heavy grazing, logging, or for cultivation are quickly occupied. Densities in optimal habitats are as high as 10 animals per mi^2 (4 per km^2), but more typical densities are 1–2 per mi^2 (0.3–1.0 per km^2).

BEHAVIOR
Highly territorial, both sexes actively defend the territory by chasing same-sex intruders and by scent marking with urine, feces, and secretions of the pre-orbital, pedal, and other glands. Vocalizations between individuals include goat-like bleats, whistles, and growls. Typically drops to the ground and freezes as a first response to approaching danger and flees in a zig-zag pattern if the threat moves near.

FEEDING ECOLOGY AND DIET
Primarily a browser, it will often feed near ground level on roots and low shrubs, but also shoots, flowers, and fruits of trees; commonly eats soil for its nutrient content. Desert-adapted, it can survive with little or no access to open water. Water balance is maintained by selection of plants of high water content and inactivity during hottest times of the day. Animals are active in day and night in wetter habitats and are most active nocturnally in very dry areas.

REPRODUCTIVE BIOLOGY
Adults are solitary or occur as pairs, and rarely as small, polygynous groups, on territories of 10–37 acres (4–15 ha). Breeding pairs are sometimes stable for several years. Mating is followed by gestation of about 170 days, at which time one lamb is born. Young lay hidden for three to five months before joining their mother. Birth commonly coincides with rainy seasons. Females in some areas have been observed to breed twice per year.

CONSERVATION STATUS
Lower Risk/Least Concern. Declining in unprotected parts of its range where it suffers from overhunting, but it is stable and well represented in protected areas. Overall, the outlook for the species appears good if protected areas remain intact. Like other neotragines, this species is vulnerable to predation by domestic dogs.

SIGNIFICANCE TO HUMANS
Included in traditional African folklore, skin used for drums, traditional clothing, and crafts. Meat is considered to be of good quality by humans; this species is eaten throughout its range. ◆

Klipspringer
Oreotragus oreotragus

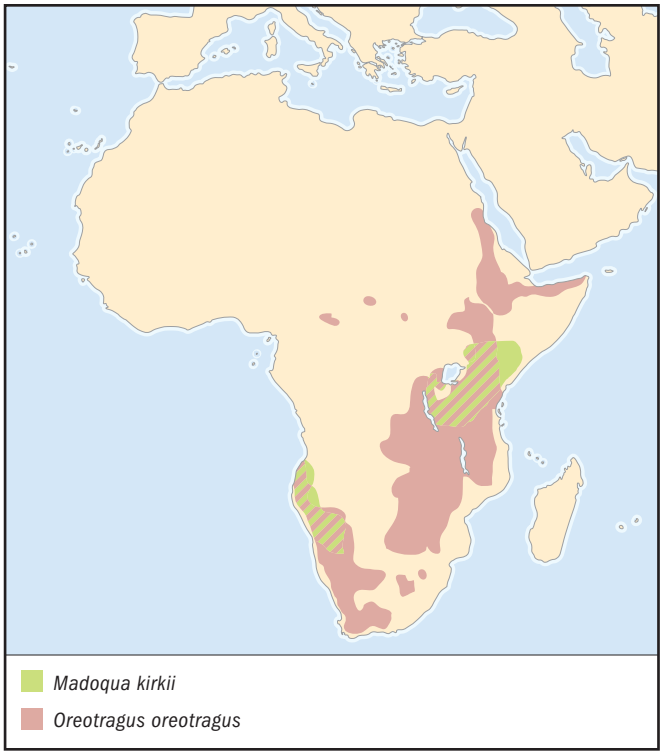
TAXONOMY
Antilope oreotragus (Zimmermann, 1783), Cape of Good Hope, South Africa. Eleven proposed subspecies.

OTHER COMMON NAMES
French: Oreotrague; German: Klippspringer.

PHYSICAL CHARACTERISTICS
Small, compact antelope with rounded hindquarters and blunt muzzle. Walks on tips of extended hooves. Length 32–39 in (82–100 cm); height 18–24 in (45–60 cm); weight 20–35 lb (9–16 kg). Fur is coarse, hollow, and tawny to gray in appearance. Underside and ear linings light gray to white. Horns straight and annulated in males, up to 6 in (15 cm) in length, though typically no longer than 3.5 in (9 cm). Unique among Neotraginae, females of some populations are horned.

DISTRIBUTION
Patchily distributed in rocky and mountainous terrain from northern Sudan, Eritrea, Ethiopia, Somalia, south through Kenya, Uganda, and Tanzania into central and southern Africa. The largest populations today occur in Namibia.

HABITAT
Rocky hillsides, cliffs, and ravines from sea level to 14,800 ft (4,500 m) and at a broad range of temperature and rainfall regimes. Vegetation type is considerably less important than access to steep, rocky slopes for escape and cover. Occur at densities up to 36 per mi^2 (14 per km^2) in ideal habitats, but more often seen at densities of 0.3–0.8 per mi^2 (0.1–0.3 per km^2).



BEHAVIOR
Nimble and fast, supremely adapted for life in rocky terrain. Fiercely territorial, territory boundaries are scent marked routinely by all family members by placing feces, urine, and pre-orbital gland secretions in highly visible areas. Physical aggression exhibited as fights and chases are common and occur between both sexes. Bonds between monogamous pairs are strong and often last years. Vigilance is shared among group members and they signal the approach of a predator with an alarm whistle.

FEEDING ECOLOGY AND DIET
Selective browsers, prefer leaves, buds, flowers, fruits, and seeds with high-protein, low-fiber content. Up to 90% of diet consists of fruit and flowers in wet season, while leaves of shrubs, trees, and sometimes grasses form larger portion of diet in dry seasons. Will leave the safety of rocky terrain to feed or drink during harshest times of the year.

REPRODUCTIVE BIOLOGY
The typical breeding group is a male-female pair on a territory 3.5–22 acres (1.4–9 ha) in size. Monagamous pairs are sometimes joined in a territory by one or two un-dispersed offspring. Estrus is thought to last roughly one week and gestation is estimated at five months, after which one lamb is born. Newborns lay hidden for up to three months before joining parents and are weaned at four months. Seasonality of reproduction varies across the broad geographic range of this species, but is generally coordinated with rainy seasons.

CONSERVATION STATUS
Lower Risk/Conservation Dependent. Their preference for steep, rocky habitats and their ability to detect and avoid predators (human or otherwise) has allowed this species to avoid the common pitfalls of habitat loss and over hunting. However, the subspecies *O. o. porteousi* represents an exception and is classed as Endangered where it occurs in Nigeria and the Central African Republic. Predictable routes of travel by animals also makes snaring an effective and potentially devastating form of hunting.

SIGNIFICANCE TO HUMANS
Sturdiness and agility have made it a popular mascot and hero in traditional and modern African folklore. It has little economic value through much of its geographic range and its meat is not generally preferred. It comprises a relatively small part of the bushmeat trade in Nigeria. ◆

Dwarf antelope
Neotragus batesi

TAXONOMY
Neotragus batesi de Winton, 1903, Efulen, Bulu Country, Cameroon. Two recognized subspecies.

OTHER COMMON NAMES
English: Bate's pygmy antelope, Bate's dwarf antelope, pygmy antelope; French: Antilope de Bates; German: Batesbockchen; Spanish: Antílope de Bates.

PHYSICAL CHARACTERISTICS
Tiny, delicate antelope with large eyes, small, rounded ears, and short, pointed muzzle. Length 19–23 in (47–58 cm); height 7.5–11.5 in (19–29 cm); weight 4–10 lb (1.8–4.5 kg). Body is reddish to golden-brown, darker on back and head; belly, throat, and chin and spots below ears are white, as is underside of tail. Horns on males short and conical.

DISTRIBUTION
Patchily distributed in two distinct regions, the first in western Africa from Nigeria, Cameroon, Gabon to Central African Republic and Congo (Brazzaville), and the second in central Africa from eastern Congo (Democratic Republic of the Congo) to western Uganda.

HABITAT
Tree gaps or areas of heavy undergrowth in moist lowland forests. Includes dense habitats along rivers, roads, plantations, gardens, and in secondary growth following logging. Occur at densities up to 194 per mi^2 (75 per km^2) in ideal habitats, but more often seen at densities of 4–8 per mi^2 (1.5–3 per km^2).

BEHAVIOR
Cryptic and shy, this antelope is adapted to life in closed habitats. Has a slow, high-stepping gait when moving through the forest, responds to danger by freezing and then darting for cover if the threat approaches closely. Quick for short distances, but lacks stamina to outlast predators if caught in larger clearings. Males mark territories with black, tar-like secretions of the pre-orbital gland. Short, nasal moans are used to maintain contact between individuals, and they sometimes bark when fleeing from danger.

FEEDING ECOLOGY AND DIET
Selective browsers of high-quality leaves, stems, and shoots from a vast number of food plants. Crops such as sweet potatoes, peanuts, and peppers are also consumed, as are fruits. Foraging occurs both day and night in remote locations and more often only at night in areas near human habitation.

REPRODUCTIVE BIOLOGY
Males form exclusive home ranges of 5–10 acres (2–4 ha). Reproduction occurs year round but with two peaks coinciding with the arrival of rainy seasons. As many as 80% of breeding-age females are pregnant at any given time. Young are hidden for months and weaning typically occurs during the rainy season.

CONSERVATION STATUS
Lower Risk/Near Threatened. This antelope's ability to use and sometimes thrive in human-dominated habitats has enabled it to survive in areas where other mammals cannot. However, heavy hunting and the loss of forest habitat present major threats. It is captured in nets and snares by hunting parties and also taken by dogs in areas near human settlements.

SIGNIFICANCE TO HUMANS
Linked to folklore and taboos in some areas of its distribution, which has helped protect it from over-harvest in these regions. Accounts for only a small percentage of animals sold as bush meat in western Africa, but has considerable subsistence value for communities living in and near forests. Skin is used for traditional crafts. ◆

Kirk's dikdik
Madoqua kirkii

TAXONOMY
Neotragus kirkii (Günther, 1880), Brava, Somalia. Seven proposed subspecies.

OTHER COMMON NAMES
English: Damaraland dikdik; French: Dik-dik de Kirk; German: Kirkdikdik; Spanish: Dik-dik de Kirk.

PHYSICAL CHARACTERISTICS
Small, very slender antelope with distinctive soft, elongated nose. Length 22.5–29.5 in (57–75 cm); height 14–18 in (35–45 cm); weight 6–14 lb (2.7–6.5 kg). Fur on back is grizzled gray with black and white flecks, face and legs are tan, and the chin, belly, and underside of small tail are white to off-white. Crest of fur on head is dark yellow-orange, as are face and legs. Ears large and lined with white fur; large eyes bordered by ring of short white fur. Males with prominent glands beneath the eyes; horns on males sharp, straight, and annulated, growing to 4 in (10 cm).

DISTRIBUTION
Found patchily in two distinct areas separated by more than 1,000 mi (1,600 km); the first in Tanzania, Kenya, and Somalia, the second in Angola and Namibia. Largest populations in Namibia.

HABITAT
Restricted to arid regions of dense scrub and mixed woodland habitats. Thickets and thorn scrub are used for cover and food. Also found in riverine woodlands and thickets, along the base of hills and rocky outcroppings. Densities in optimal habitat recorded at up to 282 per mi^2 (109 per km^2), but more typically 26–104 per mi^2 (10–40 per km^2) in suitable habitat.

BEHAVIOR
Pairs defend territories cooperatively by chasing same-sex intruders. Territory borders observed to be stable for years in some areas. Territory holders use urine, dung, and secretions from pre-orbital and other glands to mark territory boundaries. Fights common between males along shared borders but seldom involve actual contact between combatants. During fights, males butt vegetation and raise the hair tuft on their heads. Has six known vocalizations, including a shrill double whistle alarm call, and bleats, mews, and screams.

FEEDING ECOLOGY AND DIET
Browses selectively on a broad array of herbs, leaves, flowers, shoots, and fruits; grasses only rarely eaten. Feeds actively at day and night, though generally avoids heat of midday. Often rises onto two legs to reach foods otherwise out of reach. Visits saltlicks and consumes soil and bones to acquire needed minerals. They are renowned for their ability to survive with no access to open water.

REPRODUCTIVE BIOLOGY
Typical breeding unit is a monogamous pair sometimes joined by one or two young on territories of 3–25 acres (1–10 ha). Pair bonds known to last till the death of one member; genetic studies confirm fidelity of females to their mate. Polygynous groups occasionally occur where animal densities are high. Estrus is thought to last only one to two days. One young is born after a gestation period 166–174 days. Young are precocious and join parents after five or six weeks of hiding in dense vegetation. Birth peaks coincide with the arrival of rainy seasons.

CONSERVATION STATUS
Lower Risk/Least Concern. Total population is estimated from hundreds of thousands to one to two million. This animal has declined in some areas as a result of land development for agriculture and hunting but is generally widespread and common. Hunted primarily with nets and snares and occasionally guns and dogs.

SIGNIFICANCE TO HUMANS
The high population densities make it a common item in bushmeat markets. It is a common source of meat for sustenance and commerce throughout its distribution. ◆

Salt's dikdik
Madoqua saltiana

TAXONOMY
Antilope saltiana (Desmarest, 1816), Ethiopia. As many as six proposed subspecies.

OTHER COMMON NAMES
French: Dik-dik de Salt; German: Eritrea-Dikdik; Spanish: Dik-dik de Salt.

PHYSICAL CHARACTERISTICS
Small, delicate antelope, with short, blunt muzzle. Length 19–24 in (49–60 cm); height 13–16 in (33–40 cm); weight 5.5–9 lb (2.5–4 kg). Fur on back is grayish brown and freckled, shading into a pale orange on sides and legs. Belly, interior of legs, underside of tail, and chin are white. Ears large and lined with white fur. Longer fur on head is reddish brown; conspicuous white ring around the eye. Horns on males up to 3.5 in (9 cm) and straight.

DISTRIBUTION
Restricted to arid bushlands and semi-desert scrub in Horn of Africa south from Sudan, Eritrea, Ethiopia, Djibouti, Somalia

to northern Kenya. Occurs from sea level up to 5,000 ft (1,500 m). Largest populations in Somalia and Ethiopia.

HABITAT
From evergreen bushlands to sub-desert scrub habitats, often found on valley bottoms and hillsides. Suggested densities in optimal habitat up to 36 per mi^2 (14 per km^2), but more typically 5–10 per mi^2 (2–4 per km^2).

BEHAVIOR
Families share territorial defense and all members use urine and dung to mark territory boundaries. Subordinate males and females mark dominant males with pre-orbital secretions in what is thought to be submissive behavior. Erection of crest of fur on head thought to be display of dominance by males and is often associated with a high-stepping strut and flashing of orange fur along limbs and flanks. Vocalizations include a double whistle used to warn other group members of approaching danger.

FEEDING ECOLOGY AND DIET
Browses on herbs, leaves, shoots, fruits, and roots often close to ground. Feeding occurs primarily at night and during early morning and late afternoon hours. Generally able to survive without access to open water.

REPRODUCTIVE BIOLOGY
Typically occurs as monogamous pairs or family groups of pairs with one or two young on territories of 10–50 acres (4–20 ha). Breeding pairs are likely stable over long periods. One young born after a gestation period estimated at five or six months. Weaning thought to occur at three to four months.

CONSERVATION STATUS
Lower Risk/Least Concern. Despite its restricted distribution, the global population is estimated in the hundreds of thousands. However, this animal is vulnerable to over-hunting, habitat alteration, and competition with domestic livestock. Numbers have declined in areas of high human settlement. Hunted with nets and snares.

SIGNIFICANCE TO HUMANS
Little is known about cultural significance of this species. Contributes to subsistence hunting throughout its range. Other economic significance is small. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Guenther's dikdik *Madoqua guentheri* English: Guenther's long-snouted dikdik; French: Dik-Dik de Guenther; German: Günther Dikdik; Spanish: Dikdik de Gunther	Small and slender with extended, elastic nose. Coat grizzled gray mixed with brown, yellow, and white, with white undersides and red-orange crest of fur on head. Males with sharp, annulated horns up to 4.5 in. (9.8 cm), slanted backwards. Length 22–26 in (55–65 cm); height 14–18 in (35–45 cm); weight 8–12 lb (3.5–5.5 kg).	Dry brush and scrub habitats where thickets provide food and cover. Territorial, occurs in monogamous pairsor singly.	Locally common in parts of Sudan, Ethiopia, Somalia, Uganda, and Kenya.	Primarily a browser of green leaves, buds, and shoots.	Lower Risk/ Least Concern
Silver dikdik *Madoqua piacentinii* French: Dik-Dik d'argent; German: Piacentini Dikdik; Spanish: Dikdik de argentado	Smallest dikdik, with short, blunt muzzle. Back and sides grizzled silver with sandy-tan legs, undersides and crest. Males with short, sharp horns up to 3 in. (7 cm), slanted backwards. Length 17–20 in (45–52 cm); height 12–14 in (30–35 cm); weight 6–9 lb (2.5–4 kg).	Low, dense coastal scrub thickets.	Confined to the coastal plain of Somalia.	Browses on leaves, buds, and shoots.	Vulnerable
Royal antelope *Neotragus pygmaeus* French: Antilope royale; German: Kleinstbockchen; Spanish: Antílope de real	Smallest of the horned bovids; rabbit sized. Crouched in appearance. Reddish to golden brown fur, darker on head and along back; white on underside of body and tail and on chest and chin. Small horns up to one inch (2 cm) present on males and slanted backwards. Length 18–22 in (45–55 cm); height 9–12 in (22–30 cm); weight 4–8 lb (2–3.5 kg).	Dense undergrowth, forest, and forest edges in moist and humid environments. Occur singly or in pairs on small territories. Shy and secretive, hides to avoid detection and escapes with short bursts when approached.	Occurs patchily in Guinea, Sierra Leone, Liberia, Ivory Coast, and Ghana.	Fresh leaves and buds, shoots, fungi, and fruit.	Lower Risk/Near Threatened
Suni *Neotragus moschatus* French: Antilope musquee; German: Moschusbockchen; Spanish: Suni	Crouched in appearance. Shiny fur is dark brown to rufous and speckled; white to gray undersides extending from tail to chin and including interior of limbs. Males possess thin, annulated horns up to 5 in (13 cm) and greatly enlarged facial glands. Length 22–25 in (55–63 cm); height 13–16 in (32–40 cm); weight 9–13 lb (4–6 kg).	Coastal forest and areas of heavy undergrowth. Occur as pairs or small polygynous groups on territories of 5–15 acres (2–6 ha). Males fiercely territorial, demarcate territories with scent, auditory and visual displays. Most active at night.	Occurs patchily east of the Rift Valley from Somalia to northeastern South Africa.	Browses on fresh leaves and shoots, flowers, roots, and fungi.	Lower Risk/ Conservation Dependent
Sharpe's grysbok *Raphicerus sharpei* English: Sharpe's grysbuck, Sharpe's steinbok, Tropiese grysbok; French: Grysbok du Sharpe; German: Sharpegreisbock; Spanish: Grysbok de Sharpe	Body is reddish brown to tan speckled with white; whitish to gray face, throat and undersides. Large, white-lined ears; "skirt" of white-tipped fur extending over the hindquarters. Males with short conical horns up to 4 in (10 cm), widely spaced and vertical. Length 24–31 in (60–80 cm); height 16–24 in (40–60 cm); weight 15–26 lb (7–12 kg).	Prefers areas of considerable cover such as secondary growth, brush, riverine habitats, and thickets. Occur as pairs or singly on small territories demarcated with dung middens. Most active at night.	From Lake Victoria south to the Transvaal west through the Zambezi valley, east to the coast of Mozambique.	Browses on leaves and shoots, flowers, fruits.	Lower Risk/ Conservation Dependent
Cape grysbok *Raphicerus melanotis* English: Grysbok, Cape grysbuck; French: Grysbok du cap; German: Kaapgreisbock; Spanish: Grysbok de capa	Body is reddish brown speckled with white; whitish to gray chin, throat, ears, and undersides. Short, compact muzzle. Males with short, smooth horns up to 5 in (13 cm), angled vertically. Length 26–32 in (65–80 cm); height 18–24 in (45–60 cm); weight 18–29 lb (8–13 kg).	Occurs in scrub and brush on sand dunes, at the base of hills and in riverine habitats. Occur singly or as loosely associated pairs. Males and females share territories or overlapping home ranges. Most active at night.	Restricted to the southern Cape of South Africa.	Primarily browses on shrubs, flowers and fruit. May go long periods without water.	Lower Risk/ Conservation Dependent
Beira *Dorcatragus megalotis* French: Beira, dorcatrague; German: Beira; Spanish: Beira	Slender, long-legged, and long-necked. Fur thick and gray on back developing into a darker band along sides from front elbow to back thigh. Throat, chin and underparts off white; limbs and head rufous. Ears large and lined with white fur. Sharp, broad-set horns up to 5 in (13 cm) on males. Length 2.6–2.8 ft (80–86 cm); height 1.6–2 ft (50–60 cm); weight 20–25 lb (9–11.5 kg).	Arid, rugged mountain habitats where rock and low brush provides forage and cover. Occur singly, in pairs, or in groups of up to 12 animals on large home ranges.	Restricted to mountainous regions of northern Somalia.	Leaves of small shrubs and bushes, also grasses.	Vulnerable

Resources

Books

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Justin S. Brashares, PhD

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Bovids V
Duikers
(Cephalophinae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subfamily Cephalophinae

Thumbnail description
Timid small, tropical antelopes; females often larger than the males; coat color is usually reddish brown, but can be gray, black, or striped; most species have a tuft of hair between a pair of horns; maxillary glands used for scent marking; considered browsers; agile jumpers and hiders; reflect the primitive, ancient lifestyle of bovids

Size
Body length 22–59 in (59–145 cm); shoulder height 12–34 in (30–85 cm); 9–176 lb (6–80 kg)

Number of genera, species
2 genera; 18 species

Habitat
Dense forest, lowland or high montane forest, savanna, and open bush; closely tied to dense cover for hiding

Conservation status
Endangered: 1 species; Vulnerable: 3 species; Lower Risk/Near Threatened: 9 species; Lower Risk/Conservation Dependent: 3 species; Lower Risk/Least Concern: 2 species

Distribution
Sub-Saharan Africa

Evolution and systematics

The Cephalophinae belong to the neotragine radiation of bovids. The ancestors of these browsing antelope first appeared during the Miocene, and later invaded Africa and Asia. Although their fossil record is sparse, Cephalophinae share many similarities with early bovids.

Modern Cephalophinae include 18 species represented by two genera, *Sylvicapra* and *Cephalophus*. Sixty-five subspecies have been identified. *Cephalophus* can be divided into four subgenera, which can be described as the conservative dwarfs, the diverse red duiker lineage, the fiber duiker lineage, and the giant duiker species. Several researchers have argued that the conservative dwarf subgenus is, in fact, a unique genus, *Philantomba*.

Physical characteristics

The Cephalophinae vary considerably in size. Their body shape is consistent across species, and designed for traveling through dense vegetation. They have arched bodies, short forelegs, long hind limbs, and strong hindquarters. Females are often as much as 4% longer and may be taller than males. Cephalophinae weigh 9–176 lb (6–80 kg) and reach shoulder heights of 12–34 in (30–85 cm). Their coats are coarse and generally reddish brown, with a white underbelly. However, their coloring can range from pale gray to dark brown or black, and several species have unique coat colors and patterns. Tails may be as short as 1.5 in (4 cm) or as long as 6 in (15 cm). A hair tuft between a pair of short, ridged horns is common. Duikers have large, gash-like scent glands beneath the eye.

Distribution

Cephalophinae have a widespread distribution across sub-Saharan Africa and on the islands adjacent to these coastal regions. The areas of greatest density are in equatorial Africa within the rainforest belt that stretches from Guinea to the Democratic Republic of the Congo.

Maxwell's duiker (*Cephalophus maxwelli*) watches for predators while browsing. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Habitat

Duikers prefer habitats of rainforest or dense bushland, although some species choose to live in swamps or mountainous regions. Urbanization has forced some populations to relocate or adapt to the local ecology. Others, more susceptible to habitat loss and ecological exploitation, have patchy distributions.

Behavior

Duikers earned their name for their tendency to flee in a series of diving jumps or to duck for cover beneath bushes and in fallen tree trunks when frightened. The name is derived from the Afrikaans word for diver. Most duiker species are nocturnal, foraging for food and surveying their territory from dusk to dawn. They remain sedentary during the daylight hours, often hidden inside hollow trees or behind fallen trunks.

In addition to being skittish, both male and female duikers are highly territorial animals. They are typically found alone, in pairs, or in pairs with one youngster, and they live in precisely defined habitats. Some species have fixed core territories with dynamic boundaries that overlap with other pairs, while others keep stricter borders. Duikers will patrol their territories alone or in pairs, and chase away any intruders. In zoos, male duikers are intolerant of other males and they fight violently if housed in the same pen. Females seem more tolerant of one another in captive settings.

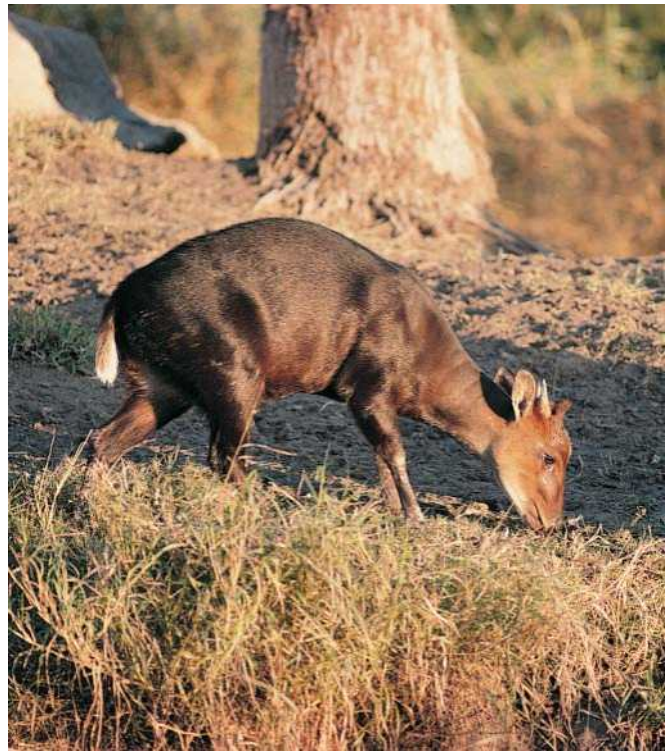
Duikers mark their territorial boundaries, their mates, and their calf with olfactory cues secreted from the maxillary glands, located below the eye. Pedal glands, located within the hooves, and feces also serve as territorial scent markers. Bucks mutually mark by pressing their glands against each other prior to fighting.

Feeding ecology and diet

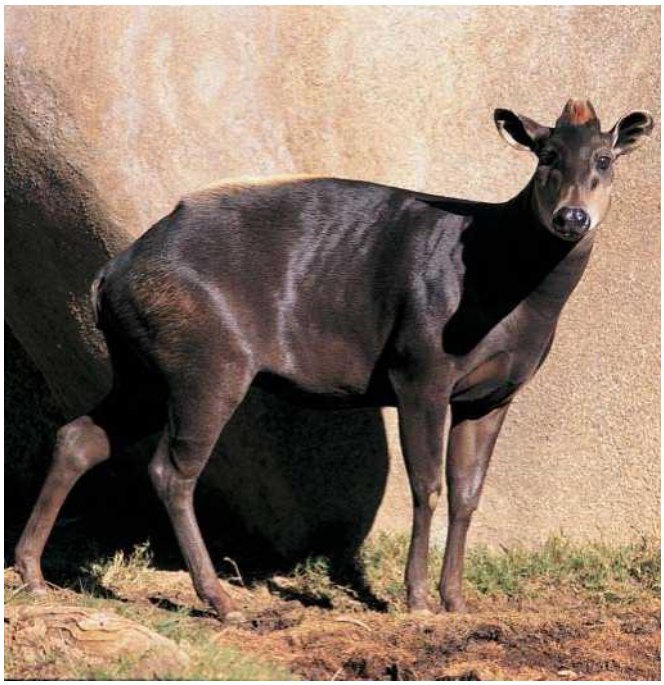
Cephalophinae have diverse diets and notable feeding habits, preferring the leaves, shoots, and tender branches of

A male blue duiker (*Cephalophus monticola*) drinks at a small stream. (Photo by Leonard Lee Rue III. Bruce Coleman, Inc. Reproduced by permission.)

The bush duiker (*Sylvicapra grimmia*) is also known as Grimm's duiker. (Photo by Kenneth W. Fink/Photo Researchers, Inc. Reproduced by permission.)

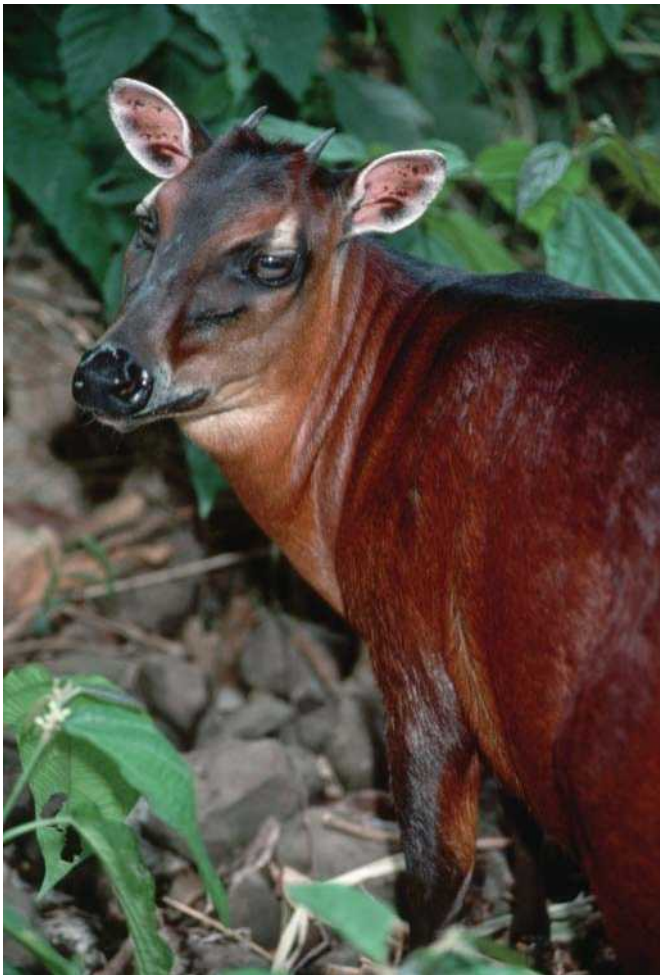


A black duiker (*Cephalophus niger*) grazing in the late afternoon. (Photo by Kenneth W. Fink. Bruce Coleman, Inc. Reproduced by permission.)



A yellow-backed duiker (*Cephalophus silvicultor*) in central Africa. (Photo by Kenneth Fink. Bruce Coleman, Inc. Reproduced by permission.)

The zebra duiker (*Cephalophus zebra*) is found in forested areas of the midwestern part of Africa (Photo by Kenneth W. Fink. Reproduced by permission.)



The bay duiker (*Cephalophus dorsalis*) eats primarily fruits and seeds. (Photo by © Kevin Schafer/Corbis. Reproduced by permission.)

Bush duikers (*Sylvicapra grimmia*) are one of the most adaptable antelope. (Photo by T. Wolf. Bruce Coleman, Inc. Reproduced by permission.)

trees and bushes, fruits, and seeds. As much as 90% of the animal's diet may be derived from fruits and leaves, with some seasonal variation. They can often be found grazing beneath trees on the fruits and seeds dropped by monkeys. Occasionally, they will eat insects, eggs, birds, and small mammals. Cephalophinae are known to raid plantations adjacent to forests for palm nuts, mangoes, and cocoa pods.

Cephlophinae conduct most foraging between dusk and dawn. The rainy season deposits enough moisture on the leaves of bushes and trees for the animals to meet their fluid needs.

Reproductive biology

All members of the Cephalophinae subfamily are monogamous, generally producing one litter per year. Females are sexually mature at approximately nine months of age, males between 12 and 18 months. Cephalophinae are non-seasonal breeders, but in some species such as the bush duiker (*Sylvicapra grimmia*), calf births may peak during the summer months. Gestation among the Cephalophinae can be as short

Jentink's duiker (*Cephalophus jentinki*) showing the characteristic white stripe encircling the upper back. (Photo by Anthony Mercieca/Photo Researchers, Inc. Reproduced by permission.)

A red-flanked duiker (*Cephalophus rufilatus*) among foliage. (Photo by Animals Animals ©David Welling. Reproduced by permission.)

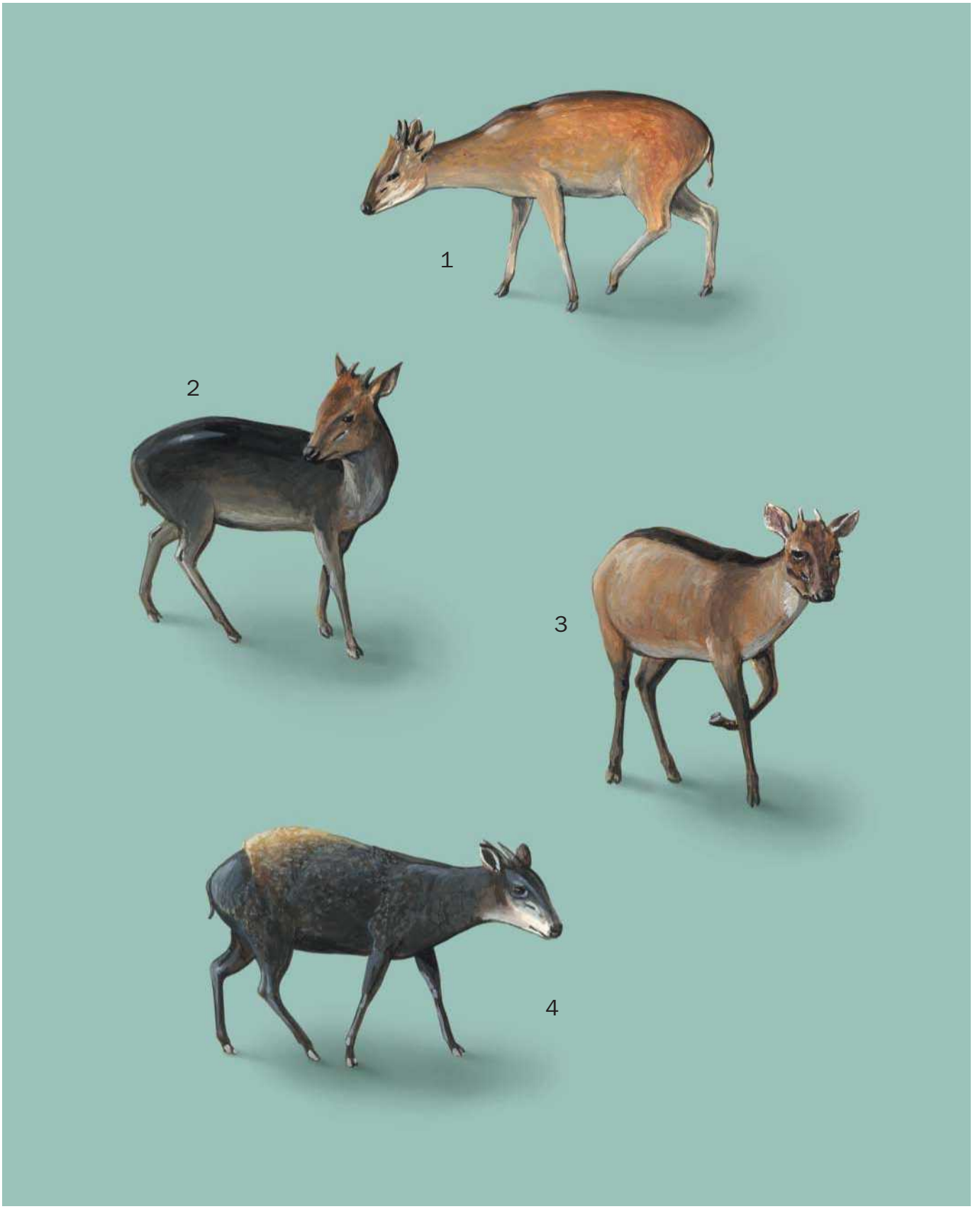
as four months or as long as nine months. Single births are the norm, but it is not unheard of for bush duikers to bear twins. Male duikers do not participate in rearing apart from delivering warnings about nearby predators and defending the trio's territory. Most calves are weaned from their mothers between five and nine months of age.

Conservation status

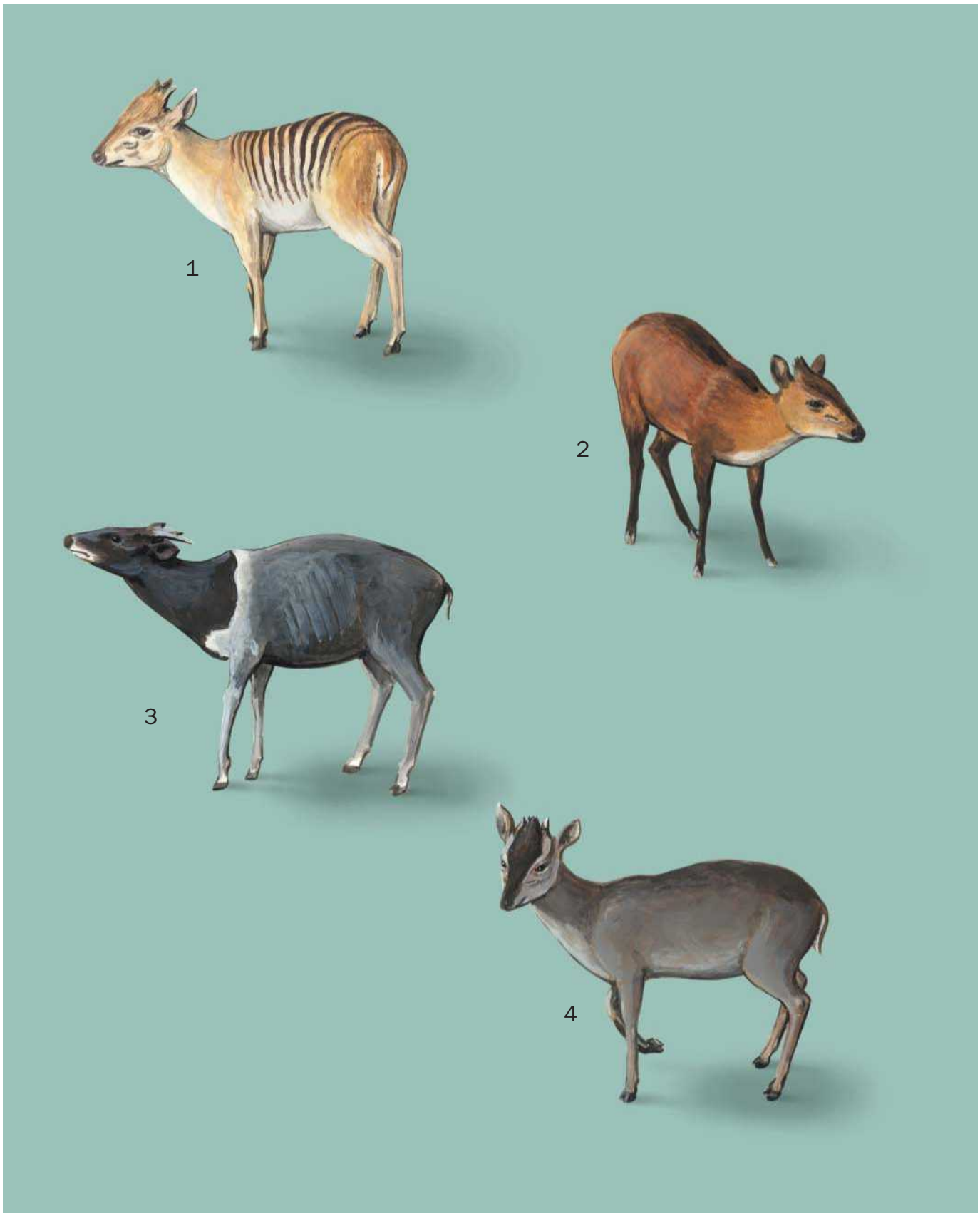
Due to their timid nature, it is difficult to estimate the population sizes of many species of Cephalophinae. Species with wide habitat ranges and those that are highly adaptable to changing ecological conditions are not threatened. However, 16 of 18 species have been placed on the IUCN Red List of Threatened Species. Most of those listed are Lower Risk, but *C. adersi* is Endangered and *C. jentinki*, *C. spadix*, and *C. zebra* are Vulnerable. Loss of habitat and bushmeat hunting continue to be the greatest threats to Cephalophinae.

Significance to humans

The Cephalophinae represent an essential source of protein and income throughout the forest regions of Central and West Africa. There is ample evidence that the current levels of hunting are unsustainable. In addition, the dwarf duikers are prized by trophy hunters, who seek to add full body mounts of the smaller animals to their collections.



1. Ogilby's duiker (*Cephalophus ogilbyi*); 2. Black duiker (*Cephalophus niger*); 3. Bay duiker (*Cephalophus dorsalis*); 4. Yellow-backed duiker (*Cephalophus silvicultor*). (Illustration by Brian Cressman)



1. Zebra duiker (*Cephalophus zebra*); 2. Red-flanked duiker (*Cephalophus rufilatus*); 3. Jentink's duiker (*Cephalophus jentinki*); 4. Maxwell's duiker (*Cephalophus maxwelli*). (Illustration by Brian Cressman)

Species accounts

Maxwell's duiker
Cephalophus maxwelli

TAXONOMY
Cephalophus monitcola maxwelli (Smith, 1827), Sierra Leone.

OTHER COMMON NAMES
French: Céphalophe de Maxwell.

PHYSICAL CHARACTERISTICS
Once thought to be a subspecies of the blue duiker. Length 25–30 in (63–76 cm); height 14–16.5 in (35–42 cm); weight 11–22 lb (5–10 kg). Slate gray or gray-brown coat, with a pale belly, throat, and chin. Coloring is dark brown or charcoal-colored nose bridge and forehead, with striking white lines running from the eyes to the nose. Thin, fringed tail is 5–6 in (12–15 cm) long. Horns on both males and females are spike-like with ridges at the base. Only 2 in (5 cm) long, the horns are often hidden by the dark brown tuft of hair that grows between the horns.

DISTRIBUTION
Limited to western Africa, west of the Niger River.

HABITAT
Secondary forests and moist savanna.

BEHAVIOR
Live in pairs in well-defined territories. Both sexes mark the boundaries of their ranges with secretions from the maxillary glands. Bonded pairs often mark one another by rubbing their heads together.

FEEDING ECOLOGY AND DIET
Selective browser that consumes a varied diet of fruits, shrubs, and herbs. May also consume some small animals and insects.

REPRODUCTIVE BIOLOGY
Bonded pairs mate one time per year. Gestation is approximately 120 days, and one calf is born from each mating. The number of births in a population peaks between January and March, with a second peak occurring between August and September. Young are weaned by one year.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Humans hunt it for the bushmeat trade, and have contributed to its population decline. ◆

Black duiker
Cephalophus niger

TAXONOMY
Cephalophinus niger Gray, 1846, Ghana.

OTHER COMMON NAMES
French: Céphalophus noir; German: Schwarzducker.

PHYSICAL CHARACTERISTICS
Heavily built antelope: length 31–42 in (80–90 cm); height 18–20 in (45–55 cm); weight 33–66 lb (15–20 kg). Glossy dark brown to black coat that pales to gray around the neck and chin. Undersides are lighter in color, often with an orange patch between the forelegs. Nose bridge and forelock reddish brown. Head is slightly elongated with straight pointed horns, 3–7 in (8.5–21 cm) in males and 1–1.2 in (2.5–3 cm) in females. Tail approximately 5 in (12.5 cm).

DISTRIBUTION
Found throughout lower West Africa, in Benin, Ivory Coast, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, and Togo. Populations once found in the Kalakpa and Shai Hill reserves in central and southeastern Ghana have disappeared.

HABITAT
Found on the edges of forests, secondary forests, and in bushes and thickets of lowland tropical rainforest. May also frequent riverine galleries, isolated forest patches, and semi-deciduous forests.

BEHAVIOR
Seldom observed in the wild, its behavior has not been well studied. There are conflicting reports about whether it is a nocturnal or diurnal species. A solitary animal.

FEEDING ECOLOGY AND DIET
Its saw-like teeth permit it to browse many different types of vegetation. In addition to feeding on fallen fruits and on the flowers, leaves, herbs of forest trees and shrubs, it will use its teeth to strip the bark from trees. Will sometimes eat insects and small birds.

REPRODUCTIVE BIOLOGY
Monogamous. Captive individuals indicate that the gestation period is 126 days, with an average of 7.5 months between births. Females give birth to a single offspring, which is weaned at six months.

CONSERVATION STATUS
Listed as a Lower Risk/Near Threatened species. In 1999, approximately 100,000 black duikers remained in Africa, and the population continued to decline.

SIGNIFICANCE TO HUMANS
Hunted for the bushmeat trade. ◆

Zebra duiker
Cephalophus zebra

TAXONOMY
Cephalophus zebra Gray, 1838, Sierra Leone.

OTHER COMMON NAMES
English: Banded duiker, zebra antelope; French: Céphalophe zèbre; German: Zebraducker.

PHYSICAL CHARACTERISTICS
Muscular duiker with unique coloration. Length 27.5–36 in (85–90 cm), height 16–20 in (40–50 cm), weight 33–44 lb (15–20 kg). Easily distinguished from other duikers by its vertical black banding. Between these stripes, the pelage is a light gold, off white, or auburn. The bands do not cross the pale yellow to white belly and undersides. Head, shoulders, and lower legs are a rich tan color. Long tail is approximately 6 in (15 cm). Horns are conical and pointed, and the head lacks the characteristic hair tuft.

DISTRIBUTION
Distribution restricted to small region in West Africa, between the Moa River of Sierra Leone to the west, and the Niouniourou River of Ivory Coast to the east, and concentrated in Liberia.

HABITAT
Primarily resides in lowland canopy forests, but will venture to the forest edges and into clearings, or live in montane and upland forests.

BEHAVIOR
Both sexes will defend their territory and their offspring from competitors or other dangers. Captive zebra duiker show diurnal behavior.

FEEDING ECOLOGY AND DIET
Feeds on fruit and nuts, and may crack large, thick-shelled nuts with its forehead. Known to eat mice.

REPRODUCTIVE BIOLOGY
Monogamous. Gestation is about 225 days, after which a single calf is born. Newborns have a bluish tint to their coat and do not develop adult-like coat coloring and stripes before seven months of age. Weaning occurs close to three months after birth.

CONSERVATION STATUS
Considered to be a Vulnerable species. Only 28,000 remain and are restricted to a small geographical area of 12,000 mi^2 (31,000 km^2).

SIGNIFICANCE TO HUMANS
Threatened by bushmeat hunters. ◆

Ogilby's duiker
Cephalophus ogilbyi

TAXONOMY
Cephalophus ogilbyi (Waterhouse, 1838), Bioko, Equatorial Guinea. Three subspecies recognized.

OTHER COMMON NAMES
French: Céphalophe d'Ogilby, céphalophe de Fernando Poo; German: Ogilbyducker, Fernando-Poo-Ducker; Spanish: Duiquero de Ogilby.

PHYSICAL CHARACTERISTICS
Large crouched, slab-shaped body: length 34–46 in (85–115 cm); height 22 in (55 cm); weight 31–40 lb (14–18 kg). Coat color is golden brown to mahogany, darker on the hindquarters, and stippled with gray hairs along the back. Chest and undersides are pale brown or gray. Black stripe traces the length of the spine. Leg color can vary between regions and subspecies. Black muzzle has chestnut-colored arches over the eyes, and short curved horns.

DISTRIBUTION
Common on Bioko Island, particularly along the mountain slopes, but patchy elsewhere. Found in Cameroon, Congo, Ivory Coast, Equatorial Guinea, Gabon, Ghana, Guinea, Liberia, Nigeria, and Sierra Leone.

HABITAT
Closed canopy rainforest, and lowland forest and montane forest to altitudes of 2,400–3,600 ft (800–1,200 m) on Bioko Island, Equatorial Guinea.

BEHAVIOR
Found alone or in pairs, it is presumed to be active during daylight hours.

FEEDING ECOLOGY AND DIET
The vast majority of its diet is made up of fruits, including those dropped by monkeys. Other vegetation and flowers make up the remainder of its diet.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Classified as a Lower Risk/Near Threatened species. Total population estimate is 35,000.

SIGNIFICANCE TO HUMANS
It is a pest to crop growers and a target of bushmeat hunters. ◆

Jentink's duiker
Cephalophus jentinki

TAXONOMY
Cephalophus jentinki Thomas, 1892, Liberia.

OTHER COMMON NAMES
French: Céphalope de Jentink; German: Jentinkducker; Spanish: Duiquero de Jentink.

PHYSICAL CHARACTERISTICS
One of the largest of the *Cephalophus*: length 54 in (135 cm); height 30–33.5 in (75–80 cm); weight up to 154 lb (70 kg). Gray to gray-brown coloring with glossy black head and neck; shoulders are draped with a swath of white or gray hair that descends to the chest. Similar markings encircle the nose and lips. Large ridged horns angle backward from the ears.

DISTRIBUTION
Found in western Guinea, but restricted to scattered populations.

HABITAT
Fragmented habitats, consisting of fruiting trees and thick canopies. A group is said to be living in the forests outside of Freetown, Sierra Leone.

BEHAVIOR
Limited interaction with Jentink's duiker suggests that they are nocturnal animals. Hide in hollow trees by day. Solitary, but often found in pairs.

FEEDING ECOLOGY AND DIET
Relies primarily on the tree seedlings and fruits, including kola nuts, cherry mahogany, and sand apples. Will forage in secondary growth forests, scrub, farmlands, and plantations when fruits are scarce.

REPRODUCTIVE BIOLOGY
Reproductive behavior is relatively unstudied. Gestation estimated at 7–8 months. Calves are born with dark brown coats that adopt the adult coloration by one year of age.

CONSERVATION STATUS
Classified as Vulnerable. An estimated 3,500 individuals remain.

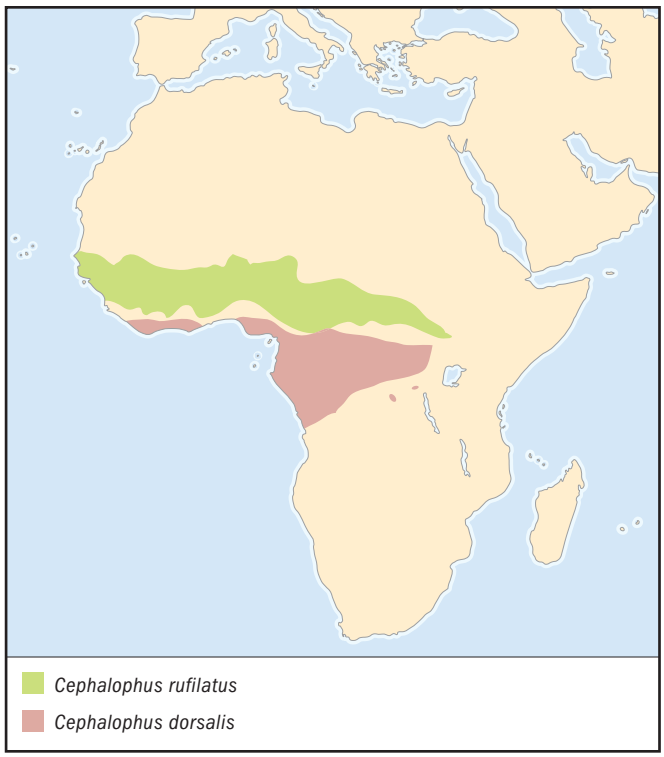
SIGNIFICANCE TO HUMANS
A pest to farmers and plantation owners, it is also a target for hunters in the bushmeat trade. ◆

Red-flanked duiker
Cephalophus rufilatus

TAXONOMY
Cephalophus rufilatus Gray, 1846, Waterloo Village, Sierra Leone. Two subspecies.

OTHER COMMON NAMES
French: Céphalophe à flancs roux; German: Rotflankenducker, Blaurückenducker; Spanish: Duiker de flancos rojos.

PHYSICAL CHARACTERISTICS
Medium-sized antelope: length 24–28 in (60–70 cm); height 12–16 in (30–40 cm); weight 20–26 lb (9–12 kg). Dark gold to reddish brown coat with dark brown to black legs; bluish black band along the spine; dark nose and face, with blue-black



stripe running from the forehead to the muzzle, and a white upper lip and lower jaw. Maxillary glands.

DISTRIBUTION
Found in the eastern coastal forests of KwaZulu-Natal, Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Ivory Coast, Gambia, Ghana, Guinea-Bissau, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan, and Togo.

HABITAT
Lives in gallery forests in West and Central Africa, in coastal forests of highly confined regions of southern Africa, along forest edges, and in woodlands.

BEHAVIOR
Territorial animal that marks boundaries, young, and mate with scent cues. Emits shrill bark when alarmed.

FEEDING ECOLOGY AND DIET
Leaves make up approximately 60% of the diet, which is supplemented by twigs, flowers, and fruits. Consumes grasses and fungi in small quantities.

REPRODUCTIVE BIOLOGY
The average gestation time is 240 days. Assumed monogamous.

CONSERVATION STATUS
Classified as a Lower Risk/Conservation Dependent species; less threatened by habitat loss than any other species. An estimated 170,000 remain.

SIGNIFICANCE TO HUMANS
Purchased from bush meat markets in the Ivory Coast for dietary protein. ◆

Bay duiker
Cephalophus dorsalis

TAXONOMY
Cephalophus dorsalis Gray, 1846, Sierra Leone. Two subspecies.

OTHER COMMON NAMES
English: Black-striped duiker; French: Céphalophe à bande dorsale noire, céphalophe bai; German: Schwarzrückenducker.

PHYSICAL CHARACTERISTICS
Medium to large duiker: length 28–40 in (70–100 cm); height 16–22 in (40–55 cm); weight 33–44 lb (15–20 kg). Has reddish brown coat, with blue or brown-gray legs and black dorsal stripe; white underside; white lips and lower chin. Smooth, short horns. Large maxillary glands.

DISTRIBUTION
Guinea-Bissau to the Democratic Republic of the Congo, and as far south as Angola.

HABITAT
Dense lowland forests of West and Central Africa.

BEHAVIOR
Found alone or paired with mate or calf. Forage for food only between dusk and dawn.

FEEDING ECOLOGY AND DIET
Consumes mainly fruits, leaves, grasses, young branches and saplings, buds, and some insects and eggs. Occasionally will chase and kill small rodents, or other small animals.

REPRODUCTIVE BIOLOGY
Monogamous. Females reach sexual maturity between nine and 12 months of age, approximately 3–6 months earlier than the male. Calves are weaned early, by five months.

CONSERVATION STATUS
Labeled as a Lower Risk/Near Threatened species.

SIGNIFICANCE TO HUMANS
Hunted for bushmeat. ◆

Yellow-backed duiker
Cephalophus silvicultor

TAXONOMY
Cephalophus silvicultor (Afzelius, 1815), Sierra Leone and the Pongas and Quia Rivers of Guinea. Two subspecies.

OTHER COMMON NAMES
French: Céphalophe à dos jaune; German: Gelbrückenducker, Riesenducker.

PHYSICAL CHARACTERISTICS
Largest of the duikers: length 46–58 in (115–145 cm); height 25–34 in (65–85 cm); weight 99–176 lb (45–80 kg). Dark brown to black coat with white or orange short tufts of hair along the back; gray muzzle and white lips, and maxillary glands. Ridged, wedge-shaped horns grow on both males and females.

DISTRIBUTION
Senegal to southwestern Sudan, western Uganda and Rwanda, south to Angola and Zambia, and western Kenya.

HABITAT
Forests with heavy undergrowth.

BEHAVIOR
Territorial and aggressive; both females and males defend the defined region, which is heavily marked with scent cues. When scared, it will emit shrill bleats and grunts, and erect its stiff orange back hairs. Nocturnal.

FEEDING ECOLOGY AND DIET
Prefers local vegetation from the forest undergrowth, and also eats fruit, seeds, fungi, and grasses.

REPRODUCTIVE BIOLOGY
Like many duikers, females reach sexual maturity 3–6 months before the male. Monogamous. Calves are weaned by five months of age.

CONSERVATION STATUS
Listed as a Lower Risk/Near Threatened species.

SIGNIFICANCE TO HUMANS
Bushmeat hunting continues to threaten the population. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Aders's duiker *Cephalophus adersi* French: Céphalophe de Aders; German: Adersducker	Overall coloration is tawny red, grayer in neck area. Wide, white band on rump runs cranially, underparts are lighter. Head has reddish crest with simple, spiked horns. Muzzle is pointed, nose has flat front. Marked cowlick on nape of neck. Head and body length 26–28 in (66–72 cm), shoulder height 11.8 in (30 cm).	Coastal forests, lowlands, and thickets. Live in pairs, defends territory, generally completely diurnal.	Zanzibar, Tanzania, and Sokoke Forest, Kenya.	Fallen flowers, fruits, and leaves.	Endangered
Peters's duiker *Cephalophus callipygus* French: Céphalophe de Peters; German: Petersducker	Reddish brown pelage with thick, stocky body and long, slender legs. Head and body length 35–45 in (90–115 cm), tail length 4.7–6.3 in (12–16 cm), shoulder height 19–24 in (50–60 cm).	All forest biotopes in lowlands and mountains up to 9,840 ft (3,000 m). Very little information on behavioral and reproductive patterns.	West of Congo and Ubangi Rivers in Congo; southern Central African Republic; and Gabon and southern Cameroon.	Mainly grasses.	Lower Risk/Near Threatened
White-bellied duiker *Cephalophus leucogaster* French: Céphalophe du Gabon	Coloration of pelage is reddish brown. Stocky body with longer, slender legs. Head and body length 23–39 in (90–100 cm), tail length 4.7–6 in (12–15 cm), shoulder height 16–18 in (40–45 cm).	Primary and secondary forests. Highly intolerant of same sex, fights are frequent.	Cameroon, Gabon, Congo, and southwestern and eastern Democratic Republic of the Congo (Zaire).	Grass and leaves.	Lower Risk/Near Threatened
Blue duiker *Cephalophus monticola* German: Blauducker	Fur is short, red in kids, bluish gray in adults. Underside is white. Triangular horns on both sexes with ridges towards the bases. Head and body length 21–35 in (55–90 cm), weight 8.8–22.0 lb (4–10 kg).	Hedgerow timber, bush, and gallery forests, both large and small forests. Sedentary, solitary, and territorial.	Eastern Nigeria to Kenya and Tanzania, south to Angola, Zambia, Malawi, eastern Zimbabwe and Mozambique; Natal and eastern Cape Province, South Africa; Zanzibar; Bioko; and Pemba Island.	Buds, young shoots, leaves, herbs, berries, grasses, fruits, termites, ants, snails, eggs, and probably birds.	Not threatened
Natal duiker *Cephalophus natalensis* French: Céphalophe rouge	Reddish brown pelage, stocky body with slender legs. Head and body length 31–39 in (80–100 cm), tail length 4–6 in (10–15 cm), shoulder height 14–18 in (35–45 cm).	Thick bush and dense woodlands on the plains and in the mountains. Sedentary, solitary, and territorial.	Southern Tanzania, southern Malawi, Mozambique, and Natal, South Africa.	Fruits, insects, and carrion.	Lower Risk/ Conservation Dependent
Black-fronted duiker *Cephalophus nigrifrons* French: Céphalophe a front noir; German: Schwarzstirnducker	Reddish brown in coloration, black tint on forelegs and tail. Black stripe runs from nose to two, short, pointed horns. Inner ear is exposed and white. Tail is short and tipped in black. Head and body length 35–43 in (90–110 cm), tail length 4–6 in (10–15 cm), shoulder height 18–22 in (45–55 cm).	Forest, swamp forest and marshes at both low and high altitude; sometimes found in gallery forest. Sedentary, solitary, and territorial.	Cameroon to Democratic Republic of the Congo, Rwanda and western Uganda, south to northern Angola; Mt. Elgon (Uganda/Kenya); Aberdare Range and Mt. Kenya, Kenya.	Leaves, shoots, seeds, fruit, buds, and bark.	Lower Risk/Near Threatened
Abbott's duiker *Cephalophus spadix* French: Céphalophe d'Abbott; German: Abbottducker	Stocky body with short, sturdy legs and a thick neck. Pelage is dark chestnut brown to black over most of body. Underparts are lighter brown with a reddish hue. Wedge-shaped face with pale gray forehead. Both sexes have horns.	Montane forests and high altitude marshes. Little known of reproductive and behavioral patterns. Very shy, will become violent if cornered.	Highlands of northeastern and central Tanzania.	Flowers, green shoots, and herbs.	Vulnerable

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Weyns's duiker *Cephalophus weynsi* French: Céphalophe de Weyns	Coloration of upperparts varies from almost buffy to brown to black. May have stripe along middle of back. Smooth, short neck hair.	Open country with scattered trees and brush. Sedentary, solitary, and territorial.	Democratic Republic of the Congo, Uganda, Rwanda, and western Kenya.	Mainly grasses.	Lower Risk/Near Threatened
Harvey's duiker *Cephalophus harveyi*	Long, coarse upper neck fur. Coloration of upperparts varies from almost buffy to brown to black. May have stripe along middle of back.	Open country with scattered trees and brush. Sedentary, solitary, and territorial.	Southern Somalia, eastern Kenya, eastern and southern Tanzania, northern Malawi, eastern Zambia, and sight records from eastern Ethiopia.	Mainly grasses.	Lower Risk/ Conservation Dependent

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Organizations

IUCN—The World Conservation Union. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41 (22) 999 0000. Fax: +41 (22) 999 0002. E-mail: mail@hq.iucn.org Web site: <http://www.iucn.org>

Other

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Hannah Hoag, MS

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Bovids VI
Sheep, goats, and relatives
(Caprinae)

Class Mammalia
Order Artiodactyla
Suborder Ruminantia
Family Bovidae
Subfamily Caprinae

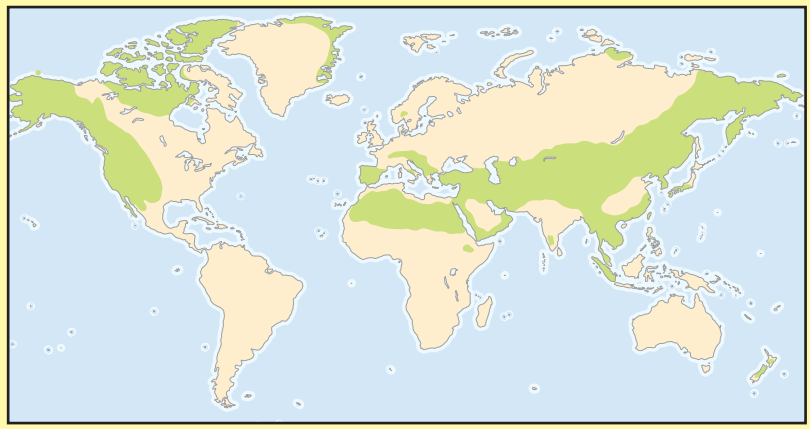
Thumbnail description
Medium- to large-bodied herbivorous, usually mountain-adapted mammals with either short sharp horns or large and ornate horns

Size
35–94 in (90–240 cm); 44–836 lb (20–380 kg)

Number of genera, species
11 genera; 31 species

Habitat
Mountains, deserts, forest, and tundra

Conservation status
Critically Endangered: 1 species; Endangered: 7 species; Vulnerable: 11 species



Distribution
North America, North Africa, and Eurasia; introduced to New Zealand; domesticated varieties on all continents except Antarctica

Evolution and systematics

The taxonomy of the Caprinae is complex and several arrangements have been proposed. Three tribes are generally recognized: Rupicaprini, Ovibovini, and Caprini. Molecular analysis in 1997 suggested that Tibetan antelope or chiru (*Pantholops hodgsonii*), previously classified in a tribe of its own or with saiga (*Saiga tatarica*), was closer to the Caprinae than the Antilopinae and may be a basal member of the Caprinae. As of 2003 its phylogenetic relationship to the rest of the Caprinae had not been definitively assigned. There is more disagreement among taxonomists at species and subspecies levels. IUCN's Caprinae Specialist Group (CSG) adopted a working classification for the Caprinae Action Plan in 1997 that contained 31 species and 81 subspecies. CSG subsequently established a Taxonomy Working Group to examine outstanding problems.

The tribe Ovibovini contains two genera, each with a single species: musk ox (*Ovibos moschatus*) and takin (*Budorcas taxicolor*). Musk ox has two listed subspecies and takin has four. The Rupicaprini has four genera and nine species: serows (*Capricornis*), three species; gorals (*Naemorhedus*), three species; mountain goat (*Oreamnos*), one species; and chamois (*Rupicapra*), two species. Serow (*Capricornis sumatraensis*) has five subspecies. Some authors include Formosan serow (*C. swinhoei*) with the Japanese species (*C. crispus*). Himalayan goral (*Naemorhedus goral*) has two subspecies; *N. baileyi* has two, and *N. caudatus* has four. No subspecies have been identified in *Oreamnos*. Seven subspecies are listed for northern chamois (*R. rupicapra*), but by the end of 2002 the validity of all of these had not been confirmed. Southern chamois (*R. pyrenaica*) has three listed subspecies. The Caprini has five genera and 20 species: Barbary sheep (*Ammotragus*), one species; tahrs (*Hemitragus*), three species; blue sheep (*Pseudois*), two species; true goats (*Capra*), seven species; and wild sheep (*Ovis*), five species. *Ammotragus* has six subspecies, but again the validity of all of these is unconfirmed. No subspecies are recognized in the tahrs. Two subspecies of blue sheep (*Pseudois nayaur*) are listed. The specific status of dwarf blue sheep (*P. schaeferi*) has been questioned on the ground that it may be only an ecotype. The taxonomy of *Capra* is complex. Earlier arrangements placed Alpine ibex, Siberian ibex, Nubian ibex, Walia ibex, and west Caucasian tur (*C. caucasica*) together in a single species, *C. ibex*, but they are separated here. Markhor (*C. falconeri*) has three subspecies and wild goat (*C. aegagrus*) has four. Spanish ibex (*C. pyrenaica*) has four known subspecies, two of which are already extinct.

The genus *Ovis* is even more complex, with a variety of arrangements proposed. All recent authors have recognized the distinctiveness of the larger argalis (*O. ammon*) from the smaller mouflon and urials. The mouflon and urial group is classified as either one species (*O. orientalis*) or as two (*O. orientalis* for the mouflons and western forms, and *O. vignei* for the eastern urials). Twelve subspecies were recognized in the IUCN's Caprinae Action Plan. It has proved difficult to establish a generally agreed classification of the argalis at the subspecies level, with a large number of forms having been named. Eight are listed in the Caprinae Action Plan. Seven subspecies (one now extinct) are listed for the bighorn sheep (*O. canadensis*) and four for the snow sheep (*Ovis nivicola*). Thinhorn sheep (*O. dalli*) has two subspecies. Techniques of molecular genetic analysis are expected to help validate these forms and further clarify relationships within the subfamily.

Bighorn sheep (*Ovis canadensis*) fighting. (Photo by Bob & Clara Calhoun. Bruce Coleman, Inc. Reproduced by permission.)

The fossil record is incomplete. Musk ox and takin are descendants of a formerly widespread group in Eurasia and both evolved in the late Pliocene or early Pleistocene. Rupicaprini apparently evolved in Asia, with the Pliocene Pachygazella as a possible ancestor, though the earliest fossils of chamois are known only from the late Pleistocene. An ancestral rupicaprine must have crossed the Bering land bridge into North America and given rise to *Oreamnos*, which first appeared there during the Wisconsin glaciation. There is general agreement that the Caprini evolved from the Rupicaprini.

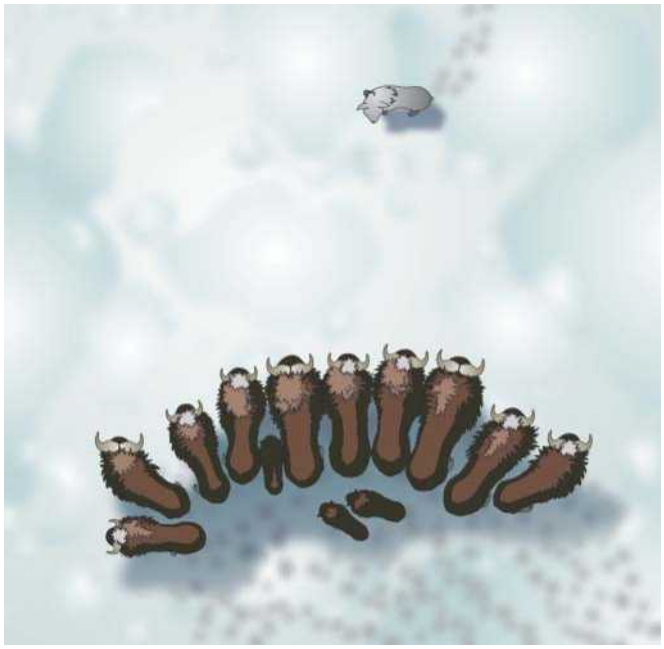
The genus *Tossunnoria* from the early Pliocene of China shows characters intermediate between gorals and Caprini and is regarded as the probable ancestor of modern *Ovis* and *Capra*. Nadler and colleagues confirmed in 1973 Geist's 1971 hypothesis that the Caprini evolved via two main lineages: one through a Barbary sheep-like form to true sheep and another goat-like line.

Members of the genus *Capra* first appeared in the mid-Pleistocene, probably from a tahr-like ancestor. From the fossil evidence, its distribution once reached the Atlantic coast of Europe. There are few fossils of *Ovis*. The earliest ones known were found in China and Europe and date from the Pliocene. The genus evolved in the mountains of Eurasia from where they radiated northwards and northeast, crossing the Bering land bridge into North America. Earliest evidence of *Ovis* in North America dates from about 100,000 years ago. Most modern Caprini evolved during the Pleistocene, a time when there were 18 major glaciations and Geist suggested in 1989 that Caprini differ from Rupicaprini as a result of adaptation to colder climates and to open rather than closed habitats.

Physical characteristics

The Caprinae are medium- to large-sized herbivores. Sizes range from around 44 lb (20 kg) in goral to 836 lb (380 kg) in adult musk ox. Captive musk ox have attained weights of 1,430 lb (650 kg). In gorals and serows, males and females are around the same size. In other Caprinae species, males average larger than females, this difference being most marked in the Caprini. The general body plan shows a strong, stocky build with powerful limbs that facilitate rapid movement through precipitous terrain. Argali and urial sheep (*Ovis ammon* and *O. orientalis*) are exceptions, and have a lighter, more agile build reflecting their reliance on speed to escape from predators. All Caprinae bear horns and in many species, growth rings are present that can be used to age the animal.

Male ibex (*Capra ibex*) test each other's strength using their massive horns. (Photo by Aaron Ferster/Photo Researchers, Inc. Reproduced by permission.)



Musk ox form a defensive ring when threatened. Here, a wolf threatens their young. (Illustration by Emily Damstra)

Rupicaprini have short, sharp horns that rise straight from the top of the head. These curve slightly backwards in gorals and serows, and are sharply hooked in chamois. Ovibovini have thicker, more massive horns. In the musk ox, they curve downwards and out and in takin curl outwards then back. Caprini have the largest and most developed horn shapes. In *Ovis*, *Pseudois*, and *Capra*, they show a high degree of sexual dimorphism with horns of the females much shorter and slimmer than those of the males. Horns are long and swept back in ibexes, twisted in markhor and curling in *Ovis*, reaching their most massive in the argalis (*O. ammon*). The maximum length recorded for the Altai argali is 66 in (169 cm). Hooves are well adapted to grip securely on rock.

Coat color is inconspicuous and many species blend easily into their background. Coloration ranges from white to black through shades of straw-yellow, sandy and brown to deep reddish brown. Male Barbary sheep have long chest ruffs, Himalayan tahrs have a thick ruff on the foreparts; argalis and urial have shorter throat ruffs. Wild goat species have beards of varying length. Tails are relatively short. Light rump patches are well developed in *Ovis*, but absent in rupicaprids, excepting the highly gregarious chamois (*Rupicapra*).

A Japanese serow (*Capricornis crispus*) with young in the snow. (Photo by PPS/Photo Researchers, Inc. Reproduced by permission.)

Distribution

The subfamily is mainly distributed in the Northern Hemisphere; in North America from the Arctic south to northern Mexico; across the whole of northern Africa and the highlands of Ethiopia; in all the mountains of Europe and Asia, extending to southern India and Sumatra. Musk ox is now restricted to North America and Greenland, but formerly occurred in northern Siberia and may have survived there until early recent times. In historic times, it also occurred much more widely in North America and in Western Europe. The takin is found in the mountains of western China and the eastern Himalaya, west to Bhutan. Rupicaprini have a disjunct distribution, with chamois distributed throughout the mountains of central and southern Europe, Turkey and the Caucasus, and gorals and serows are restricted to Asia. Their combined distribution extends from Pakistan to the Russian Far East and the Korean Peninsula. Japanese serow (*Capricornis crispus*) and Formosan serow (*C. swinhoei*) are endemic to Japan and Taiwan, respectively. *Oreamnos* is found in southeast Alaska and mountains of northwestern Canada and the northwest United States. Serow has an extensive range from the western Himalaya to Gansu and Sichuan provinces in China and through Southeast Asia to Sumatra. Barbary sheep are endemic to northern Africa and once occurred on all ranges and rocky massifs in the Sahara and subdesert zones. Himalayan tahr are distributed in a narrow band along the southern side of the Himalaya from the Indian state of Jammu and Kashmir to central Nepal. Arabian tahr are endemic to the mountains of southeast Arabia and Nilgiri tahr are restricted to a small range in the southern part of the Western Ghats in India. The distribution of *Pseudois* is centered on the Tibetan Plateau and bordering ranges. Its range extends in the west to the Karakoram Mountains of northern Pakistan and penetrates to the southern side of the Himalaya in a few places. Dwarf blue sheep have a very limited distribution in river gorges of southwest China. The genus *Capra* is distributed through the mountains of Europe and Asia, from the Alps to Lake Baikal, and in northeast Africa. Wild goat, the progenitor of domestic goats, is found in Crete and a few other Aegean islands, and through the Caucasus, Turkey, and Iran to Afghanistan and Pakistan. Markhor has a relatively limited distribution in Pakistan, Afghanistan, and Tajikistan. Spanish ibex occurs on several ranges in the Iberian Peninsula. West Caucasian tur and east Caucasian tur occupy the west and east of the Caucasus, respectively, with a narrow hybrid zone in the center of the range. Alpine ibex occur throughout the European Alps. Siberian ibex have an extensive distribution through the mountains of Central Asia from the Hindu Kush and Pamirs to the ranges of southern

Chamois (*Rupicapra rupicapra*) in Bavaria, Germany. (Photo by Animals Animals ©Peter Weimann. Reproduced by permission.)

Siberia. Walia ibex survive in a tiny area of the Simien Mountains of Ethiopia. The genus *Ovis* occurs from Western Europe across Eurasia to northeastern Siberia and into North America. Mouflons and urial are found on the islands of Corsica and Cyprus and eastwards to the upper Indus Valley in the extreme north of India and in Central Asia. Argalis also have a wide Central Asian distribution. This extends from just south of Lake Baikal in the north southwards to the northern side of the Himalaya, and from Kazakhstan in the west to Inner Mongolia in the east. Snow sheep are restricted to mountain ranges of northeast Siberia. Thinhorn sheep occur in Alaska and northwest Canada, while bighorns have a much more extensive range in western Canada and through the western United States, reaching Baja California in Mexico.

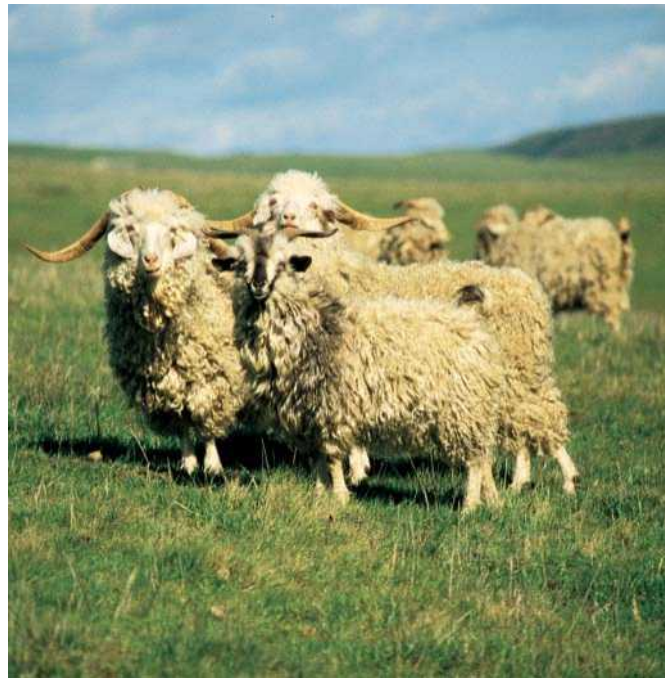
Introductions have extended this original distribution. Himalayan tahr and chamois have been introduced successfully to New Zealand. Barbary sheep are among several species of exotic bovids that have been introduced to the southwest United States for sport hunting. Barbary sheep have also been introduced to Spain, mouflons to several parts of Europe, and muskox to Norway. Feral domestic sheep and goats have established populations in several countries and on many islands.

Habitat

Caprinae are primarily associated with hilly or mountainous terrain, except for the tundra-living muskox. The altitudinal range within which they occur is wide. Nubian ibex have been recorded on cliffs around the Dead Sea down to 1,150 ft (350 m) below sea level. Long-tailed goral in the Russian Far East and snow sheep in Siberia both occur on coastal cliffs at or near sea level. In the Himalaya, Karakoram mountains, and on the Tibetan Plateau, Siberian ibex have been recorded at elevations of 22,000 ft (6,710 m), blue sheep at 21,500 ft (6,500 m), and argali at 19,000 ft (5,800 m).

Caprinae are adapted to a wide range of climatic conditions. Musk ox, thinhorn sheep, and snow sheep inhabit Arctic and subarctic regions year-round. Aoudad, Arabian tahr, Nubian ibex, and desert bighorn have adapted to the extreme desert heat of the Sahara, Arabia, and southwest United States. Urial in the deserts of Central Asia need to cope with high summer temperatures and very cold winters. All these desert-living species can obviously tolerate extreme aridity. Other species such as Nilgiri tahr, takin, and serows in subtropical Asia also live in seasonally wet habitats. Red goral (*Naemorhedus baileyi*) habitat in southeast Tibet has abundant rainfall, over 78 in (198 cm) annually.

Most species are primarily associated with rugged, precipitous terrain, either open or forested. Mountain goat, *Capra* species, Barbary sheep, tahrs, blue sheep, snow sheep, and



Angora goats (*Capra prisca*) in fields of Turkey. (Photo by Animals Animals ©Barbara Wright. Reproduced by permission.)

Mountain goat (*Oreamnos americanus*) kids leap and play in Glacier National Park, Montana, USA. (Photo by Bruce Coleman, Inc. Reproduced by permission.)

North American sheep utilize cliffs for escape and occur in steep, rocky, or broken country. Serows, gorals, and takin occupy forest or scrub-covered mountains. Some species seem to revel in the most difficult and inaccessible parts of the mountain ranges. Himalayan tahr, markhor, chamois, and goral move utilize both forests or scrub, and alpine meadows or other open areas. Argali and urial prefer more open and less rocky parts of the ranges but they do not avoid steep terrain.

Vegetation types occupied also show a wide range, from desert and semidesert through all montane zones to the high-cold environments of the Tibetan Plateau. Forested habitats include boreal evergreen, temperate deciduous, bamboo, and rhododendron scrub and subtropical forests of Southeast Asia. Walia ibex occur in giant heath scrub in Ethiopia's Simien Highlands.

Behavior

Caprinae mainly occur singly or in small- to medium-sized groups. Larger groups may form at the rut, at feeding grounds in winter, or occasionally at other times. Herds of up to 500 east Caucasian tur, 400 bharal, 300 takin, and 300 chamois have been reported, but these numbers are not typical. Musk ox, wild goat, and Nilgiri tahr all have a maximum group size of around 100. Serow are mainly solitary. Adult females, young and subadult, or young males often form groups, with adult males remaining separate, either solitary or in small groups, and joining the others for the rut. However, social systems in most species are not clear-cut, and mixed groups, nursery groups, and solitary males may all be seen at the same time of year, as, for example, in the case of the blue sheep.

Senses of sight and hearing are well developed. Alarm calls consist of a variety of sneezes, snorts, whistles, and hisses. Many species also stamp their feet in alarm. Most species are excellent climbers and adept at moving over precipitous terrain, seeking refuge from predators on cliffs. Argali and urial depend on speed for escape. When threatened by predators such as wolves, musk ox form a tight circle with heads lowered and young animals inside the ring.

Home range size varies greatly with species and habitat. Summer and winter ranges are commonly used. Bighorn sheep may use up to five home ranges annually. The maximum distance traversed by bighorns between winter and summer ranges is about 30 mi (48 km). In desert species, the location of water sources is an important influence on use of home ranges. Introduced aoudad in Texas had home ranges of 7.44 mi^2 (19.25 km^2) in summer and 1.02 mi^2 (2.64 km^2) in winter. Serow have been known to make well-marked tracks through their forest ranges. Japanese serow of both sexes mark the boundaries of their range with scent from preorbital glands. Arabian tahr mark their range with scrapes in the ground made by the forefeet and renewed regularly.

A common activity pattern is basically crepuscular, with feeding taking place mainly in the early morning and late afternoon or evening. The day is spent resting in shelter on or near cliffs, in caves, or in dense scrub. Ibex, urial, and blue sheep bed for the night in groups at the top of scree slopes, scraping out a smooth sleeping place and with adult animals facing in both directions to watch for danger.

Most species living in high mountains undertake altitudinal movements to lower elevations in winter to avoid cold temperatures or deep snow and return to higher altitudes in spring. The extent of these movements may be as much as 6,560 ft (2,000 m). Musk ox, in contrast, move to more exposed slopes in winter where winds prevent the buildup of snow.

Feeding ecology and diet

All members of the subfamily are generalist herbivores. A wide range of plant material is eaten: grasses, sedges, herbs, shrubs, buds, shoots, and twigs of trees; fruits, acorns, bark, moss, lichen, and fungi. Long-tailed goral in the Russian Far East eat marine grasses and even seaweed. The Caprinae includes both grazers and browsers and most species are both, to a greater or lesser extent. In a large proportion of the global range of Caprinae, there is a significant difference in forage quality between summer and winter. In winter, animals may be forced to eat dry vegetation, twigs, shrubs, and evergreen shoots with a low nutritional content and that may contain secondary compounds. As a result, they lose condition and may even die of starvation. Many species descend in spring to reach the first flush of green growth. Lush mountain pastures containing grasses and sedges provide rich feeding grounds, and it has been estimated that Siberian ibex in Pakistan could gain up to 44 lb (20 kg) in weight by the end of the summer. Invertebrates, including scorpions and beetles have been found in the stomachs of urial in Turkmenistan.

Blue sheep, Siberian ibex, urial, bighorn sheep, musk ox, and Japanese serow all dig through snow to reach winter for-

Nilgiri tahr (*Hemitragus hylocrius*) on the slopes of the western Ghats of India. (Photo by E. Hanumantha Rao/Photo Researchers, Inc. Reproduced by permission.)

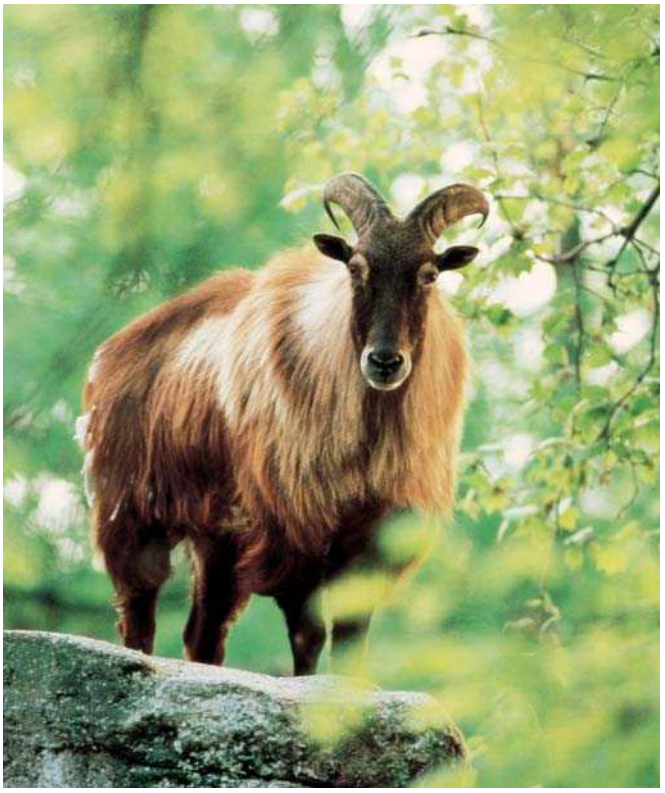
age. Wild goat species may stand up on their hindlegs to gain access to browse and use a foreleg to pull down the vegetation. Himalayan tahr and markhor have been observed climbing into oak trees to feed on the leaves, with some markhor reaching heights of 19–29 ft (6–9 m) above the ground. Serow and mountain goats are also known to climb into trees growing horizontally out of cliffs to feed. Takin are mainly browsers and they may push over young trees to reach the leaves and shoots.

While water needs may be partially met from vegetation consumed or dew that has condensed on vegetation, most species drink from streams and springs, and those living at high altitudes eat snow in winter. Salt licks are also important to many species: mountain goats, for example, may travel several miles (kilometers) to reach them. Blue sheep have been known to lick urine-soaked areas near human encampments and takin consume soil at certain seasons, possibly for its mineral content.

Reproductive biology

Most Caprinae are polygamous, with dominant males enjoying priority access to females. Dominance is established through displays, threats, and direct combat, prior to or during the rut. Fighting may involve locking horns and twisting, direct head-to-head clashes, or lateral or flank attacks. Head-on fighting may involve two animals running straight at each other before clashing horns, or rising up on their hind legs, then crashing down together. The sound may carry a long way through the mountains and all-out bouts between animals such as argali with their massive horns are an impressive spectacle. Thickened front parts of the skull protect them from damage. Rupicaprini do not use direct head butts but attack the flanks of rivals, attempting to stab with their short horns. Rut-related mortality is reported in musk ox and mountain goat. Male displays to females include tail raising, urine spraying, lip curls, low stretches, and kicks with the foreleg. Chamois males bob their head up and down in front of females and Himalayan tahr also nod and shake their heads in display. Mountain goat males mark vegetation during the rut with glands behind the horns, dig rutting pits, and paw the soil onto their flanks and undersides.

Caprinae living in northern latitudes and at high elevations show a strong seasonality in breeding. The particular period varies with locality and is timed so that births coincide with an abundance of fresh green growth in spring or early summer to meet the nutritional needs of lactation and growth of the young. Cold or wet weather at this time increases juve-



A Himalayan tahr (*Hemitragus jemlahicus*) on rocky ledge. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

nile mortality. Walia ibex and Barbary sheep may breed throughout the year, but still show seasonal peaks. Gestation period is around eight months in musk ox and five to seven months in other species. Single young are the norm, but twins are not uncommon in some species.

Pregnant females seek out secluded areas to have their young. Young Caprinae can stand soon after birth but normally hide for two to three days before following the female. Most species are weaned in four to five months.

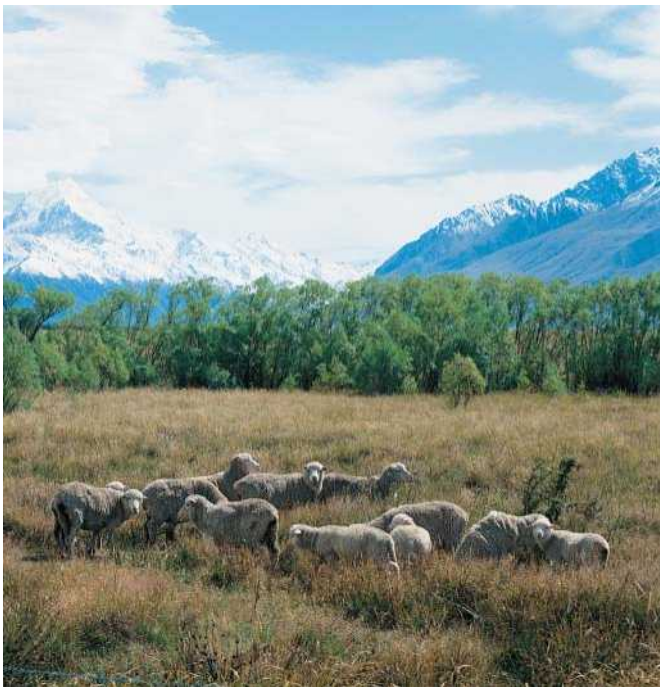
Conservation status

Nineteen species are considered threatened in the 2002 IUCN Red List. The Walia ibex (*Capra walie*) is Critically Endangered. Its population is estimated to have decreased from 400 in 1983 to 180 in 1996. Six species are Endangered, including two species of tahr. Nilgiri tahr (*Hemitragus hylocrius*) and Arabian tahr (*H. jayakari*) have small populations and limited geographic ranges. West Caucasian tur (*Capra caucasica*) is restricted to a small area of the western Caucasus, while Nubian ibex (*Capra nubiana*) and markhor (*Capra falconeri*) have suffered heavily from indiscriminate hunting. Dwarf blue sheep (*Pseudois schaeferi*) also has a very restricted distribution in the gorge of the upper Yangtze. Six of the subspecies listed in the 2002 Red List were Critically Endangered, and 15 are Endangered. Serow, Arabian tahr, Walia ibex, and several Caprinae subspecies are listed as Endangered by the U. S. Fish and Wildlife Service.

The greatest recent threat to wild Caprinae has been uncontrolled hunting, a factor that intensified sharply during the twentieth century with the introduction of powerful and accurate modern weapons and improved vehicle transport. Indiscriminate hunting has adversely affected all species, driving several towards extinction, wiping out many small populations, and reducing ranges. Other factors with a negative impact include increasing competition with livestock, loss of habitat, fragmentation of isolated populations, and road building that improves access to remote mountain areas. These must also have caused the loss of genetic diversity in most species, to a greater or lesser extent.

For many species, accurate population estimates and range details have not been established, especially for forest living species, and assessments of conservation status have to be based on partial information. At the end of 2002, Arabian tahr numbered around 2,000 and Nilgiri tahr fewer than 2,500. Strict legal protection and reintroductions in the United States and Canada have halted or reversed declines and increased mountain sheep populations by almost 50% in a quarter of a century. The Japanese government gave the Japanese serow special protected status in 1955, and its numbers increased from 2,000–3,000 at that time to about 100,000 at the end of 2002.

Introductions and reintroductions have also been successful in redressing declining situations, for example, with the muskox. Alpine ibex were hunted out in Europe by 1850, except for one herd in the Gran Paradiso area of Italy. Animals from this source have since been reintroduced to many parts of their former range in Switzerland, France, and Austria, and



Domestic sheep (*Ovis aries*) live throughout the world in association with humans. (Photo by Hans Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

these are now thriving. Many protected areas contain important populations of Caprinae and some have been established to conserve remnant populations. The surviving population of Walia ibex lives in Simien National Park. Wadi Sareen Tahr Reserve in Oman was established to protect Arabian tahr, and Eravikulam National Park in India contains the largest remaining population of Nilgiri tahr.

Innovative schemes to restore old strip mining sites in Canada have created new habitat for bighorn sheep, leading to dramatic increases in numbers, doubling of body mass in females over a period of 15 years, and big increases in male body sizes, including new record horns. The areas have also been colonized by many other large mammal species, and numbers of nesting birds have risen steadily. Well-managed sport hunting programs have also helped to conserve Caprinae populations.

Significance to humans

All species provided a valuable source of meat, hides, and wool to indigenous peoples. The frequent depiction of ibex and other species in rock drawings attests to their importance to early hunters. In addition to meat, they utilized skins and wool for rugs and clothing, sinew, bones, and horn. Virtually all the body parts of Alpine ibex were greatly valued for medicinal use, and over-exploitation drove the animal to the edge of extinction by the middle of the nineteenth century. Blood and many other body parts of serow and goral are widely used for medicinal purposes in Southeast Asia.

Most species of Caprinae have been hunted for trophies as well as meat, and the large and showy horns of wild *Capra* and *Ovis* species being especially prized. Commercial sport hunting continues to be popular and managed sport hunting programs in Mongolia and other Central Asian countries have provided a valuable source of income. The larger horns of wild sheep and goats are used for decoration and a variety of other purposes. In southern Arabia, horns of Nubian ibex are placed on the corners of houses to ward off evil spirits. In the northwest Himalaya, large numbers of horns from both wild and domestic species are placed on village altars and on cairns on top of passes as votive offerings.

A pygmy goat ewe with lambs in Ontario, Canada. (Photo by Animals Animals ©Ralph Reinhold. Reproduced by permission.)

Without doubt, the greatest significance of Caprinae for humans lies in their role as the origin of domestic sheep and goats. Wild goats were first domesticated about 2,700 years ago in the Middle East, serving ever since as a valuable source of meat, milk, and leather. Domestic sheep and goats now exist in hundreds of varieties and are found on all continents, except Antarctica. They number in the millions and far exceed populations of all wild Caprinae. They provide a source of meat, milk, wool, and hides for people throughout the world and, especially in the case of sheep, are farmed at commercial levels and their products exported. On the negative side, overgrazing by domestic sheep and goats has been widely blamed for degradation of extensive areas of the Mediterranean region and the Middle East.

1. Mountain goat (*Oreamnos americanus*); 2. Barbary sheep (*Ammotragus lervia*); 3. Himalayan goral (*Naemorhedus goral*); 4. Northern chamois (*Rupicapra rupicapra*); 5. Serow (*Capricornis sumatraensis*); 6. Blue sheep (*Pseudois nayaur*). (Illustration by Emily Damstra)

1. Takin (*Budorcas taxicolor*); 2. Siberian ibex (*Capra sibirica*); 3. Arabian tahr (*Hemitragus jayakari*); 4. Musk ox (*Ovibos moschatus*); 5. Bighorn sheep (*Ovis canadensis*). (Illustration by Emily Damstra)

Species accounts

Serow
Capricornis sumatraensis

TAXONOMY
Naemorhedus sumatraensis (Bechstein, 1799), Sumatra, Indonesia.

OTHER COMMON NAMES
French: Serow; German: Serau; Spanish: Sirao.

PHYSICAL CHARACTERISTICS
Head and body length 55–70 in (140–180 cm), height 33–37 in (85–94 cm), and weight 110–300 lb (50–140 kg). Upperparts are gray-black and undersides whitish. Horns are slim and slightly curved back, 6–10 in (15–25 cm).

DISTRIBUTION
Himalaya of India, Nepal, and Bhutan; western China; Southeast Asia (Myanmar, Laos, Thailand, Vietnam, Cambodia), and Indonesia (Sumatra).

HABITAT
Mountain forests.

BEHAVIOR
Usually solitary or in small groups up to seven. Crepuscular. Rest below rock overhangs and cliffs during the day. Known to swim between islands off the coast of Malaysia.

FEEDING ECOLOGY AND DIET
Feeds on a wide range of grasses, shoots, and leaves.

REPRODUCTIVE BIOLOGY
Polygamous. Mate in October–November, and gestation lasts about seven months.

CONSERVATION STATUS
Detailed distribution and local population estimates are unavailable. The population is considered to be declining due to illegal hunting and habitat loss, and it is listed as Vulnerable. *C. s. rubidus* and *C. s. sumatraensis* are Endangered.

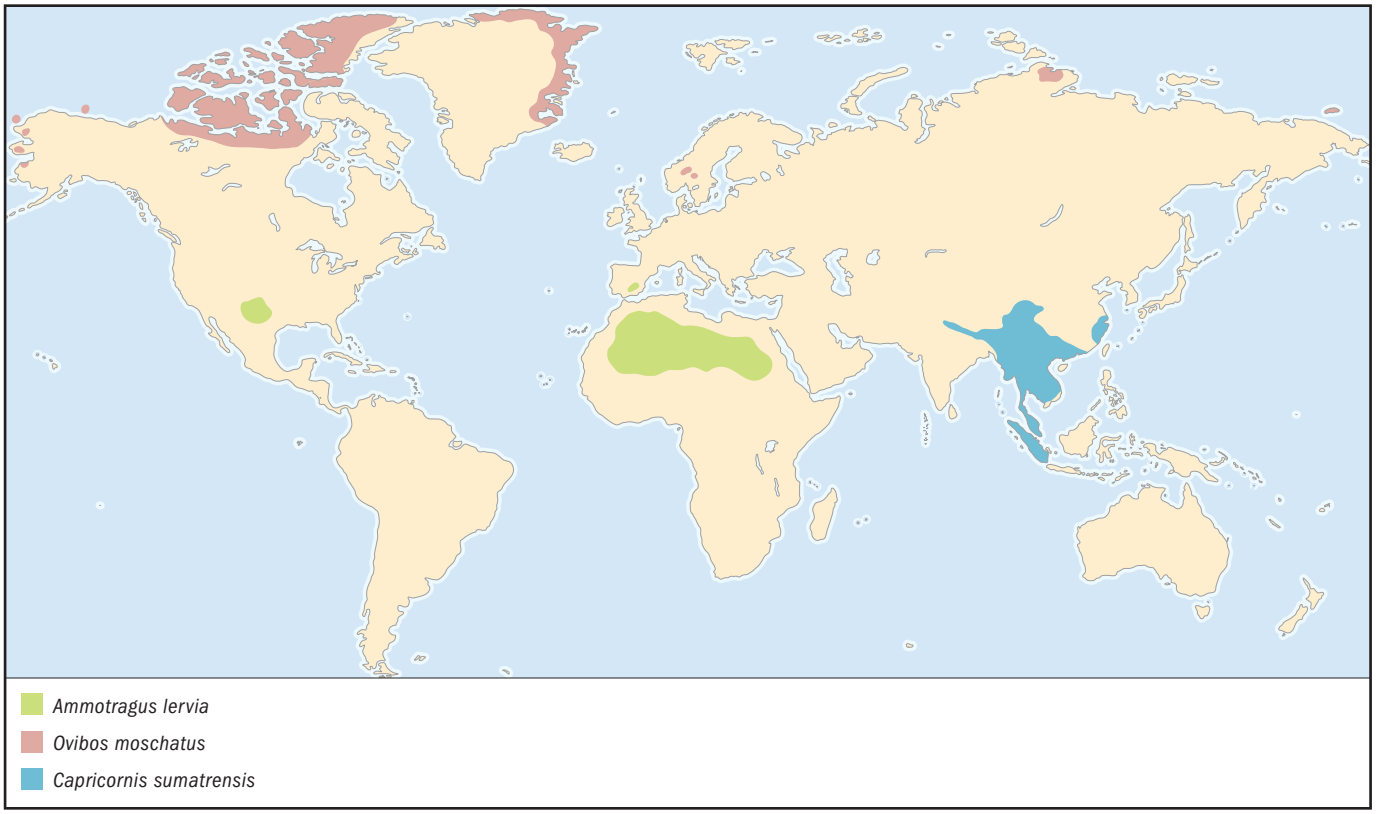
SIGNIFICANCE TO HUMANS
Hunted for its meat and other body parts that have medicinal properties. ◆

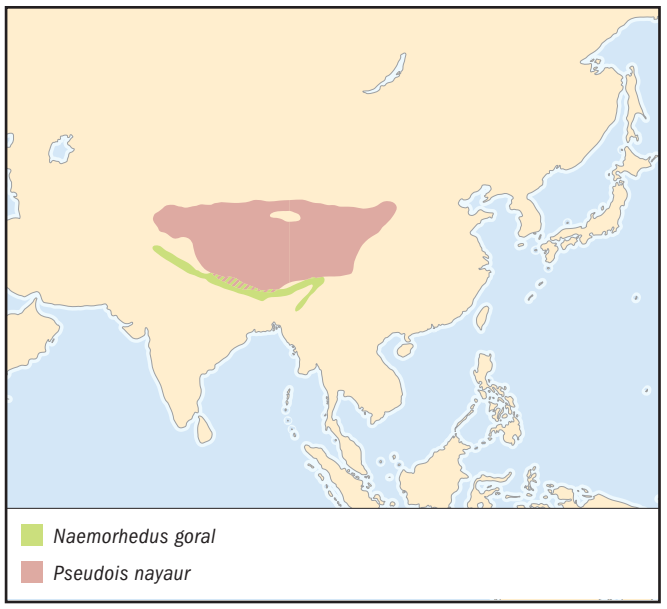
Himalayan goral
Naemorhedus goral

TAXONOMY
Naemorhedus goral (Hardwicke, 1825), Nepal.

OTHER COMMON NAMES
French: Goral; German: Goral; Spanish: Goral.

PHYSICAL CHARACTERISTICS
Goral have a stocky build. Head and body length is 32–51 in (82–130 cm), height 22–31 in (57–78 cm), and weight 55–66 lb (25–30 kg). Both sexes have short, sharp, backward-curving





horns 5–6 in (12–15 cm) long. Color is gray to dark brown with a darker stripe down the center of the back and a short crest of hairs in males. There is a conspicuous white throat patch.

DISTRIBUTION
The Himalaya from Pakistan to Arunachal Pradesh in eastern India and adjacent parts of Tibet.

HABITAT
Forested mountains from 3,280–13,120 ft (1,000–4,000 m), preferring precipitous slopes.

BEHAVIOR
Mainly active in the early morning and late afternoon. Live in small groups of up to 12; adult males are usually solitary.

FEEDING ECOLOGY AND DIET
Grass, herbs, and shrubs. The diet has not been studied in detail.

REPRODUCTIVE BIOLOGY
Polygamous. Mating takes place November–December. Young are born in April–May in the western Himalaya, later in the east.

CONSERVATION STATUS
Not threatened. No population estimates available.

SIGNIFICANCE TO HUMANS
Hunted for meat and to a lesser extent for sport. ◆

Mountain goat
Oreamnos americanus

TAXONOMY
Oreamnos americanus (de Blainville, 1816), Washington State, United States.

OTHER COMMON NAMES
French: Chèvre des montagnes; German: Schneeziege; Spanish: Cabra de las rocosas.

PHYSICAL CHARACTERISTICS
Head and body length 47–63 in (120–160 cm), height 35–47 in (90–120 cm), and weight up to 308 lb (140 kg). Males average 10–30% larger than females. There is a ridge or hump above the shoulder and males have a small beard. Color is white or yellowish white. Horns are short.

DISTRIBUTION
Original range extended from southeast Alaska and northwestern Canada to north-central Oregon and Montana. Introduced to Colorado, South Dakota, Olympic National Park, and several Alaskan islands.

HABITAT
Steep slopes and cliffs in Arctic tundra or subalpine mountains. In autumn, usually moves onto south- or west-facing slopes.

BEHAVIOR
Peaks of activity in early morning and evening. Usually in small groups up of to four animals. May gather in large groups in winter.

FEEDING ECOLOGY AND DIET
Diet consists of a broad range of plant matter, including grasses, herbs, mosses, lichens, and shrubs.

REPRODUCTIVE BIOLOGY
Polygamous. Males fight at the rut and may inflict injuries on rivals with their sharp horns. Mating takes place November–early January and young are born late May–early June.

CONSERVATION STATUS
Not currently threatened. Population was estimated at more than 80,000 and stable in 1997.

SIGNIFICANCE TO HUMANS
Has been extensively hunted for its meat. Some limited sport hunting still takes place. ◆

Northern chamois
Rupicapra rupicapra

TAXONOMY
Rupicapra rupicapra (Linnaeus, 1758), Switzerland.

OTHER COMMON NAMES
English: Alpine chamois; French: Chamois; German: Alpengemse; Spanish: Rebeco alpino.

PHYSICAL CHARACTERISTICS
Head and body length 35–52 in (90–130 cm), height 30–32 in (76–81 cm), and weight 53–110 lb (24–50 kg). Tawny-brown in summer, dark brown or blackish brown in winter, with pale undersides and whitish on head and throat. Horns are slim and hooked, 6–8 in (15–20 cm) long.

DISTRIBUTION
European Alps, Carpathians, Balkans, Turkey, and the Caucasus.

HABITAT
Rocky slopes, alpine meadows, and forest edge.

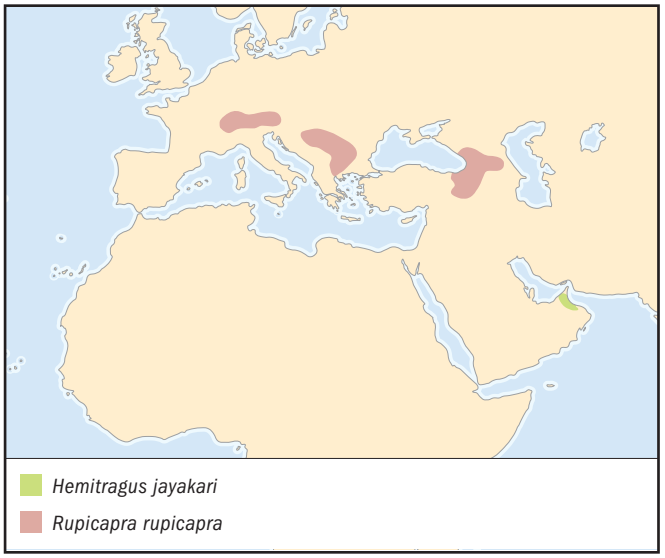
BEHAVIOR
Females and young form groups of up to 15–30 animals. Males are usually solitary and join herds in late summer.

FEEDING ECOLOGY AND DIET
Mainly herbs and grasses in summer, includes lichen, moss, and tree shoots in winter.

REPRODUCTIVE BIOLOGY
Polygamous. Mating occurs in November, the young are born May–June. Younger males are driven away from females by dominant males.

CONSERVATION STATUS
Subspecies *R. r. cartusiana* and *R. r. tatrica* are Critically Endangered, *R. r. caucasica* is Vulnerable, and *R. r. asiatica* is Data Deficient.

SIGNIFICANCE TO HUMANS
Hunted for its meat and hide, made into "chammy" leather. ◆



Barbary sheep
Ammotragus lervia

TAXONOMY
Ammotragus lervia (Pallas, 1777), Department of Oran, Algeria.

OTHER COMMON NAMES
English: Aoudad; French: Aoudad, mouflon à manchettes; German: Mähnenschaf; Spanish: Arruí.

PHYSICAL CHARACTERISTICS
Length 51–65 in (130–165 cm), height 30–44 in (75–112 cm); weight 220–320 lb (100–145 kg) in males and 88–110 lb (40–55 kg) in females. Color is reddish tawny with long white or pale mane on the throat and chest, and tufts on forelegs. Males' horns sweep out, back, then in, and reach a maximum of 33 in (84 cm). Females have shorter horns.

DISTRIBUTION
Mountains and isolated massifs of the Sahara from western Sahara to Egypt and Sudan. Introduced to southwest United States (New Mexico, Texas, California), Spain, and, unsuccessfully, to Mexico.

HABITAT
Rugged, rocky mountains from near sea level to 12,790 ft (3,900 m) in the Atlas Mountains.

BEHAVIOR
Occur alone or in small groups. Behavior in the wild is poorly known.

FEEDING ECOLOGY AND DIET
Feeds on sparse desert vegetation. Vulnerable to prolonged drought.

REPRODUCTIVE BIOLOGY
Polygamous. Males clash heads in fights for dominance for females; mating reportedly takes place throughout the year, with a peak in September–October. Gestation lasts 154–160 days.

CONSERVATION STATUS
Populations have been reduced by indiscriminate hunting and are thought to be declining. Overall regarded as Vulnerable. *A. l. ornata* (Egypt) is probably Extinct in the Wild.

SIGNIFICANCE TO HUMANS
Traditionally hunted for meat, hide, hair, and sinew. ◆

Blue sheep
Pseudois nayaur

TAXONOMY
Ovis nayaur (Hodgson, 1833), Tibetan frontier, Nepal.

OTHER COMMON NAMES
English: Bharal; French: Bharal, bouc bleu; German: Blauschaf; Spanish: Baral.

PHYSICAL CHARACTERISTICS
Head and body length is 47–55 in (120–140 cm); weight 132–165 lb (60–75 kg) in males, 77–121 lb (35–55 kg) in females. Horns of males are smooth and curve up, out, then back. Females have short, rather stout horns. Coat color is gray to slate gray in winter, and a sandy tint in summer. Males have

a black line along the flanks, a black chest and throat. Both sexes have a black front surface to the legs with white knees.

DISTRIBUTION
The whole of the Tibetan Plateau and bordering ranges. Range extends from the Karakoram Mountains of northeastern Pakistan along the northern side of the Himalaya, penetrating to the southern side of the range in a few places, and northeastwards into Inner Mongolia.

HABITAT
Rugged mountains, isolated ridges, and broken rocky terrain, with cliffs for escape. Recorded above 21,500 ft (6,500 m) in the Himalaya and Karakoram Mountains.

BEHAVIOR
Diurnal, with activity peaks in early morning and late afternoon. Mixed herds are seen all year and all-male groups are more common in summer.

FEEDING ECOLOGY AND DIET
Diet includes a range of grasses, sedges, herbs, and shrubs, and may be supplemented in winter by twigs, mosses, and lichens.

REPRODUCTIVE BIOLOGY
Polygamous. Males fight for females at the rut, rising on their hindlegs before clashing heads. The rut takes place in December–January, and gestation lasts about 160 days.

CONSERVATION STATUS
Some populations are declining, others are stable. Regarded overall as not threatened.

SIGNIFICANCE TO HUMANS
Traditionally hunted for meat by local peoples. Commercially hunted in parts of China and meat exported. Limited sport hunting program established in Nepal. ◆

Arabian tahr
Hemitragus jayakari

TAXONOMY
Hemitragus jayakari Thomas, 1894, Jebel Akhdar Range, Oman.

OTHER COMMON NAMES
French: Tahr d'Arabie; German: Arabischer tahr; Spanish: Tar arabico.

PHYSICAL CHARACTERISTICS
A rather small member of the Caprini. Height 24 in (62 cm); weight 50 lb (23 kg). Horns are short, laterally compressed, and swept back. Color is light sandy brown with pale undersides. A short dorsal crest is tipped black. The face has dark stripes up the muzzle and from mouth to eye, separated by paler patch.

DISTRIBUTION
Mountains of United Arab Emirates and northern Oman. Apparently now extinct in United Arab Emirates.

HABITAT
Precipitous mountains and cliffs from 656–5,900 ft (200–1,800 m).

BEHAVIOR
Occurs alone or in small groups. Both sexes mark their territory with scrapes in the ground that are regularly renewed.

FEEDING ECOLOGY AND DIET
Diet includes fruit, shoots, seeds, and grasses.

REPRODUCTIVE BIOLOGY
Polygamous. Mating occurs throughout most of the year and young have been observed in every month except November. Gestation lasts 140–145 days.

CONSERVATION STATUS
Tahr have disappeared from some isolated massifs but some remaining populations are well protected within nature reserves. The population was estimated at around 2,000 in 1997 and is believed to be stable, though listed as Endangered.

SIGNIFICANCE TO HUMANS
Traditionally hunted for their meat. ◆

Siberian ibex
Capra sibirica

TAXONOMY
Capra sibirica (Pallas, 1776), Sayan Mountains, Siberia, Russia.

OTHER COMMON NAMES
English: Asiatic ibex; French: Bouquetin d'Asie; German: Sibirischer steinbock; Spanish: Sakin altai.

PHYSICAL CHARACTERISTICS
The largest and heaviest member of the genus, with the longest horns. Head and body length 67 in (171 cm), height 43 in (110 cm), and weight 286 lb (130 kg). Horns are scimitar-like, swept back and laterally compressed, with prominent transverse ridges on the front surface and reach 60 in (148 cm). Horns of females are much shorter. Males have a long beard. Color is very variable, from light gray to dark chocolate brown.

DISTRIBUTION
Occurs throughout the mountains of Central Asia and the western Himalaya (Afghanistan, Pakistan, India, China, Kyrgyzstan, Kazakhstan, Mongolia, Russia). A small number have been introduced to New Mexico.

HABITAT
Rocky, rugged mountains with cliffs for escape. Occurs around 2,300 ft (700 m) in desert mountains of the Gobi, at 1,970–13,120 ft (600–4,000 m) in the Tien Shan, and 10,500–22,000 ft (3,200–6,710 m) in the Himalaya and Karakoram Mountains. Altitudinal movements in winter may cover 6,560 ft (2,000 m).

BEHAVIOR
Generally occurs in groups of 5–12, except at the rut when large groups may form (up to 150). Adult males mostly live apart from female and young until the rut.

FEEDING ECOLOGY AND DIET
Diet known to comprise 140 plant species across the range. Feeds on grasses, sedges, and herbs and also on leaves, shoots, fruit, and lichens.

REPRODUCTIVE BIOLOGY
Polygamous. Males fight for access to females by clashing horns and sideway head thrusts. Mating takes place between October and January depending on elevation and latitude. Gestation is 170–180 days. Twins occur frequently in older females.

CONSERVATION STATUS
Reduced in number in many parts of the range by indiscriminate hunting, but protected in places by precipitous terrain. Some populations are declining, while others are stable. Population estimated at more than 250,000 in 1997, and not considered threatened.

SIGNIFICANCE TO HUMANS
Traditionally an important source of meat; skin used for rugs and to make box calf; fur of young animals for fur coats; and horns utilized as wall decorations or as milk containers. Currently a victim of sport hunting. ◆

Bighorn sheep
Ovis canadensis

TAXONOMY
Ovis canadensis Shaw, 1804, Mountains on Bow River, Alberta, Canada.

OTHER COMMON NAMES
French: Mouflon d'Amerique; German: Dickhornschaf; Spanish: Carnero de la Canada, borrego cimarron.

PHYSICAL CHARACTERISTICS
Head and body length is 60–77 in (153–195 cm) in males and 49–60 in (124–153 cm) in females. Maximum weights are 300 lb (137 kg) in males and 200 lb (91 kg) in females, but usually 160–211 lb (73–96 kg) and 105–154 lb (48–70 kg), respectively. Males have massive horns curling round and forward. Color ranges from reddish brown to very dark brown. Undersides, back of legs, rump patch, and muzzle are white.

DISTRIBUTION
Mountains of western North America south to desert ranges of the southwest United States and northern Mexico. Former range was more extensive.

HABITAT
Mountains, foothills, badlands, with cliffs for escape.

BEHAVIOR
Live in small groups of two to nine, with adult males usually separate.

FEEDING ECOLOGY AND DIET
Eat a wide range of grasses, herbs, and shrubs.

REPRODUCTIVE BIOLOGY
Polygamous. Mating takes place in autumn and gestation lasts about 174 days. Females first mate aged two and a half years, males not usually before ages seven or eight. Males establish dominance prior to the rut by displaying and head clashing.

CONSERVATION STATUS
May have numbered one to two million during the nineteenth century, but much lower than that now. Numbers overall are stable and the species is classified as Lower Risk/Conservation Dependent. *O. c. weemsi* is Critically endangered, *O. c. cremnobates* is Endangered, and *O. c. mexicana* is Vulnerable.

SIGNIFICANCE TO HUMANS
Hunted for meat and trophies. ◆

Musk ox
Ovibos moschatus

TAXONOMY
Bos moschatus (Zimmerman, 1780), between Seal and Churchill Rivers, Manitoba, Canada.

OTHER COMMON NAMES
French: Boeuf musqué; German: Moschusochs; Spanish: Buey amizclero.

PHYSICAL CHARACTERISTICS
Massive build with relatively short legs and a slight hump. Height is 47–59 in (120–150 cm). Maximum weight can reach 836 lb (380 kg). Coat is dark brown and coarse, with a dense, soft underfur. Both sexes have horns that are broad and curve down and out.

DISTRIBUTION
Formerly occurred through northern Alaska, Canada, and Greenland into northern Eurasia. May have survived in northern Siberia until 3,000–4,000 years ago. Exterminated from Alaska and parts of Canada during the nineteenth and twentieth centuries, but conservation measures and reintroductions have restored them to part of this original range. Also introduced to west Greenland, Wrangel Island, and the Taimyr Peninsula in Arctic Russia, and southern Norway.

HABITAT
Tundra. Prefers moist habitats such as lakesides, valley bottoms, and wet meadows in summer. In winter, move to open slopes, ridges, and summits where winds prevent accumulation of snow.

BEHAVIOR
Gregarious, living in herds of up to 100, though usually 10–20. When threatened, they bunch together in a tight circle, facing outward, with calves in the center.

FEEDING ECOLOGY AND DIET
In summer, they feed on grasses and sedges and, in winter, browse on shrubs and dwarf willow.

REPRODUCTIVE BIOLOGY
Polygamous. The rut takes place June–September. Males display and fight with head-on clash. Dominant bulls drive other males away. Young are born mid-April–mid-June.

CONSERVATION STATUS
Not threatened. Populations now stable or increasing. Estimated to number approximately 120,000 in 1997.

SIGNIFICANCE TO HUMANS
Hunted for its meat and hide. Inuit people used its horns to make bows and its light, warm underfur *qiviut* for clothing. ◆

Takin
Budorcas taxicolor

TAXONOMY
Budorcas taxicolor Hodgson, 1850, Mishmi Hills, Assam, India.

OTHER COMMON NAMES
French: Takin; German: Rindergemse, gnuziege; Spanish: Takin.

PHYSICAL CHARACTERISTICS
Heavy, solid build with stout limbs. Head and body length is 39–92 in (100–235 cm), height at shoulder 27–55 in (68–140 cm), and weight 330–880 lb (150–400 kg). Color ranges from yellowish white through to dark brown. Horns are thick and massive in both sexes.

DISTRIBUTION
Occurs in the eastern Himalaya (India, Bhutan, northern Myanmar) north through western China (eastern Tibet, Sichuan, Shaanxi, and Gansu).

HABITAT
Lives in rugged, rocky mountains covered in scrub, bamboo thickets, and forest at altitudes of 3,280–13,940 ft (1,000–4,250 m).

BEHAVIOR
Occurs in groups of 10–35 animals, with large groups reported in summer. The sexes occur together in August–September.

FEEDING ECOLOGY AND DIET
Mainly browses, feeding on forbs and leaves in summer and twigs and evergreen shoots in winter. May travel long distances to saltlicks.

REPRODUCTIVE BIOLOGY
Polygamous. Mating takes place in July–August in Sichuan. Gestation in captivity lasts 200–220 days.

CONSERVATION STATUS
Regarded as Vulnerable. Two subspecies, golden takin (*B. t. bedfordi*) in Shaanxi, China, and Mishmi takin (*B. t. taxicolor*), are Endangered.

SIGNIFICANCE TO HUMANS
Hunted for its meat by indigenous peoples using snares, deadfalls, and spear traps. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Japanese serow *Capricornis crispus* French: Serow du Japon; German: Japonischer Serau; Spanish: Sirao de Japon	Both sexes have short horns 3–6 in (8–15 cm), slightly curved back. Length 39–59 in (100–150 cm); height about 28 in (70 cm).	Lives in montane forests at 4,920–8,200 ft (1,500–2,500 m). Occupy small home ranges marked with secretions from preorbital glands. Mate in October–November, gestation about seven months.	Southern and central Japan (Honshu, Shikoku, and Kyushu).	Leaves, shoots, buds, acorns, seeds, and grass.	Not threatened
Long-tailed goral *Naemorhedus caudatus* French: Goral à queue long; German: Langschwanzengoral; Spanish: Goral	Color variable, from gray, brown, and whitish. Short, sharp horns up to 8 in (21 cm). Body length of males up to 46 in (118 cm) and height 29 in (74 cm). Weight to 70 lb (32 kg). Females smaller and lighter.	Coastal cliffs, forested mountain slopes up to 3,280 ft (1,000 m). Move to lower elevations in winter.	Russian Far East, Korean Peninsula, and northeast China.	Graze and browse on grasses, herbs, leaves, shoots, twigs, and acorns. In coastal areas may consume marine grass and seaweed.	Vulnerable
Southern chamois *Rupicapra pyrenaica* English: Apennine chamois; French: Isard; German: Pyrenäengemse; Spanish: Rebeco iberico	Pale red-brown in summer, darker in winter; white or pale patch on throat and neck. Horns short, hooked backwards. Length 39–47 in (100–120 cm); weight 55–132 lb (25–60 kg).	Rocky mountains and meadows above tree line. Forest edges or in forests in winter. Diurnal. Usually in small groups.	Pyrenees (France, Spain), Cantabrian Mountains (Spain), and Apennines (Italy).	Grasses, herbs; browse on trees in winter.	Not threatened
Dwarf blue sheep *Pseudois schaeferi* French: Bouc bleu; German: Zwergblauschaf; Spanish: Baral	Weight 61–86 lb (28–39 kg). Height 28–31 in (70–80 cm).	Lives below the forest belt at around 8,528 ft (2,600 m) in the Yangtze Gorge.	Yangtze Gorge in Sichuan, China.	Not known.	Endangered
Nilgiri tahr *Hemitragus hylocrius* English: Nilgiri ibex; French: Tahr; German: Tahr; Spanish: Tar	Horns thick, short, curve backwards; up to about 16 in (40 cm) long in males, 12 in (30 cm) in females. Stocky build with short mane. Adult males weigh 176–220 lb (80–100 kg).	Cliffs and grassy hills, 3,936–7872 ft (1,200–2,600 m).	Southern part of the Western Ghats in Tamil Nadu and Kerala, India.	Grasses, sedges, and herbs.	Endangered

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Wild goat *Capra aegagrus* French: Chèvre egagre; German: Bezoarziege; Spanish: Egagro	Limbs strong, build stocky. Males horns are slim, scimitar-shaped and strongly keeled, to 51 in (130 cm). Length 47–63 in (120–160 cm); weight 55–209 lb (25–95 kg).	Arid rocky hills, steep slopes up to 13,776 ft (4,200 m). Active early morning and evening; also during the night in hot weather.	Crete; Turkey to Pakistan and Iran, Caucasus, and Turkmenistan.	Graze and browse on grasses, herbs, and shrubs.	Vulnerable
East Caucasian tur *Capra cylindricornis* English: Dagestan tur; French: Bouquetin du caucase oriental; German: Ostkaukasischen Tur; Spanish: Tur oriental	Massive body. Horns are large, spiral gently up, out, and back; to 51 in (130 cm) in males, 12 in (30 cm) in females. Length 51–59 in (130–150 cm); height 31–39 in (79–98 cm); weight 121–220 lb (55-100 kg).	Steep, rocky areas 2,600–13,776 ft (800–4,200 m). Seasonal migrations may cover 4,920–6,560 ft (1,500–2,000 m). Usually in small groups, larger occasionally (to 500).	Eastern Caucasus (Azerbaijan, Georgia, and Russia).	Grass, herbs; shrubs and leaves in winter.	Vulnerable
Markhor *Capra falconeri* French: Markhor; German: Schraubenziege, Markhor; Spanish: Markhor	Limbs short and thick. Males have a black beard and long mane. Distinctive horns are twisted in to a spiral, reaching 63 in (160 cm) in length. Length 55–71 in (140-180 cm), height 26–39 in (65–100 cm), and weight 176–242 lb (80–110 kg).	Live at and around the treeline on precipitous mountain slopes from 2,300 to 8,856 ft (700–2,700 m), occasionally to 13,120 ft (4,000 m). Occur in small groups of females and young. Males usually solitary.	Tajikistan, Afghanistan, and Pakistan.	Graze and browse on a range of grasses, herbs, and shrubs.	Endangered
Alpine ibex *Capra ibex* French: Bouquetin des Alpes; German: Alpen-Steinbock; Spanish: Ibice de los Alpes	Horns are scimitar shaped, and swept back, to 33 in (85 cm) in length with prominent transverse ridges on the front surface. Length 51–59 in (130–150 cm). Solidly built; weight reaches 264 lb (120 kg).	Lives above the tree line at 8,200–11,480 ft (2,500–3,500 m). May enter upper level of forests in spring in search of new grass. Use cliffs for escape. Mate in December January, gestation lasts 145–160 days.	Alps of Italy, Switzerland, Austria and Germany.	Feeds on grasses, herbs, and lichens.	Not threatened
Spanish ibex *Capra pyrenaica* French: Bouquetin d'Espagne; German: Spanischer Steinbock; Spanish: Cabra iberica	Horn shape varies; usually twisted outwards and upwards. Length 46–60 in (116–153 cm). Weight 55–176 lb (25–80 kg).	Mountains. Mainly diurnal. Rut takes place from early November to the middle of December. In groups of 50–60 outside the breeding season.	Mountains of northern, central, and southern Spain.	Grasses, herbs; occasionally shrubs and lichens.	Not threatened
Walia ibex *Capra walie* French: Bouquetin d'Ethiopie; German: Afrikanischer Steinbock; Spanish: Ibice de Ethiopia	Horns swept back, long and heavy. Weight 176–275 lb (80–125 kg).	Frequents escarpments, steep terraces, gorges, and screes at 8,200–14,750 ft (2,500–4,500 m) with montane forest or subalpine scrub. Mainly crepuscular. Mate throughout the year with a peak March–May.	Simien Mountains of Ethiopia. Range decreased significantly 1920–1970; in 2002 was restricted to 16 mi (25 km) of the northern escarpment.	Grasses, herbs, leaves, shoots, and lichens. Requires year-round availability of water.	Critically Endangered
Urial *Ovis orientalis* French: Mouflon; German: Mufflon, Wildschaf; Spanish: Muflon	Horns relatively light and curl out and round. Length 43–57 in (110–145 cm); weight 55–190 lb (25–87 kg).	Inhabits hills and mountains, mainly in arid or semiraid areas. Reaches 15,000 ft (4,570 m) in Ladakh, but usually at lower elevations. Mostly in open country but in Corsica lives in deciduous woodland.	Corsica, Cyprus, Turkey, and Iran through Central Asia and east to the upper Indus Valley. Introduced into western Europe.	Grasses, herbs, and shrubs.	Vulnerable
Argali *Ovis ammon* French: Argali, mouflon d'Asie; German: Argali; Spanish: Argali	Massive horns curl round and to the front and outwards past the face. Shape varies with subspecies. Can attain 75 in (190 cm) in length, 20 in (50 cm) in basal circumference. Body length 71–79 in (180–200 cm).	High altitude hills, valleys, and plateaux. Prefers relatively open steep terrain. Occurs up to 19,000 ft (5,800 m) in Tibet, China.	Mountains of central Asia, China, and Mongolia.	Feeds on grasses, sedges, herbs, and low shrubs.	Vulnerable
Snow sheep *Ovis nivicola* French: Mouflon du Kamtchatka; German: Schneeschaf; Spanish: Carnero de Kamchatka	Horns heavy, to 44 in (111 cm) in males, curl out and around.Length 63–70 in (162–178 cm); weight 189–220 lb (86–100 kg), may reach 308 lb (140 kg) in autumn. Females are about half the weight of males.	Coastal escarpments, rugged parts of tundra mountains; usually below 4,260 ft (1,300 m); occasionally in forest edge in winter. Sedentary; males and females separate in summer, mixed groups in winter. Herds rarely over 20.	Northeast Siberia, from just north of Lake Baikal to Kamchatka.	Sedges, rushes, grasses, herbs, ferns, lichens, shrubs, and fruit. Fifty species known in the diet.	Not threatened

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Organizations

IUCN Species Survival Commission, Caprinae Specialist Group, Marco Festa-Bianchet, Chair. Department of Biology, University of Sherbrooke, Sherbrooke, Quebec J1K 2R1 Canada. Web site: <http://www.callisto.si.usherb.ca:8080/caprinae/iucnwork.htm>

David P. Mallon, PhD

Pholidota
Pangolins
(Manidae)

Class Mammalia
Order Pholidota
Family Manidae
Number of families 1

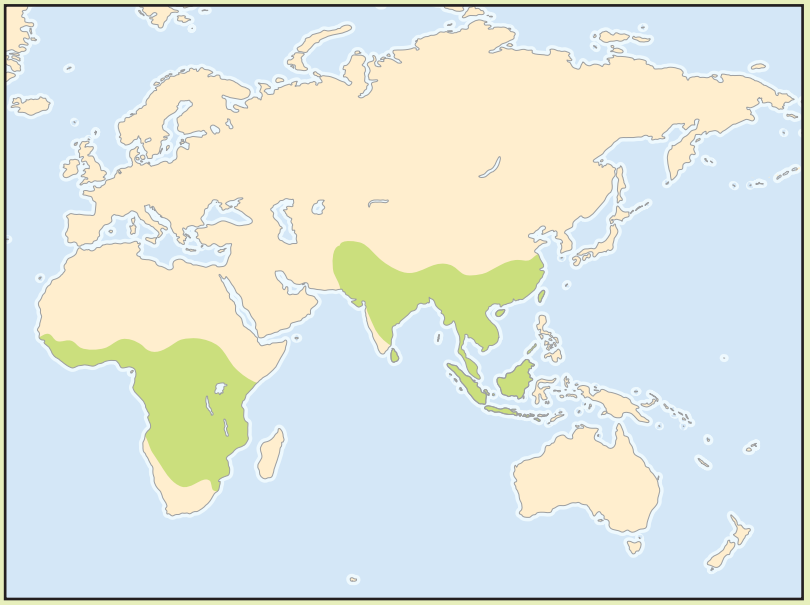
Thumbnail description
Mostly nocturnal ant- and termite-eating animals with a long and tapered body shape; they possess a unique body cover consisting of enormously overlapping scales that are movable and sharp edged (because of this they are also known as scaly anteaters); they have no teeth in their elongated heads but do have extremely long, protrusible tongues for catching prey

Size
Head and body length 12–35 in (30–90 cm), tail length 10–35 in (26–88 cm), and weight 2–77 lb (1–35 kg)

Number of genera, species
1 genus; 7 species

Habitat
Southern and Southeast Asia, tropical and subtropical parts of Africa

Conservation status
Lower Risk/Near Threatened: 4 species



Distribution
Tropics and transitional zones (subtropics) bordering the tropics to the north and south; sufficient numbers of ants and termites is paramount to survival, and is the overriding factor as to whether they will remain in a locality

Evolution and systematics

In Europe, the geological range of the order Pholidota is middle Eocene (about 45 million years ago [mya]) to Pleistocene (5–1.6 mya); in Asia, its range is Miocene (24–5 mya) to Present; in North America, it is early Oligocene (about 35 mya); and in Africa, middle Oligocene (about 30 mya) to Present. The order name Pholidota means "the scaled animal."

The origins of pangolins are largely unknown. Many of their current features (such as lack of adult teeth along with signs of primordial teeth in the embryo, chewing musculature and stomach, lack of zygomatic arch, elongated facial skeleton, worm-like tongue, forelimbs as digging tools, and prehensile tail) imply a long independent history. There is a general acceptance that they had an early separation from primitive mammals. By the Eocene era pangolins were highly specialized with such adaptations as horny scales, no teeth, and a diet of only ants and termites. The common name pangolin (possibly from Malayan or French words) refers to the animal's ability to curl up into a ball.

Physical characteristics

Pangolins have a similar shape to armadillos and anteaters. The African species are more specialized in almost every way than the Asian species. Males are usually larger than females, often 10–50% or more heavier. Pangolins are somewhat poikilothermic; that is, their body temperature directly varies with local temperature, with a low average body temperature of 89.9°F (32.2°C).

These strange reptilian-looking animals are distinct from all other Old World mammals by their unique covering of horny body scales (described as similar looking to shingles on a house roof, with all species often described as looking like "living pine cones"). The color, pattern, quantity, shape, and size of the scales differ across the seven species, and can also differ slightly within species, depending on the part of the body covered. They generally have 18 rows of overlapping (imbricate) scales around the body. The African and Asian species are distinguished by the row of scales on the tail. In all species, the row of scales is continuous to the tip of the tail, but the African species have a double row starting two-thirds of the way down to the tip. The scales and skin make up 20% or more of the body weight of most species, although on arboreal species the scales are lighter and thinner than those of the terrestrial species. The coloration of the scales includes dark brown, dark olive-brown, pale olive, yellow brown, and yellowish. Generally, the scales are bilaterally symmetrical, then flattened from the top down, and directed

A lion cub cautiously examines a pangolin, which is rolled up in its defensive posture. (Photo by George B. Schaller. Bruce Coleman, Inc. Reproduced by permission.)

towards the back of the animal. The number of scales remains the same throughout their life. When scales are lost due to wear they are replaced from the stratum germinativum (which provides for regeneration of cells) in the dermis (skin base). The process of scale replacement occurs when living cells (the epidermis) on the dermal papillae grow to the surface. The epidermis eventually cornifies (the converting of skin cells into horny material) in the depressions between the dermal papillae to make a loose stratum corneum. On top of and at the tip of the papillae, the processes of epidermal cornification lead to the formation of hard (horny) scales.

The scales protect every body part except for the underside of the head and the sides of the face, throat and neck, stomach, inner sides of the limbs, and on the snout and chin (and in some species on the outer surfaces of the forelegs). During the night the color of the scales is good camouflage. The parts of the body that are without scales are thinly covered with hair. The hair coloration is whitish, pale brown to russet, or blackish, and the skin is grayish with a bluish or pinkish tinge in some areas. There are three or four hairs present at the base of each scale in the Asiatic species, but there are no hairs at the base of the scales in the African species.

Pangolins possess small, short, but powerful limbs and each is tipped with sharp, clawed digits, with the middle digit being the largest. Their powerful front feet have large digging claws, while the shorter and stouter hind feet contain smaller claws. The digging claws of the front feet are folded upward so that the pangolins put down only the outsides of their soles. The limbs are used for digging into termite mounts and anthills. The terrestrial species also use their claws for scooping out underground burrows. In the arboreal species, the claw point grows over the finger and toe cushions. When running, all pangolins, whether arboreal or terrestrial, use primarily their hind legs. Terrestrial pangolins are able to move far distances in an erect position (without touching the ground with their front legs). In movement, they keep the body in a curved position; the tail is carried slightly above the ground and is used to maintain balance. Generally, arboreal pangolins have prehensile tails, while terrestrial ones possess semi-prehensile tails.

Pangolins have small, smooth, and tapered (conical) heads. The eyes are small, with no lubricating glands for the eyelids. The nose is fleshy and has nostrils. Depending on the species, the exterior ears may be reduced in size or absent. The skull moves smoothly into a short neck and later merges directly into the roundish body. The mouth opening (or slit) is constricted (narrowed) with an elongated snout. All species have a primitive cerebrum, and they lack a zygomatic arch or any bony crest for the attachment of muscles. Thus, the skull has few protrusions, cheekbones, bone ridges, or bone cams to

A pangolin (*Manis* sp.) drinking. (Photo by Michael Pitts/Naturepl.com. Reproduced by permission.)

which chewing muscles could be attached. The jaw contains no teeth (except for embryos that contain small primordial teeth, which eventually fall out). The underdeveloped halves of the lower jaw are reduced to thin strips of bone.

Pangolins are edenate; that is, instead of teeth, they use their tongue for foraging. The tongue is extraordinarily long and worm-like, and the salivary glands (which supplies the tongue with a tacky coating of saliva to which insects stick) are very large (measuring 22.0–24.5 in (360–400 cm) and are located in the chest. The tongue measures 6–7 in (16–18 cm) in the small species and about 16 in (40 cm) in the largest species, the giant pangolin. The tongue can be either round or flattened, depending on the particular species, and ends with a fine point. The tongue's average thickness is about 0.2 in (5 mm). When resting, the tongue is contained in a sheath supported by pliable cartilage rods that reaches from the back of the mouth to the pelvic region (the thoracic cavity) at the back of the lower belly. The muscles used by the tongue are attached to the xiphisternum (sternum).

There are 11–16 thoracid (chest) vertebrae, 5–6 lumbar (loin) vertebrae, 2–4 sacral (pelvis) vertebrae, and 21–47 caudal (tail) vertebrae. The lumbar vertebrae do not have articular processes. Pangolins have neither a clavicle nor a collarbone.

The muscular stomach is often called a "chewing apparatus" because pangolins swallow insects whole, where they are then chewed up in the stomach. This is accomplished in part by the stratified "pavement" epithelium, a horny skin layered (like pavement) on the posterior part of the stomach. Pangolins use this adaptation because the stomach must masticate the chitinous exoskeleton of insects (since they have no teeth in their mouths). Opposite to this epithelium is a muscular organ that is studded with horny teeth. Mucus glands and a large gastric gland also contribute to digestion. To also assist in digestion, pangolins swallow sand and stone bits in order to help the grinding action of the stomach.

The sword-like process of the sternum has undergone a modification in all pangolins in order to accommodate the large elongation of the tongue. In the Asian species, the sternum is fairly long (resembling a shovel) and ends in a laterally broadened disc. In the ground species, it forms a long cartilage rod extending to behind the end of the rib cage. In the African arboreal species (the long-tailed pangolin and the tree pangolin), it consists of two very long cartilaginous rods extending outside the diaphragm, first toward the rear and then arcing toward the head again.

The powerful tail is quite mobile, even though it is covered with scales. In the arboreal species it is considered fully prehensile (that is, it can be turned around either way, like a corkscrew) and is sometimes about twice the length of the body. The terrestrial species have a shorter, more blunt tail that is not considered fully prehensile. The mobility of tails assists the animals in climbing and supporting themselves when standing upright on the ground. The tail is sensitive at the tip, and can be hooked over a support such as a branch. It can also be used to strike out at an adversary, and when used along with its sharp scales can inflict much damage onto its enemies.

Pangolins can also spray attacking animals with a foul-smelling musky fluid from its bean-shaped perineal (anal) glands located in and around its posterior. These glands also play an important part in intraspecific (within the same species) relations throughout the animal's life. They provide important information concerning the psychophysiological

A close up view of a ground pangolin's (*Manis temminckii*) scales. (Photo by W. A. Sheppe/Mammal Images Library of the American Society of Mammalogists.)

The ground pangolin (*Manis temminckii*) eats mainly ants and termites. (Photo by © Peter Johnson/Corbis. Reproduced by permission.)

state of pangolins. For example, the scents prevent aggressive males from approaching each other too closely, helps facilitate the locating of a mate, and are important in mother-young relationships.

Males have a scrotum housed inside abdominal skin so as to avoid heat loss. Females possess two mammae with their auxiliary teats. The urine of pangolins has a pungent odor, and when dried it makes a whitish spot. The dung of pangolins is sausage-shaped and dry in texture. It is black in color when the diet consists mostly of ants, but brown when its main food is termites. Pangolins are often infested with external and internal parasites.

Distribution

Pangolins are found in tropical and subtropical areas south of the Sahara in Africa (excepting the southwest part of Africa), and in southern and southeastern Asia including India, Myanmar, Thailand, southern China, the Malay Peninsula and nearby islands, and through Indonesia to the Philippines.

Habitat

Depending on the species, they inhabit diverse habitat including tropical rainforests, subtropical and deciduous forests, grasslands, thick bush, wooded shrubby slopes, sandy areas, steppes, and open or savanna country. Whatever the area, it must contain ants and termites. They are creatures who usually roam within individual territories, when known, of 38–63 acres (15–25 ha) for males and 8–10 acres (3–4 ha) for females. Ground burrows are about 5.9–7.9 in (15–20 cm) in diameter, usually attain a depth of about 8 ft (2.5 m), terminate in round chambers as much as 6.6 ft (2 m) in circumference, and generally are closed off with dirt when occupied. Arboreal pangolins regularly travel between the ground level and upper layers of the jungle canopy ranging from 5–20 ft (1.5–6.1 m) above ground.

Behavior

Some species of pangolins, the larger ones, are classified as terrestrial (ground-dwelling) (*Manis gigantea*, *Manis temminckii*, *Manis crassicaudata*, and *Manis javanica*) while others, the smaller species, are classified as arboreal (tree-climbing) (*Manis pentadactyla*, *Manis tetradactyla*, and *Manis tricuspis*). Whether classified as terrestrial or arboreal, some species can dwell both on the ground and in trees.

All species of pangolins are nocturnal except for the predominantly diurnal *Manis tetradactyla*. Because pangolins are active mostly at night, they have poor vision. Their ability to

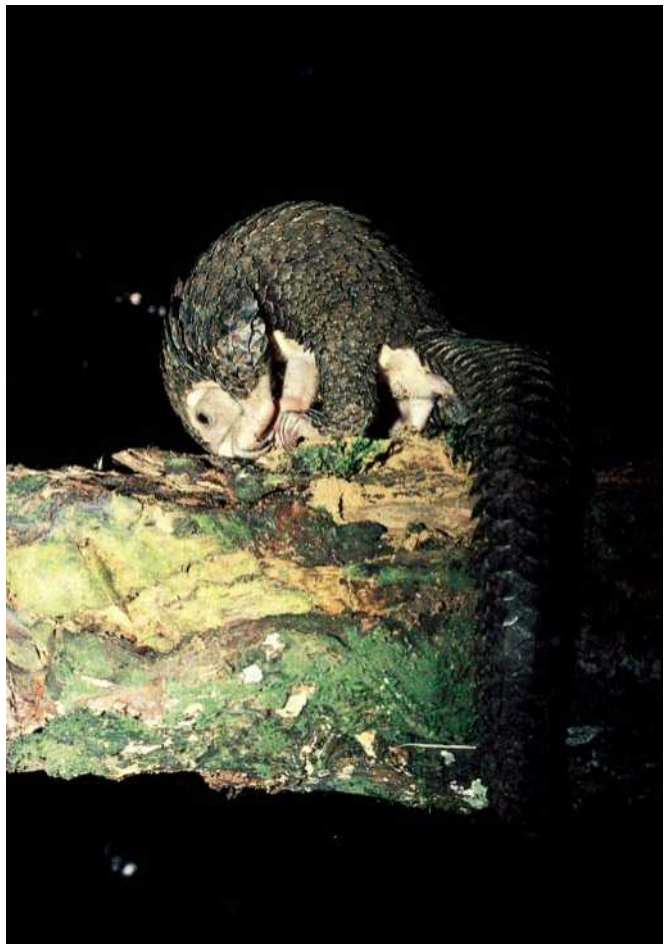
Pangolins may use their prehensile tails to anchor themselves in a tree while they break open termites' tree nests. (Photo by A. Blank/ Photo Researchers, Inc. Reproduced by permission.)

hear is only average, and is used little in intraspecific relationships. They make no well-distinguished sounds; with the only noticeable utterances being hisses and snorts. However, large olfactory lobes allow their sense of smell to be exceptionally sharp, playing the major role in finding food and, in all likelihood, playing a major role in intraspecific communication. They have very few expressive behaviors, the most frequent being the closing of the eyes and the sticking out of the tongue. Pangolins are generally shy, solitary, and unsociable creatures who only rarely associate with a conspecific.

Panglolins are slow and deliberate movers. Most are good climbers, and some also swim. The terrestrial species will rest and sleep during the day in burrows that they have previously dug (or those dug by other animals), while the arboreal species find haven in hollow trees. For additional protection from small- and medium-sized enemies, they roll up (basically) into a ball when sleeping. They do not actively defend a fixed territory from neighboring animals of the same species. However, they do repeatedly mark selected trees, branches, and rocks with secretions from their anal glands and urine, which announces to neighboring and trespassing animals that the area is already occupied. The terrestrial species regularly mark their territories with droppings, and arboreal species may do so as well.

All species can move quickly when alarmed. If unable to reach shelter, they will often curl into a tight ball with their scaled limbs and tail protecting the soft under-parts. When in this position the sharp-edged scales are erected as protective armor. Movements of the scales and twitches of the tail apparently deter predators. They do not appear to use their fore-claws in defense. The animals will also expel urine and posterior gland secretion in defense of their immediate safety. Often a stream of urine is released if a pangolin is unrolled by force. Feces may also be released, which is often combined with secretion from the anal glands.

Pangolins are plantigrade; that is, they walk on the soles of their feet with heels touching the ground. When they walk on all four limbs their toes are doubled under and the tips of the long nails are placed on the ground. The large digging claws of the forefeet are held inward by terrestrial species, which walk on the outer sole. The arboreal species bend the claw downward when traveling on the ground. In walking on the ground, primarily the hind limbs are used. They stop periodically and raise themselves up, supporting themselves on



A pangolin searches for insects in the Democratic Republic of the Congo (Zaire). (Photo by K & K Ammann/Photo Researchers, Inc. Reproduced by permission.)

Ground pangolins (*Manis temminckii*) live in central Africa to northern South Africa. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

their hind legs and tail. In this position, with the front of the body erect and the head protruding, they smell or look out for possible enemies. At a fast pace, the tail is lifted from the ground.

The giant pangolin (*M. gigantea*), ground pangolin (*M. termminckii*), long-tailed pangolin (*M. tetradactyla*), and tree pangolin (*M. tricuspis*) are all good swimmers, holding only the head above water while swimming with a "doggy paddle" motion. They are able to cross narrow rivers easily, but tire on longer journeys.

Feeding ecology and diet

Pangolins are insectivorous, with a very limited diet almost exclusively of insects, mostly termites and ants (and some soft-bodied insects and larvae) that are located by scent. The larger species sometimes eat larger insects. Variations in diet may be due to the availability of local supplies or on seasonal variations. Pangolins show a strong preference for particular species of ants and termites to eat, often rejecting all others. All species drink water regularly, lapping it up with their tongue in a flicking motion.

Pangolins developed special adaptations because of their particular diet. Live insects are caught with their long, proboscis-like tongue, which is sheathed in a special membrane attached to the pelvis. The tongue is about 27 in (70 cm) long when it is fully extended from its mouth. The tongue remains coiled up in the animal's mouth when at rest. In preparation to catch prey, pangolins will secrete viscous saliva from special glands in the abdomen onto the tongue. When the tongue is darted into the chambers of a mound, the sticky tongue will trap insects living inside. Since they have no teeth, all food is crushed in the lower section of the stomach that leads to the intestines. This area normally contains small pebbles that function to crush food. While eating, thickened membranes protect the eyes of pangolins from insects, and special muscles seal its nostrils and ear openings to shield it from the bites of ants. Ants that reach the scales are often shaken off.

Terrestrial pangolins scrape funnel-shaped holes around a termite hill until they find termites. They do this by using their tail and hind legs as a "tripod," digging with their front feet. With the feet held close to the right and left sides of the head, the claws tear open the insect nest. The snout gradually penetrates the mound. With its long, sticky tongue, the animal catches the insects with fast movements. The termite hill is seldom destroyed completely, so pangolins will return to the same termite hill after the remaining insects have rebuilt the hill. When pangolins locate old

animal droppings containing termites, they take the pellets with their forelimbs and turn over onto their backs. They then hold the dropping between their claws above its stomach, and raise their head and lick off the termites. Arboreal pangolins often break up tree nests by anchoring themselves in the branches with their hind legs and prehensile tail. The claws of the forefeet then dig precisely to the left and right of the mouth, which slowly advances into the cavity formed in the nest. The worm-like tongue is constantly stabbing into the narrow passages of the termite nests. Strictly tree-dwelling pangolins hunt and feed only in the nests of arboreal termites, unable to break open the nests of ground termites. They might eat ground termites, however, if another animal has previously opened the nest.

Reproductive biology

Female pangolins have a bicornuate uterus (a heart shaped uterus with two horns) and two pectoral (breast) nipples. Males have inguinal (near the groin) testes. Several research studies suggest that some populations are capable of breeding throughout the year but most species are believed to be born between November and March. The gestation period is 120–150 days. Females usually give birth to one young, sometimes two, and rarely three, with a birth weight of 3–18 oz (90–500 g). Newborns have soft scales that do not overlap. The scales are lighter in color than in the adult, and harden after a couple of days.

There is no reliable information available on weaning or sexual maturity, but weaning is believed to begin at three months and sexual maturity believed to occur at two years. While sleeping and when alarmed, the mother rolls up around the young, which also rolls up. Beginning in the first few days, the baby makes short excursions with the mother, riding at the base of the tail or on the back and grabbing onto the scales. The mother will occasionally leave the baby behind on a branch, while feeding, and then pick it up later. The juvenile first eats insects found between the mother's scales, and later picks insects while the mother is breaking open a nest. Closer to maturity, it will dig for itself. At five months of age, the youngster will leave its mother. Females will readily take over orphans of other females. Males share a burrow with females and young ones. Life span in the wild in not known, but they can live up to 12 years in captivity. The mating system is not known.

Conservation status

The Indian pangolin (*Manis crassicaudata*), Malayan pangolin (*Manis javanica*), Chinese pangolin (*Manis pentadactyla*), and ground pangolin (*Manis temminckii*) are listed as Lower Risk/Near Threatened by the IUCN. Sanctions often apply to trade in pangolins and their products. Much of their habitat is being depleted due to the eroding of tropical rainforests and other areas. Their main threats are humans, large cats (especially leopards, lions, and tigers), hyenas, and pythons. The population densities and territorial ranges of all pangolins continue to decline.

Significance to humans

All species are hunted and trapped for their meat, which is often a favorite delicacy of indigenous people, and for their skins and scales, which are involved in international trade. Their scales are often used for adornment and good-luck charms; for example, they are made into rings and used as charms against rheumatic fever. In Asia, powdered scales are believed to be of medicinal value. The Chinese people have extensively hunted pangolins because the animal's scales are traditionally thought to contain medicinal attributes, such as an antiseptic in fighting fever and skin disease. Its skin is thought to be an aphrodisiac by some hill tribes.

1. Long-tailed pangolin (*Manis tetradactyla*); 2. African tree pangolin (*Manis tricuspis*); 3. Malayan pangolin (*Manis javanica*); 4. Indian pangolin (*Manis crassicaudata*); 5. Chinese pangolin (*Manis pentadactyla*); 6. Giant pangolin (*Manis gigantea*); 7. Cape pangolin (*Manis temminckii*). (Illustration by Brian Cressman)

Species accounts

Chinese pangolin
Manis pentadactyla

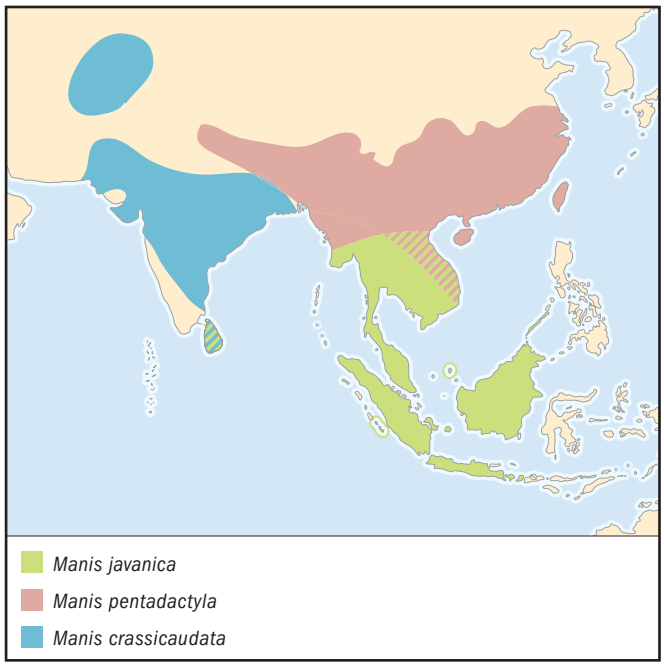
SUBFAMILY
Maninae

TAXONOMY
Manis pentadactyla Linnaeus, 1758, Taiwan.

OTHER COMMON NAMES
French: Pangolin de Chine; Spanish: Pangolín chino.

PHYSICAL CHARACTERISTICS
Chinese pangolins have a head and body length of 21–32 in (50–80 cm), a tail length of 10–16 in (26–40 cm), and a weight of 4–20 lb (2–9 kg). They have about 18 rows of overlapping scales. The yellow-brown scales are bony, up to 2 in (5 cm) across, and encompass all of the body (including the tail) except for its snout, cheeks, throat, inner limbs, and belly. They have hairs at the base of the body scales. Their limbs are slender with comparatively long and sharp claws, an important aid in climbing. Chinese pangolins have a small, pointed head, a very round body, and a narrow mouth. The nose is fleshy and has nostrils at the end, and the thin tongue, as long as 16 in (40 cm), scoops up ants and termites. Their small, external ears are better developed than are those of the other pangolins. The strongly prehensile tail and long claws make this pangolin very agile in trees and a powerful burrower.

DISTRIBUTION
Westward through Nepal, Assam and Sikkim (in northeastern India), eastern Himalayas, Myanmar, northern Thailand and Indochina, southern China, Taiwan, and Hainan.



HABITAT
They inhabit subtropical and deciduous forests and grasslands. Burrows are often built adjacent to termite nests and extend further below the surface during the cold winter months. During the summer months they sometimes occupy burrows for just a few days. It is unclear whether the winter burrow is maintained during warmer months. Although predominantly a terrestrial species, it has been observed in the jungle canopy up to 20 ft (6 m) above the ground.

BEHAVIOR
Chinese pangolins are extremely shy, and are very agile tree climbers. They are classified as arboreal and often hang by the tip of their tail. Chinese pangolins generally are not aggressive, but males can fight over mating rights. They dig tunnels up to 9 ft (3 m) long (sometimes in as little as 3–5 minutes) that terminates in a den. The den is closed off while they are inside. They swim rapidly with undulating movements. When rolled into a ball, no soft areas are exposed.

FEEDING ECOLOGY AND DIET
They feed primarily on the ground, mostly digging for termites and ants with its strongly clawed feet. Their range corresponds to those of its preferred subterranean termite species *Coptotermes formosanus* and *Cyclotermes formosanus*. They forage through a surrounding area that is about 165–330 ft (50–100 m) in circumference, and then move onto another area when food becomes scarce.

REPRODUCTIVE BIOLOGY
Males fight violently over females. Mating occurs during a 3–5 day period in late summer or early autumn. Young are born in a winter burrow, and emerge with the mother in the spring. The gestation period is unknown, but in Nepal, Chinese pangolins were found to reproduce during April and May. Females give birth to 1–2 young at a time. Birth weight and head-and-body length are generally unknown but have been reported to be about 1 lb (0.5 kg) and about 18 in (45 cm) respectively. Scales in young animals are purplish brown. When a baby Chinese pangolin nurses, the mother lies on her back or side. While resting, she holds the baby pressed to her abdomen. Young are able to walk at birth, but are carried on the mother's tail or back. When the mother is feeding, the offspring is left alone. Weaning, sexual maturity, and life span are unknown. Males have been observed to exhibit good parental instincts and share a burrow with the female and young.

CONSERVATION STATUS
Lower Risk/Near Threatened. Their main enemies are humans, large cats (especially leopards, lions, and tigers), hyenas, and pythons. They live in many protected forests throughout their range. Land development often threatens unprotected habitats.

SIGNIFICANCE TO HUMANS
Chinese pangolins are hunted for their meat, which is considered a delicacy in many areas such as Vietnam and Hong Kong. ◆

Indian pangolin
Manis crassicaudata

SUBFAMILY
Maninae

TAXONOMY
Manis crassicaudata Gray, 1827, India.

OTHER COMMON NAMES
English: Thick-tailed pangolin; French: Grand pangolin de l'inde; Spanish: Pangolín indio.

PHYSICAL CHARACTERISTICS
Indian pangolins have a head and body length of 2.0–2.2 ft (60–65 cm), a tail length of 1.5–1.8 ft (45–55 cm), and a weight of 17.6–19.8 lb (8–9 kg). Male Indian pangolins may be as much as 90% heavier than females. They have large, pale yellowish brown or yellow-gray scales, with brownish skin and hair; with about 14–16 rows of scales on the tail. Scales make up about one-fourth to one-third of body weight. The head is small and triangular in shape, and the body is slender and long. They possess small, undeveloped, external ears, have a scale-clad tail, and also have hairs at the base of the body scales. Each limb contains five powerful claws that are adapted for digging burrows or locating their prey's nests. They have no teeth so their two-chambered stomach crushes all their food. The tongue is 9–10 in (23.0–25.5 cm) long, and is their main way to capture food. Because the tongue is so long they have muscular attachments extending all the way to the pelvis.

DISTRIBUTION
India, Nepal, Pakistan, Bangladesh, and Sri Lanka.

HABITAT
They prefer hilly regions and plains, mostly in tropical areas. The species has been seen in tropical rainforests, subtropical thorn forests, plains, and the lower slopes of mountains. Burrows range in depth and depend on soil type. Soft soils will allow the animal to dig burrows about 20 ft (6 m) deep, while rocky, hard soils will allow depths of about 6 ft (2 m). They usually close the burrow entrance with loose soil when they are inside, which hides the entrance from predators..

BEHAVIOR
Indian pangolins are largely nocturnal, sleeping and resting in burrows or among rocks during the day. They are predominantely terrestrial but also have great agility for climbing with their prehensile tail and sharp claws. They are good diggers, often making tunnels that end in an enlarged cave. Indian pangolins live mostly alone with the exception of the mating and breeding season, when adult male and female pangolins are found in the same burrow. They protect themselves from predators by curling up into a ball, exposing only its scales. Anal glands emit a foul smelling, yellow fluid for additional defense against enemies.

FEEDING ECOLOGY AND DIET
Indian pangolins eat termites, ants, termite and ant eggs, and other insects from ground mounds and hills.

REPRODUCTIVE BIOLOGY
Their gestation period is about 65–70 days. Births may occur throughout the year, with births having been recorded in January, March, July, and November. Females give birth to 1–2 young at a time. Weight at birth is 8.2–8.6 oz (230–240 g). Scales of young are soft, with fully functioning eyes and legs. At about one month of age, young are carried on the dorsal base of the mother's tail when foraging. At about three months of age the young are (believed to be) weaned. Sexual maturity and life span in the wild for Indian pangolins are unknown.

CONSERVATION STATUS
Lower Risk/Near Threatened, and listed on CITES Appendix I. Their main enemies are humans, large cats (especially leopards, lions, and tigers), hyenas, and pythons.

SIGNIFICANCE TO HUMANS
They are hunted for meat, especially in Pakistan because some of their body parts are used for medicinal purposes. Scales are thought to be an aphrodisiac, and often used to make necklaces and shoes. ◆

Malayan pangolin
Manis javanica

SUBFAMILY
Maninae

TAXONOMY
Manis javanica Desmarest, 1822, Java, Indonesia.

OTHER COMMON NAMES
French: Pangolin javanais; Spanish: Pangolín malayo.

PHYSICAL CHARACTERISTICS
Mayalan pangolins have a head and body length of 1.6–2.0 ft (50–60 cm) and a tail length of 1.6–2.6 ft (50–80 cm). Their weight is unknown. They have amber-yellow to blackish brown scales, with whitish skin and fine, light hairs at the base of the body scales. The species possesses small, undeveloped, external ears and a scale-clad tail.

DISTRIBUTION
Myanmar, Thailand, Indochina, Malay Peninsula and many small nearby islands, Sumatra and Nias and Pagai islands to west, Bangka and Belitung islands, Java, Bali, Borneo, Palawan and Culion islands (Philippines), and Lombok.

HABITAT
This species prefers sandy open country.

BEHAVIOR
Malayan pangolins are nocturnal, and are predominantely terrestrial but also like to climb. During the day they sleep, often curled up in forked branches, in ferns, or in other plants growing on trees. They move with agility both on the ground and in trees. They are also able to hang by the tip of their tail.

FEEDING ECOLOGY AND DIET
Some zoologists report that they eat mostly termites, while others say that their primary food is ants and their pupae.

REPRODUCTIVE BIOLOGY
Their gestation period is unknown. Females give birth to 1–2 young at a time. Weight at birth is unknown. Weaning, sexual maturity, and life span are unknown.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
They are hunted for meat. ◆

Giant pangolin
Manis gigantea

SUBFAMILY
Smutsiinae

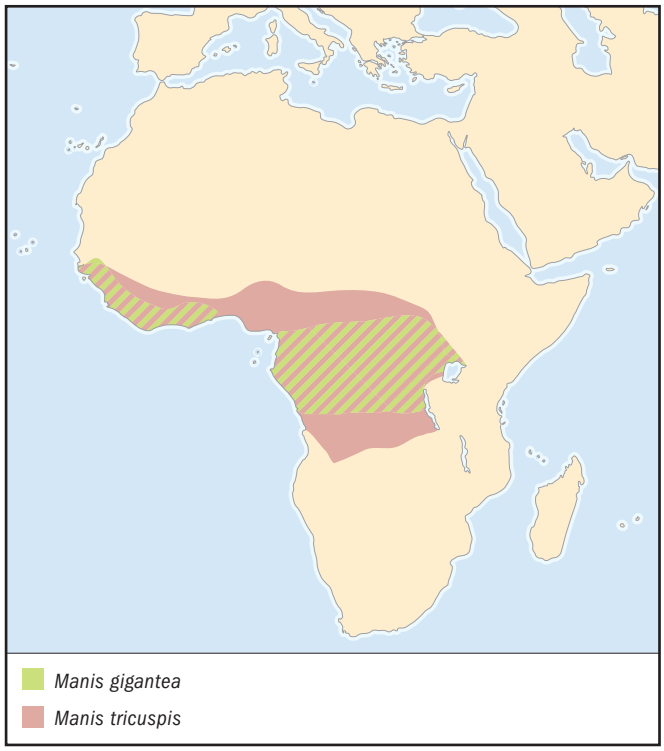
TAXONOMY
Manis gigantea Illiger, 1815, type locality not known.

OTHER COMMON NAMES
French: Pangolin géant; Spanish: Pangolí gigante.

PHYSICAL CHARACTERISTICS
Giant pangolins have a head and body length of 30–36 in (75–90 cm), a tail length of 18–30 in (50–80 cm), and a weight of 55–80 lb (25–35 kg). The female is smaller than the male. They are strictly ground dwelling (terrestrial) animals with broad sole cushions and blunt claws on the hind feet, and with forefeet containing large digging claws. The species is the largest of the order Pholidota. They have large grayish brown scales, with whitish skin and sparse hairs. The tongue measures the longest of the seven species, at about 16–27 in (40–70 cm), and can be pushed out 14–16 in (36–40 cm). The salivary glands, which supply the tongue with tacky saliva to which ants and termites adhere, are the size of goose eggs. They do not have external ears, have scales on the tail (but do not have scales beneath the tail), and have a breastbone that is very long.

DISTRIBUTION
Along the equator in Africa, from Senegal to Uganda and Angola.

HABITAT
Giant pangolins prefer tropical rainforests, but will also inhabit forests and savannas. They do not occupy high altitudes. They usually live near water. Burrows may be up to 16 ft (5 m) deep and 130 ft (40 m) long.



BEHAVIOR
They are nocturnal and ground-dwelling (terrestrial) animals, being active mainly between midnight and dawn when searching for food. Giant pangolins generally are observed singly, but pairs can be found with young. Terrestrial burrows are dug in which to sleep inside during the day. They often dig around large termite nests, both above and below the ground, using powerful fore-claws. The species uses slow and deliberate movements. When walking on all four legs, they curl in their front paws to protect the sharp front claws, actually walking on the outside of the wrists rather than on the palms. They can walk only on the hind limbs, with the help of their long tail for balance. Giant pangolins often hide inside or under stilt or platform roots of large trees.

If threatened, giant pangolins will often roll themselves into a ball, a technique that protects themselves against most enemies. If necessary, they will lash out against enemies with their sharp-scaled tail and spray urine and anal gland secretions. If near water, they will plunge into the water, rather than roll up, where they can stay underwater for considerable time, either swimming below the surface or walking along the bottom. At times a giant pangolin may rise on its hind legs and even attempt to defend itself by waving its immense fore-claws at its adversary. Unfortunately, with poor eyesight and hearing, they usually have problems identifying where their possible attackers are located.

FEEDING ECOLOGY AND DIET
They have a limited diet, feeding mostly on termites and ants but also sometimes eating larger insects. Their large digging claws enable them to tear open the subterranean and mounds-type nests made by ground termites. They may eat up to 200,000 ants in a night, with a stomach capacity of 0.5 gal (2 l). A ready access to drinking water is a necessity.

REPRODUCTIVE BIOLOGY
The gestation period is about five months. Females give birth to one young at a time. Young are usually born in an underground nest. Weight at birth is 14.2–17.8 oz (400–500 g). Newborns have soft scales, which will harden in several days. Newborns cannot walk on their legs, but are active and can crawl around on their stomachs. They will accompany their mother on feeding trips, often sitting on the base of her tail. Weaning, sexual maturity, and life span are unknown.

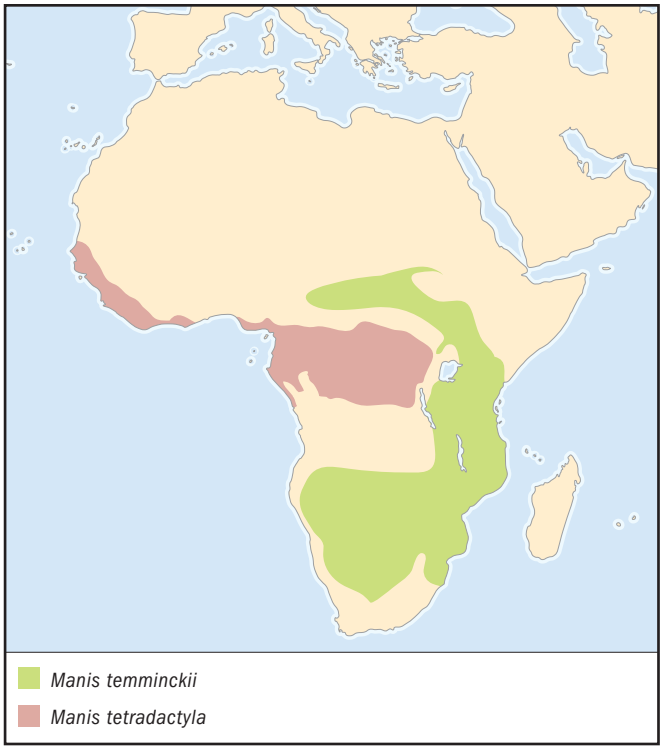
CONSERVATION STATUS
Not threatened, but deforestation for timber, agricultural development, and urban development have decreased the size of their habitat.

SIGNIFICANCE TO HUMANS
They are hunted for meat, however in some tribes its meat is forbidden to be eaten. ◆

Ground pangolin
Manis temminckii

SUBFAMILY
Smutsiinae

TAXONOMY
Manis temminckii Smuts, 1832, northern Cape Province, South Africa.



OTHER COMMON NAMES
English: Cape pangolin, South African pangolin, Temminck's ground pangolin, scaly anteater; French: Pangolin de Temminck; Spanish: Pangolín del cabo.

PHYSICAL CHARACTERISTICS
Ground pangolins have a head and body length of 20–24 in (50–60 cm), a tail length of 14–20 in (35–50 cm), and a weight of 33.0–39.6 lb (15–18 kg). (Ground pangolins are similar in most respect to Chinese pangolins.) They do not have external ears, have scales on the tail (but do not have scales underneath the tail), and the rear part of the breastbone is very long. The hind feet have broad sole cushions and blunt claws, and the forefeet contain large digging claws. Their sharp scales are large and moveable, with colorations of grayish brown to dark brown. Scale coloration helps them to blend into many different surroundings. The skin is whitish with fine, dark hairs. Ground pangolins have small, pointed heads and small eyes that are protected by specialized thick eyelids. They bury their feces in small depressions that it scrapes in the ground.

DISTRIBUTION
From Chad and Sudan in central Africa, south through Kenya and Tanzania, to Namibia and the northern parts of South Africa.

HABITAT
Ground pangolins prefer steppes, prairies, thick brush, open grasslands, and savannas with both high and low rainfall amounts. They show little territorial behavior. Burrows are usually about 6–8 in (15–20 cm) in diameter, and extend several feet (meters) underground.

BEHAVIOR
Ground pangolins are nocturnal, ground-dwellers (terrestrial) animals that occasionally climb bushes and trees. They are solitary animals, only joining together during mating. The species dig burrows inside which to sleep during the day. Ground pangolins move rapidly over the ground, sometimes up to 160 ft (50 m) per minute. They often halt, rise with the support of the tail, sniff the air, and look for possible predators.

FEEDING ECOLOGY AND DIET
They tear open termite mounds and ant nests, both in trees and on the ground, with their large claws, and lick up insects and their larvae. They are selective in what species of termites they eat. The termites of the genera *Amitermes*, *Ancistrotermes*, *Macrotermes*, *Microcerotermes*, *Microtermes*, *Odontotermes*, and *Trinervitermes* are most often eaten by first detecting (with their keen sense of smell) these preferred genera before opening the hill.

REPRODUCTIVE BIOLOGY
Males may fight for the opportunity to mate. Females breed at any time of the year, even if they are still rearing other young. The gestation period is about 120–140 days. Females give birth to one, sometimes two, young at a time. Young are born in ground dens. Birth weight is 10.7–14.2 oz (300–400 g). They are carried outside on the mother's back or tail at 2–4 weeks of age. Young will begin to feed on their own by three months of age, but are still carried until they weigh about 7 lb (3 kg). Weaning, sexual maturity, and life span are generally unknown.

CONSERVATION STATUS
Lower Risk/Near Threatened. This species is very vulnerable to population decreases because of its great economic value to humans and habitat loss to agriculture.

SIGNIFICANCE TO HUMANS
They are often killed for their flesh and scales. Ground pangolins are called *bwana mganga* "bwana doctor" in East Africa because every part of their body is said to possess healing properties. ◆

Long-tailed pangolin
Manis tetradactyla

SUBFAMILY
Smutsiinae

TAXONOMY
Manis tetradactyla Linnaeus, 1766, West Africa.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Long-tailed pangolins have a head and body length of 12–16 in (30–40 cm), a tail length of 22–28 in (55–70 cm), and a weight of 2.6–5.5 lb (1.2–2.5 kg). They are the smallest of the order Pholidota. The scales are dark brown in color with yellowish edges. Nine to 13 rows of scales encompass the entire top of the species. Their hair is dark brown to black. They have a very long, prehensile tail, the longest tail of all of the species and almost two-thirds of its entire body length. There is a short, bare patch at the tip of the tail. This species possess 46–47 caudal vertebrae, the largest number of all mammals. They do not have external ears, have scales on the tail (but do not have scales underneath the tail), and the rear part of the breastbone is very long. The sternum consists of two extraordinarily long cartilaginous rods extending outside the diaphragm,

first toward the rear and then arcing toward the head again. They have short, thick limbs and digits with long curved claws.

DISTRIBUTION
From Senegal to Uganda and Angola.

HABITAT
They prefer tropical rainforests, and not the edges of forests. Their territory is restricted within the forest canopy, but it is unknown if they maintain a home territory.

BEHAVIOR
They are the only species of pangolin that is not nocturnal: they are predominantly diurnal, eating during the day. They are very good climbers (arboreal), able to easily scale vertical tree trunks. Contact with the ground is rare. They climb with the front legs gripping the tree simultaneously, and with the body curved. The hind feet are then loosened up and are anchored close behind the front feet. With the hind feet and the tail giving the body necessary support, the front feet grip the bark further up. They are also able to hang by the tip of their tail. When hanging by its tail and wanting to resume climbing, they will often climb up their tail. They sleep in hollow trees, liana curtains, forks in trees, or epiphytes (plants growing on trees), often rolled up in the shape of a ball. The animals often sun themselves while stretched out on a tree limb or branch.

FEEDING ECOLOGY AND DIET
They eat mostly ants, preferring tree ants of the genera *Camponotus*, *Catalacus*, and *Crematogaster*. They will seek the soft, hanging nests of ants and termites, or will attack the ant columns that move among the leaves.

REPRODUCTIVE BIOLOGY
It is believed that they breed throughout the year. When mating, the male and female will intertwine tails and face each other ventrally. The gestation period is unknown. Females give birth to one young at a time. Birth weight is 3.6–5.4 oz (100–150 g). The young will ride on the mother for up to three months. Weaning and life span are generally unknown, and sexual maturity is thought to be around two years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
They are hunted for meat. ◆

Tree pangolin
Manis tricuspis

SUBFAMILY
Smutsiinae

TAXONOMY
Manis tricuspis Rafinesque, 1821, West Africa.

OTHER COMMON NAMES
English: African tree pangolin, small-scaled pangolin, three-pointed pangolin, white-bellied pangolin.

PHYSICAL CHARACTERISTICS
Tree pangolins have a head and body length of 13.75–17.75 in (35–45 cm), tail length of 19.3–23.5 in (49–60 cm) 16–20 in (40–50 cm), and weight of 3.9–5.3 lb (1.8–2.4 kg). Pangolin scales are comparatively small, with a brown-gray to dark brown color. Their distinctive dorsal scales have three fairly pronounced points (hence the name "tricuspis") on the free edge. The scales are often worn down in older individuals. They have white skin and hair; do not have external ears, have scales on the tail (but do not have scales beneath the tail), and have a very long rear part of the breastbone. Their limbs are slender with comparatively long claws, an important aid in climbing, as is their very long prehensile tail. They sleep during the day on branches of trees or in holes, which they dig out of the ground. They emerge at night to feed. The sternum consists of two extraordinarily long cartilaginous rods extending outside the diaphragm, first toward the rear and then arcing toward the head again. The long sternum is an adaptation to accommodate the animal's extremely elongated tongue. The intestine of the tree pangolin is about 6 ft (2 m) long. They drop their feces anywhere. Body temperature fluctuates between 86–95°F (30–35°C), primarily due to the outdoor temperature.

DISTRIBUTION
From Senegal to western Kenya, and south to Angola and Zambia.

HABITAT
They prefer tropical rainforests, sometimes living along the forest edges and the savannas in the southern parts of Congo (formerly Zaire) and in Zambia. The territory of males covers 37.5–62.5 acres (15–25 hectares), while the territory of females covers 7.5–10.0 acres (3–4 hectares); both generally in the lower strata of the forest.

BEHAVIOR
Tree pangolins are nocturnal and truly arboreal. With the aid of a very prehensile tail they climb with the front legs gripping the tree and with the body curved; the hind feet are then loosened up and are anchored close behind the front feet; and with the hind feet and the tail giving the body support, the front feet grip the bark further up. They are also able to hang by the tip of their tail. When hanging by its tail and wanting to resume climbing, they will climb up the tail, placing its gripping claws between the side scales of its tail. They climb down head first, in the same way as going up. Rest periods are spent in hollow trees, epiphytes, or excavated termite hills. Sleeping places are usually located 30–40 ft (10–15 m) above the ground, and they sleep rolled up in the shape of a ball. They spend most of their active time searching for termites on the ground.

Females are active for 3–4 hours every night and usually travel an average of 1,300 ft (400 m) in one night. They follow zigzag or circular courses, usually returning to their previous shelter. As a result, females usually only utilize a portion of their territory. Because of this pattern (and because of markings left by secretions of the posterior glands), different females rarely meet. If a female should locate fresh markings of another female, she will return to her own territory. Males are active for 2–10 hours every night and travel an average of 2,200 ft (700 m) in one night. Males use much more of their territory each night, with their paths being longer and straighter. This pattern allows males to encounter females more frequently. As a result male territory overlaps several female territories. During the rainy season they may become inactive for several days.

Tree pangolins move rapidly over the ground, sometimes as fast as 180 ft (60 m) per minute. They often stop, rise with

the support of the tail, sniff the air, and search for enemies. When sensing an enemy they often climb trees until the danger has passed.

FEEDING ECOLOGY AND DIET

They feed on ground and tree ants and termites, preferring tree ants of the genus *Nasutitermes* and *Microcerotermes*, and ignoring ground ants such as *Crematogaster*. The quantity of insects consumed daily is 5–7 oz (150–200 g) with 3–4 hours of daily foraging for females and up to 10 hours for males. Their stomach can hold up to 0.5 gal (2 l) of insects. They use their powerful forelimbs to sweep up insects with swift movements of their long tongues. They drink water often.

REPRODUCTIVE BIOLOGY

When a female is ready to mate, both female and male will intertwine during mating, and the pair will lie ventrally opposed. The gestation period is about 140–150 days. Females give birth to one young at a time. Birth weight is 3.2–5.4 oz (90–150 g). The weaning period takes about five months. Sexual maturity and life span are unknown. The young will crawl up on the mother immediately after birth in order to find her pectoral nipples. They are able to hold on by the claws of the forefeet, either to the mother or to a limb. At this time, they are unable to walk, but will use their tail to cling to the mother.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

They are important to local indigenous people for its meat. The scales are thought to have medicinal value in the form of antiseptic to counter fever and skin disease by Chinese cultures. Their hide is used for making shoes and other leather goods.

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Rodentia
(Rodents)

Class Mammalia
Order Rodentia
Number of families 28
Number of genera, species 443 genera; 2,021 species

Photo: A Malagasy giant rat (*Hypogeomys antimena*) emerges from its burrow. (Photo by Harald Schütz. Reproduced by permission.)

Evolution and systematics

Of the 4,629 species of mammals recognized by Wilson and Reeder, rodents represent 43% of species diversity within the class Mammalia. Several diagnostic characteristics associated with general morphology define rodents as a monophyletic group (e.g., group sharing a common ancestry). The primary characteristic is the pair of long incisors, resulting from the loss of canines and the creation of a diastema or gap between the incisors and cheek teeth, consisting of premolars and molars. Other characteristics of the skull and skeleton, dentition, and basic soft anatomy tend to support monophyly. Although the monophyly of Rodentia appears well supported on the basis of examinations of morphological traits of living forms as well as fossil lineages, several studies based primarily on amino acid sequence data from nuclear genes and some limited analysis of nucleotide sequence data have suggested that the order Rodentia is not monophyletic. According to these molecular studies, the guinea pig and its relatives group closer with other orders of mammals than they do to families of rodents, especially rats and mice of the family Muridae. However, as more extensive molecular studies have been initiated and more sophisticated analyses that take into account complex patterns of variation within rodents have been performed, molecular support for rodent monophyly has been forthcoming.

The order Rodentia presents some serious problems with respect to classification, especially the recognition of suborders. As specializations in rodents tend to focus on the masticatory apparatus (e.g., structure of the lower jaw, shape of the infraorbital foramen on the anterior end of the skull, and placement of musculature associated with jaw action), early classifications were based on the origin and insertion of jaw muscles (e.g., masseter muscles) and the arrangement of changes in portions of the skull associated with this musculature. Therefore, the more basic classifications focus on either changes in the infraorbital foramen and the placement of masseter muscles or structure of the lower jaw. Using these characteristics, the number of recognized rodent suborders has varied, depending upon the proposed classification scheme, from three (Sciuromorpha, squirrels; Myomorpha, rats and mice; and Hystricomorpha, guinea pigs and relatives) to as many as 16. Considering that the origin and insertion of jaw muscles and the structure of the skull relate directly to feeding, these features reveal high levels of parallel evolution (similar features independently derived). Molecular data, derived from nucleotide sequences, have confirmed the fallacy of using features that tend to converge in structure in response to similar functions. As a consequence of problems related to the origin and insertion of jaw muscles and modifications of the skull to accommodate such changes, the most consistent morphological feature is associated with the lower jaw. Based on this feature, two suborders of rodents can be identified, Hystrocognathi and Sciurognathi. The former suborder contains South American caviomorph rodents (guinea pigs and their relatives) and several Old World families including porcupines (Hystricidae), cane rats (Thryonomyidae), African mole-rats (Bathyergidae), and African dassie rats (Petromuridae). The remaining rodent families are placed in Sciurognathi.

In many cases, the phylogenetic relationships among families and genera of rodents are still controversial. Based on morphology and recent molecular data, families in the suborder Hystricognathi appear most closely related to the gundis of the family Ctenodactylidae. Several additional groups sharing a common ancestry appear to be well supported including: rats and mice of the superfamily Muroidea (families Muridae and Dipodidae); pocket gophers (family Geomyidae) and pocket mice and kangaroo rats (family Heteromyidae) of the superfamily Geomyoidea; squirrels (family

The South American bush rat, or degu (*Octodon degus*). (Photo by J-C Carton. Bruce Coleman, Inc. Reproduced by permission.)

Sciuridae) and mountain beavers (family Aplodontidae). The placement of other families like the Castoridae (beavers), Pedetidae (springhares), Anomaluridae (scaly-tailed squirrels), and Myoxidae (dormice) are more tentative. The final outcome of ongoing studies of rodent relationships will alter our current knowledge of the classification and evolution of the order, especially with respect to interpretations of how morphology and life-history traits have changed throughout the rodent radiations.

Paleontologically, the order Rodentia dates to the Paleocene era at approximately 57 to 60 million years ago (mya). The earliest known family is the Paramyidae, containing sciurid-like rodents. In the Eocene (38 to 45 mya), rodents experienced a rapid rate of diversification, corresponding in time to the extinction of the Mesozoic order Multituberculata, a group containing rodent-like mammals. Many lineages appearing at this time still have living representatives. On several continents, including Africa, Australia, and South America, members of the family Muridae experienced rather recent adaptive radiations.

One biogeographic enigma pertains to the origin of the South American caviomorph families of suborder Hystricognathi. According to fossil evidence, the family is no older than late Eocene to early Oligocene (36 to 40 mya), yet the closest relatives of this group occur in Africa, a continent separated from South America by thousands of miles (kilometers) during the period at which caviomorphs first appear in South America. Although some paleontologists suggest that caviomorph rodents evolved the characteristics shared with African hystricognaths in parallel, all recent morphological and molecular data suggest that these two groups share a common ancestry. Based on shared ancestry, other paleontologists and biogeographers have suggested an over-water interchange between Africa and South America. Recent molecular data confirm a shared common ancestry for all families of South American caviomorph rodents, thus refuting earlier hypotheses of multiple origins from Africa. In addition, these molecular studies support African hystricognaths as being the closest relatives of caviomorphs. The timing of events associated with the exchange between Africa and South America is still controversial and is part of a broader debate over the origin of rodent lineages in genera. More recent studies based on amino acid and nucleotide sequences have employed a "molecular clock" to estimate divergence times for rodents. Rather than the 57 to 60 mya estimated from fossils for the origin of Rodentia, the molecules suggest a considerably older origin between 100 to 110 mya. Despite this contradiction, the origin of caviomorph lineages still appears younger than the dates at which Africa and South America were connected.

Physical characteristics

Rodents are gnawing mammals, and as such, all species share several features in common. The number of teeth in rodents seldom exceeds 22. The canine teeth are absent, and all rodents possess a single pair of upper and lower incisors characterized by enamel on the anterior surface and dentine on the posterior surface, allowing for differential wear of the teeth to maintain sharpness. A diastema or gap separates the incisors from premolars and molars, and this separation facilitates both gnawing with the incisors and grinding with the cheek teeth. Size and cusp patterns of cheek teeth in rodents relate to diet. Herbivorous rodents have high-crowned cheek

Coypu (*Myocastor coypus*) huddled for warmth on feeding platform. (Photo by Bill Goulet. Bruce Coleman, Inc. Reproduced by permission.)

teeth, whereas omnivorous species have low-crowned cheek teeth and well-defined arrangements of cusps. The arrangement of two primary jaw muscles, the masseters and pterygoideus, allow for duel jaw action whereby chewing can be either transverse or front to back in motion. As noted earlier, the arrangement of these muscles relative to the infraorbital foramen has been used as a major diagnostic feature in many classifications of rodents, with the most primitive arrangement seen in the mountain beaver. Hamsters, pocket gophers, and pocket mice have cheek pouches that allow the animal to collect and transport food.

Rodents demonstrate considerable variation in size, ranging from a length of 4.7 in (12 cm) and weight of 0.1 oz (4 g) for the pygmy mouse (*Baiomys taylori*) to 39.4 in (100 cm) and 10 lb (50 kg) for the capybara (*Hydrochaeris hydrochaeris*). Extinct lineages of the family Dinomyidae reached 882–1323 lb (400–600 kg) in size. In terms of their postcranial skeleton, unspecialized rodents have five digits, short limbs, a long tail, and a plantigrade foot posture (walk with the soles of feet on the ground). More specialized species tend to show considerable modification associated with their particular mode of locomotion and general lifestyle. Many unrelated fossorial species like pocket gophers, tuco-tucos (Ctenomyidae), coruros (Octodontidae), African mole-rats (Bathyergidae), bamboo rats (Muridae, Rhizomyinae), and blind mole-rats (Muridae, Spalacinae) show considerable convergent evolution for a subterranean lifestyle. Most species have a fusiform body with short limbs, small ears, and with eyes either reduced or absent. The tail is generally shorter than the head and body, and the feet are broad. The forefeet of many species have large clawed digits for digging, whereas some species dig with their incisors. Some species of rodents are modified for saltatorial (hopping) locomotion. Kangaroo rats, jerboas, springhares, and gerbils have long tails that serve as a counterbalance during hopping. In addition, the hind feet are generally large and the hind limbs are muscular, whereas the front limbs are shorter. Saltatorial locomotion has evolved several times in rodents and appears to be an adaptation to desert environments with patchily distributed resources. In addition to modifications of the postcranial skeleton, saltatorial rodents tend to have enlarged auditory bullae. Modifications for gliding locomotion can be seen in several species of squirrels (Sciuridae) and scaly-tailed squirrels (Anomaluridae). Gliders have modified membranes extending along the sides of the body and attached to the front and hind feet. The tail is generally well developed and is used as a rudder during the glide as well as a brace when landing. Several species of rodents reveal specializations for living in aquatic environments. These species have webbed feet and tails modified for swimming. The beaver's tail is flattened dorsoventrally, whereas the nutria and muskrat have tails that are laterally compressed. Tree squirrels show specializations for an arboreal lifestyle, revealing sharp claws on the digits and a modification of the bones in ankles that allows for the hind foot to be rotated as the animal descends from a tree head first. Some species of rodents are highly cursorial (fast running) and have highly modified limbs and feet. The mara, a fast running species that lives in steppe region of Patagonia and Argentina, appears rabbit-like with long hind legs, hoof-like claws, and a digitigrade foot posture (run on digits with heel off the ground).

A black rat (*Rattus rattus*) with baby rats on straw. (Photo by Hans Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

Distribution

The order Rodentia has a worldwide distribution, and species within this order can be found in every habitat ranging from Arctic tundra to desert. Nearly 70% of all rodent species are rats and mice of the family Muridae, and representatives of this family are found on all continents as well as Australia and oceanic islands. The house mouse (*Mus musculus*) and the black rat (*Rattus rattus*), two species that live in close association with humans, are cosmopolitan and have been transported to all areas frequented by humans. Squirrels of the family Sciuridae have a worldwide distribution except for Australia, the desert region of Africa, and the southernmost region of South America. The mountain beaver, a relative of squirrels, is more restricted in distribution, being confined to the Pacific Northwest of the United States. The two living species of beaver occur either in North America or parts of Europe and Asia. Pocket gophers are restricted to North and Central America, and members of the family Heteromyidae (kangaroo rats and pocket gophers) occur in North and Central America as well as the northern portion of South America. Scaly-tailed squirrels (*Anomalurus*), African mole-rats (family Bathyergidae), and springhares (*Pedetes capensis*) occur in parts of sub-Saharan Africa. Members of the family Dipodidae occur in portions of the Middle East and northern Africa, and jumping mice of the family Zapodidae occur in both North America and parts of Europe and Asia. Several families of caviomorph rodents originated in South America, and many are restricted to the southern half of South America. At least one family, Capromyidae, is restricted to islands in the Caribbean, and the North American porcupine (*Erethizon dorsatum*) is the only caviomorph with a range extending throughout most of North America. The nutria (family Myocastoridae) also occurs in North America, but it is the consequence of an introduction by humans.

The bushy-tailed woodrat (*Neotoma cinerea*) uses its tail for warmth. (Photo by Phil A. Dotson/Photo Researchers, Inc. Reproduced by permission.)

Habitat

Most types of habitats are occupied by rodents. Some species are desert specialists. For instance, the red viscacha rat (*Tympanoctomys barrerae*) of the family Octodontidae occupies harsh desert habitats in parts of Argentina and demonstrates adaptations for feeding on plants with a high salt content. Kangaroo rats (*Dipodomys*) reveal several behavioral and physiological modifications for living in harsh desert environments, including a highly modified kidney that allows for concentration of urine and features of the nasal passage that aid in the extraction of water prior to exhaling through the nostrils. This species is active at night and occupies a closed burrow system during the day, and all the water necessary for survival is acquired through selective foraging of seeds high in water content. Other saltatorial rodents occupying similar desert habitats show strong physiological, behavioral, and morphological convergence, possessing many features analogous to the North American kangaroo rat. Squirrels are quite diverse in terms of habitat. Tree squirrels occur in most forested areas. Some species of squirrels (e.g., prairie dogs, ground squirrels, marmots) create elaborate burrow systems and can live in habitats ranging from grasslands to semidesert regions. The antelope ground squirrel (*Ammospermophilus nelsoni*) is a diurnal species that occupies desert areas in the southwestern United States. This particular species displays short activity bouts interrupted by periods in the shade where excess heat is released prior to the next foraging bout. The beaver, muskrat, and nutria prefer riparian habitats and wetlands. Some species of lemmings occur in tundra, and other microtines prefer either forest or grassland habitats. In many cases, rodents are essential components of the habitats that they occupy, and through their activities, plant communities can be modified as a result of foraging behavior, seed dispersal, and enhancing components of the soil. For instance, the plains viscacha (*Lagostomus maximus*) alters plant communities with forbs becoming more dominant than grasses in areas that are heavily grazed. Other studies on North American kangaroo rats have revealed significant changes in plant diversity in areas where a particular species has been removed.

Behavior

The social structure in rodents is highly variable. Some species, like pocket gophers, pocket mice, and kangaroo rats, are solitary. In the case of many fossorial species like pocket gophers (family Geomyidae) and Mediterranean blind mole-rats (*Nannospalax*), individuals tend to occupy burrow systems that do not overlap spatially, except for males and females during the breeding season. Multiple individuals in a burrow system are usually restricted to mother and offspring. In most cases, individuals tend to demonstrate high levels of aggression when confined in the same cage. Some fossorial species are considerably more social and maintain overlapping burrow systems. Many of these forms are highly colonial. For instance, African mole-rats of the family Bathyergidae have some solitary forms, yet several species including the naked mole-rat (*Heterocephalus glaber*), the Damaraland mole-rat (*Cryptomys damarensis*), and the common mole-rat (*C. hottentotus*) are highly colonial. In fact, the naked mole-rat and the Damaraland mole-rat have a social system analogous to eusocial insects (e.g., ants and termites). Multiple females of social tuco-tucos (*Ctenomys sociabilis*) share the same nest and burrow system along with their young. Group size in these social fossorial rodents varies greatly, to over 100 in some species. The degree of group living and the length of times that individuals remain in the group are influenced by multiple factors related to resource availability and cost of dispersal. In fact, individual naked mole-rats that disperse from their natal group appear to have a different phenotype characterized by large fat stores.

Other species of rodents tend to be gregarious. Prairie dogs, ground squirrels, and marmots live in colonies that have a well-defined structure consisting of related females that tend to stay within their natal group and males that disperse from neighboring groups. All of these species demonstrate sophisticated alarm calls in response to predators and other disturbances to alert other members of the colony, especially related individuals. In the case of Belding's ground squirrel (*Spermophilus beldingi*), the frequency of alarm calls, a behavior that can prove detrimental to the caller, tends to increase among related individuals. Under certain circumstances, both ground squirrels and prairie dogs display a form of infanticide known as marauding behavior, whereby adult individuals kill the young of a lactating female. In the case of ground squirrels this behavior appears to be directed towards non-kin.

Beavers live in colonies consisting of offspring and an adult male and female, and each colony occupies a defined territory. Individuals in the colony assist with construction of dams and lodges. Other rodents are also found to tend towards monogamy, e.g., South American acouchis and pacas, although they are less social than beavers. Additionally, some species of voles and deermice live in family groups like beavers. These species show strong incest avoidance.

Many species of South American caviomorph rodents are colonial, living in colonies with established male linear hierarchies maintained through dominance and aggression. Nearly all colonial species of caviomorph rodents are highly vocal and use a series of sounds to communicate warning, courtship, play, and aggression. Even some species of mice and rats are colo-

nial and have dominance-based social systems similar to other unrelated social species of rodents.

Species of the order Rodentia communicate using visual, aural, olfactory, and vocal signaling. Vocalizations such as squeaks, grunts, and barks are used as alarm calls, for sexual and aggressive functions, and for seeking misplaced young. Tree squirrels of the family Sciuridae have been known to use visual communication during mating by waving and shivering their tails. Several Rodentia species employ footdrumming, a characteristic thumping or stamping pattern made with the feet, to differentiate between neighbors and outsiders—though in African mole-rats (Bathyergidae), footdrumming is also used during the breeding season to announce an individual's presence to potential mates. Olfactory messages are also vital in marking territorial boundaries and recognizing colony members. Scent-producing facial and anal glands, as well as urine and fecal matter, are used to produce these signals.

Feeding ecology and diet

Many species of rodents are herbivorous and feed on a variety of plant materials. These rodents tend to have a highly developed stomach and large intestines, and nutrients from plants are extracted through a fermentation system found in the enlarged cecum occurring in the large intestines. Some rodents, like the grasshopper mouse (*Onychomys*), are insectivorous, and others eat aquatic insects, mollusks, and fish. Like carnivores, dormice lack a cecum and appear to be more omnivorous in their diet, eating a variety of insects, worms, eggs, and fruits.

A dwarf hamster (*Phodopus sungorus*) foraging. (Photo by Hans Reinhard/Okapia/Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

Rodent reproduction can be subdivided into two forms. The families Muridae (mice and rats), Geomyidae (pocket gophers), and most other sciurognaths have short life expectancies, short gestation periods (17 to 45 days), produce multiple litters per year (one to four), and have large numbers of altricial (helpless) offspring per litter. Most hystricognath rodents such as the Caviidae (guinea pigs and relatives), Erethizontidae (porcupines), and other caviomorph families, have longer life spans, have long gestation periods (ranging from 60 to 283 days), produce few litters per year (generally one to two), and give birth to smaller numbers of precocial offspring per litter. Although body size is generally a good predictor of the form of reproduction employed, hystricognath rodents tend to have longer gestation periods than similar size sciurognath rodents. Hystricognath rodents also produce precocial young that are weaned and reach sexual maturity at an early age. Although species of rodents with large altricial litters tend to gamble in terms of reproduction, many species of rodents in more unpredictable environments tend to synchronize reproduction in an effort to produce offspring under optimal conditions (e.g., during periods of maximum plant productivity). Hibernating species in the families Sciuridae (squirrels) and Zapodidae (jumping mice) generally produce one litter per year, whereas non-hibernating species can be polyestrous, breeding more than one time per year. These hibernators have a narrow window where resources are optimal for reproduction and raising offspring. For instance, the jumping mouse hibernates for nine months and has a three-month window for successful reproduction and weaning of offspring. Even within the same species of small rodent, such as the California meadow vole (*Microtus californicus*), the old-field mouse (*Peromyscus polinotus*), the Eastern woodrat (*Neotoma floridana*), timing of reproduction and litter size can vary with respect to environmental conditions such as rainfall and food abundance.

Chemical communication is important to the reproductive biology of rodents. Female house mice tend to experience increased ovulation in the presence of males. In rodents with short life spans, flexibility in the timing of ovulation to increase the chance of fertilization by a male optimizes reproductive success. The "strange male effect" (or Bruce effect, after the author who described it) in mice occurs when pregnancy is blocked in an inseminated female upon encountering an unknown male. After the new male inseminates the female, reintroduction of the previous male fails to block implantation. It has been proposed that the female presumably has "an olfactory memory" that prevents the female from blocking implantation upon encountering her first mate. Young prairie vole females do not come into heat until they are separated from their family and encounter an unfamiliar male (or his odor).

The mating system in rodents varies, depending upon the species. Many rodents are promiscuous, with offspring from

A black rat (*Rattus rattus*) threatening with its teeth bared. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

a single litter often being sired by more than one male. Recent genetic studies using DNA fingerprinting have confirmed a high incidence of multiple paternity in many promiscuous species. Some species of rodents have a monogamous mating system. For instance, male and female South American mara or Patagonian cavy (*Dolichotis patagonum*) establish pair bonds that can last for multiple mating seasons, and throughout this period the male and female stay in close proximity to each other as they forage. This same species has a tendency to form communal nurseries where several pairs house their young, visiting each day to provision their own young. Some species of rodents that demonstrate monogamy also show a correlation between male parental care and successful rearing of offspring. For instance, the California mouse (*Peromyscus californicus*) female is successful at raising a litter if the male is present. Male and female beavers also tend to form long-lasting pair bonds. Many species of caviomorph rodents have a harem based mating system defined by a linear hierarchy of males. Rock cavies (*Kerodon rupestris*) have a resource-based form of polygyny, whereby males defend rocky outcrops that are considered ideal resources, thus attracting females. Capybaras (*Hydrochaeris hydrochaeris*) are semi-aquatic rodents that live in social groups lasting multiple years. Breeding within these groups is harem-based with a dominant male and several females and subordinate males.

The naked mole-rat (*Heterocephalus glaber*), a species occupying regions of eastern Africa, has an unusual mating system, analogous to social insects, with a single reproductive female and a few reproductive males. Although mole-rat colonies can be quite large, breeding is suppressed in subordinate females, and the entire social system is based on reproductive and non-reproductive individuals. In this system, non-reproductive individuals perform duties related to excavation of the underground burrow system, foraging for food, and tending pups of the reproductive female. In captive populations, the same female can remain reproductive for multiple breeding seasons, and she uses a combination of aggression and possibly chemical communication to suppress reproduction by other adult females. This unusual social system has been considered analogous to the eusocial system seen in social insects that also have overlapping adult generations, recruitment into the natal group, and well defined reproductive and non-reproductive individuals. Apparently, several other species of African mole-rats have similar mating systems. These rodents have stimulated much debate regarding the prerequisites for such complex social behavior, including the possibility that unpredictable arid environments and monogamy may be early precursors that foster the eventual evolution of complex social systems.

Conservation

The IUCN lists 669 species of rodents under varying degrees of threat and endangerment. Thirty-two species from 23 genera are considered Extinct, and 22 of these extinct species occurred on either Oceanic islands or islands in the Caribbean. Causes of extinction relate primarily to loss of habitat and the introduction of feral predators. Ninety-five species of rodents are listed as Endangered throughout the world, with three species in the squirrel family Sciuridae considered Endangered in North America. Vulnerable and Lower Risk species number 166 each.

Significance to humans

Many species of rodents are considered nuisance animals. Burrowing activities of nutria and muskrats can undermine water retention structures like earthen dams and levies. Woodchucks (or ground hogs), eastern chipmunks, prairie dogs, and ground squirrels also burrow, resulting in potential damage to vegetable gardens and structures. Tree squirrels are incredible pests in urban areas. They are true artisans at exploiting "squirrel–proof" bird feeders. Upon invading houses, tree squirrels can damage attics, especially insulation and wiring. Woodrats (genus *Neotoma*), sometimes known as packrats, frequent barns and other buildings associated with humans. These rodents are notorious for decorating their nests with objects taken from various parts of their territory, including human artifacts. North American pocket gophers of the family Geomyidae are both a pest and a benefit. These

subterranean rodents are beneficial in terms of increasing soil fertility, aeration, and water infiltration. Their rotation of soil also reduces compaction. At the same time, pocket gophers cause serious damage to underground cables and irrigation lines by their gnawing activities. Underground telephone cables are vulnerable unless either protected by a gopher retardation device or buried below the soil's A zone. The common house mouse, *Mus musculus*, is a fixture in many homes, warehouses, and other human-made structures. In some circumstances, house mice can contaminate stored food, damage materials maintained in warehouses, and cause structural damage through their nest building and habit of gnawing.

Some rodent species cause serious damage to commercial forest operations. The mountain beaver, *Aplodontia rufa*, a species occurring from southern British Columbia to northern California, is a serious pest that feeds on conifers. Primary damage occurs as a result of girdling trees, damaging seedlings, and gnawing roots. It has been estimated that this rodent has extensively damaged over 300,000 acres (120,000 ha) of coniferous trees in parts of Washington state and Oregon. At a value of $10,000 per acre, this species has caused millions of dollars in damage. Voles also eat conifer seedlings at sites of reforestation and Christmas tree farms. These small rodents require high grass for cover. Therefore, prevention of damage to seedlings can be accomplished by minimizing the amount of grass cover. Although less damaging, nutrias are known to girdle trees, and in forest plantations and fruit orchards, the North American porcupine can cause damage. Like the pocket gopher, the porcupine also is beneficial by creating diverse habitat for many forms of wildlife, especially birds. Cotton rats (*Sigmodon*) occur throughout regions of the southern and western United States. These rodents are herbivorous and prolific breeders. When cotton rat populations are high, these rodents can cause damage to alfalfa and other crops. Although prairie dogs generally prefer overgrazed or disturbed habitat, they can impact rangelands by reducing the amount of forage available to livestock. At the same time, the burrow of prairie dogs supports many species of vertebrates and invertebrates, and the prairie dog is a major prey item of both the endangered black-footed ferret and birds of prey.

Rodents cause considerable damage to cash crops in several countries. Studies have shown that rodents consume from 1 to 20% of crops in industrialized nations and as much as 50% in less developed countries. In parts of Southeast Asia, where rodents destroy large portions of the rice crop, reduction of rodent populations resulted in a 200% increase in rice crops. The reproductive ability of many species of the family Muridae make these rodents especially harmful to crops in many parts of the world. For instance, rodent outbreaks can dramatically increase population densities of rodents, with numbers being in the thousands per 400 acres (1 ha), thus posing a serious threat to crops. For instance, a population of the European hamster (*Cricetus cricetus*) in Hungary resulted in nealy 988,422 acres (400,000 ha) being impacted. Several genera in the murid subfamily Gerbillinae (e.g., *Meriones*, *Tatera*, and *Rhombomys*) are considered major pests of cultivated crops from northern Africa to regions in India. These gerbils can severely damage cereal as well as vegetables, olive saplings, and other economically important crops.

A North American red squirrel (*Tamiasciurus hudsonicus*) carries a pine cone, from which it may extract the seeds. (Photo by Bob & Clara Calhoun. Bruce Coleman, Inc. Reproduced by permission.)

North America's largest rodent, the beaver (*Castor canadensis*), has some positive and negative attributes. Historically, the beaver has been prized for its pelt, and beaver trapping had a severely negative impact on natural populations throughout portions of its range in North America. As "nature's engineers," beavers are capable of modifying habitat that favors wetlands. Through their dam building activities, beavers create habitat suitable for waterfowl and other wetland species. However, alteration of habitat and harvesting trees for food and support materials also threatens both agricultural and forest interests. Dams can initiate flooding in some areas resulting in the loss of trees that are intolerant of high water levels. In addition, beavers can pose a threat to human health. They are known to carry *Giarda*, an intestinal parasite, transmitted to humans through drinking water, and exposure to beaver lodges can result in humans contracting Gilchrist's disease, which causes pneumonia-like symptoms.

Many species of rodent endanger human health. Bubonic plague or the "Black Death" is a dreaded disease that created havoc during the sixth and fourteenth centuries in Europe by killing almost one third of its population. The total number of deaths from bubonic plague was approximately 137 million people. Thousands died as a result of this rodent-borne bacterial disease. Plague is transmitted by the bite of an infected flea as well as through inhalation of the bacteria or direct contact with body fluids, and during the European epidemic, the primary rodent host was the black rat, *Rattus rattus*, of the family Muridae. Even today, several species of rodents carry bubonic plague, even though the frequency of human infections has declined. Squirrels and chipmunks are the major rodent hosts of plague in California, and humans most at risk live in the more rural areas of the state. Prairie dogs are also bubonic plague carriers, and although they rarely transmit the

Tunney's rat, or pale field rat (*Rattus tunneyi*). (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

disease to humans, whole prairie towns have ceased to exist as a result of plague epidemics.

Lyme disease is another bacterial infection transmitted indirectly from rodent reservoirs to humans through tick bites. This disease occurs worldwide and has become endemic throughout the United States. The symptoms are flu-like and can become chronic. Rodents, especially the white-footed mouse (*Peromyscus leucopus*), act as reservoirs by supporting the larval and nymphal stages of tick species known to transmit the disease. In the northeastern United States, the cycle of Lyme disease involves a rodent intermediate host followed by the adult stage of the tick infesting white-tailed deer. Humans catch the disease through incidental bites from infected ticks.

Hantavirus causes pulmonary distress in humans and is contracted through exposure primarily to the urine and droppings of several species of mice. This exposure generally occurs as a result of breathing the virus during contact with dust in areas of heavy rodent infestation. In North America, there are several rodent hosts of the subfamily Sigmodontinae (family Muridae) including the deer mouse (*Peromyscus maniculatus*), the white-footed mouse (*Peromyscus leucopus*), the cotton rat (*Sigmodon hispidus*), and the rice rat (*Oryzomys palustris*). The most recent and famous hantavirus outbreak in North America occurred in the "Four Corners" of the southwestern United States. In South America, outbreaks of viruses related to hantavirus have occurred in Chile. Again, the primary rodent hosts are sigmodontines, such as the genus *Oligoryzomys*. Even in parts of Europe and Asia, several species of rodents harbor similar viruses that cause pulmonary disorders and hemorrhagic fever in humans. In many cases virus outbreaks are cyclical and are more virulent during population increases in response to increased rainfall and plant production.

Prairie dogs watch for predators. (Photo by © Nancy Stanford/Corbis. Reproduced by permission.)

Rodents provide both indirect and direct benefits to humans. Many species serve as the primary prey of many vertebrate predators, and through their burrowing, dam building, seed hoarding, and other activities, rodents can have a positive impact on wildlife habitat. In terms of human health, rodents provide excellent animal models for studying human disease. In fact, approximately 95% of animals used in research are either rats or mice. The house mouse, in particular, provides a very useful animal model for biomedical research. Inbred strains, first developed by pet fanciers, of rats and mice are widely used to study human diseases. Transgenic and knock-out mice represent genetically manipulated strains of the house mouse that are used in research on a variety of human diseases (e.g., Parkinson's diseases, cancer, heart disease, etc.). Similar rodents are being used to study Alzheimer's disease, aging, and cystic fibrosis, and they are also useful for testing potentially beneficial cancer treatments and other drugs used to combat human disease. Research supported by the National Aeronautics and Space Administration uses rodent models to study bone loss in response to being in an environment without gravity.

In addition to serving as research models, many rodents are popular pets, including rats, mice, gerbils, hamsters, and guinea pigs. Rodents are also eaten in many parts of the world. For example, roasted, fried, or stewed cuy (guinea pig) is popular in Ecuador, Peru, and other South American countries.

Resources

Books

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Foundation for Biomedical Research. 818 Connecticut Avenue, NW Suite 200,, Washington, DC 20006 USA. Phone: (202) 457 0654. Fax: (202) 457 0659. Web site: <http://www.fbresearch.org/education/species-sheet-rodents.htm>

National Center for Infectious Diseases, Division of Bacterial and Mycotic Diseases. 1600 Clifton Road, Atlanta, Georgia 30333 USA. Web site: <http://www.cdc.gov/ncidod/dbmd/mspb.htm>

Rodney L. Honeycutt, PhD

Mountain beavers
(Aplodontidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Aplodontidae

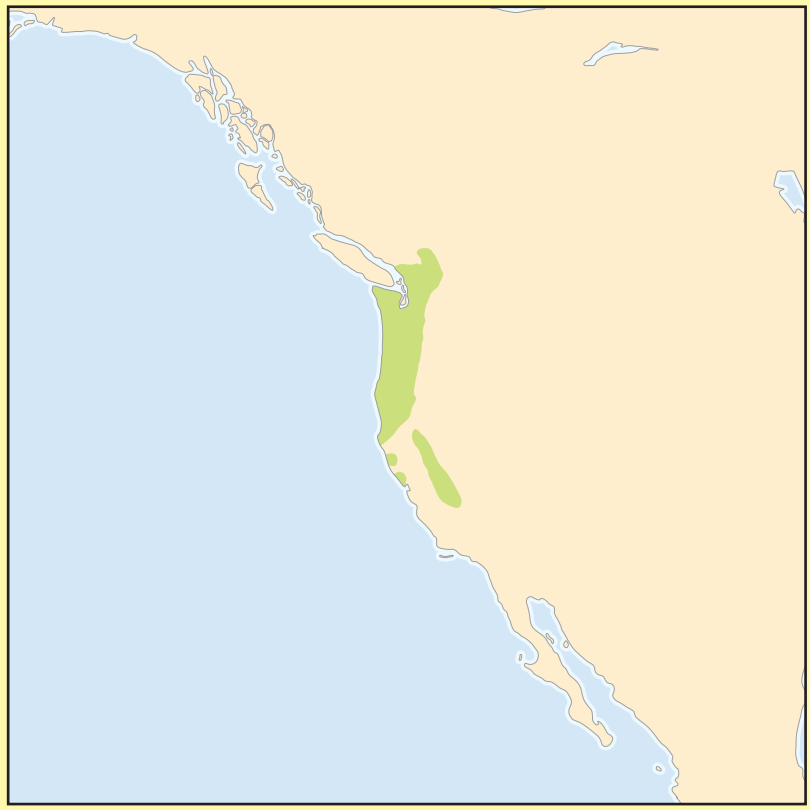
Thumbnail description
Medium-sized burrowing rodent with a stocky body, blunt nose, and short stubby tail; small ears, short legs, and long claws; dark brown pelage with sparse coarse guard hairs, and small white patch below the ears

Size
Body length average 14.3 in (364 mm), range 9.3–19.7 in (238–500 mm); tail length average 1.2 in (29.8 mm), range 0.4–2.2 in (10–55 mm); weight average 2.6 lb (1,158 g), range 1.8–4.0 lb (800–1,800 g)

Number of genera, species
1 genus; 1 species

Habitat
Temperate forest with dense understory of herbs and shrubs

Conservation status
Lower Risk/Near Threatened



Distribution
Western North America

Evolution and systematics

The mountain beaver, or sewellel (*Aplodontia rufa*), is not related to the beaver but is in its own distinct family. Classification of suborders of rodents is based, in part, on the anatomy of the jaw muscles. In early classification schemes, three suborders are recognized. Alternative schemes recognize two suborders, with no assignment given to several families whose lineage is uncertain. Regardless of which scheme is used, Aplodontidae are substantively different from other families of rodents, and considered the most ancient of living rodents. Their origins trace back 50 million years to the Eocene. They and related groups flourished through to the Miocene and once occupied parts of Asia, Europe, and western North America. Today, the family is represented by a single species, mountain beaver, confined to a small portion of western North America.

The taxonomy for this species is *Aplodontia rufa* (Rafinesque, 1817), Oregon, United States.

Physical characteristics

The mountain beaver has a robust, cylindrical body and is approximately the size of a muskrat without its tail. It is adapted for burrowing with a rounded head, blunt nose, long vibrissae, short ears and small eyes. The furred tail is so short that at first glance the animal appears to be tailless. The pelage is dark brown with coarse but sparse guard hair and lighter brown thick underfur. There is a small white patch of short fur at base of the ears. The underparts are slightly lighter than the back, except on pregnant and lactating females where three pairs of mammae are surrounded by zones of darker fur. The legs are short and strong for digging. The front and hind feet have five toes terminating in long strong claws, except the pollex (thumb), which has a short stubby claw and is somewhat opposable.

Distribution

Mountain beavers inhabit forestlands along the Pacific Coast of North America, from sea level to as high as 7,000 ft (2,000 m) in subalpine forests. They range south from 50°N in southwestern British Columbia through western Washington and Oregon to northern California where inland they extend further south to 36°40'N along the Sierra Nevada Mountains. Two disjunct populations occur on the coast of California north of San Francisco Bay.

Mountain beaver (*Aplodontia rufa*). (Illustration by Brian Cressman)

Habitat

Habitats used by mountain beavers vary, but are typically forests with dense patches of herbs and shrubs. This vegetation supplies not only forage, but also security and thermal cover. On forested slopes, mountain beaver are frequently found in thickets of diverse vegetation near streams. In closed canopy forests, mountain beaver tend to be associated with canopy gaps created by disturbances such as root-rot and windfall. These openings allow light to penetrate the forest and promote growth of herbs and shrubs. The fallen trees form the main structures beneath which mountain beaver construct tunnels and runways to access foraging sites in their home range. Mountain beavers readily occupy early seral stages after logging as long as there is sufficient cover and food.

The mountain beaver (*Aplodontia rufa*) relies heavily on its sense of smell and touch. (Photo by V. B. Scheffer/Mammal Images Library of the American Society of Mammalogists.)

A mountain beaver (*Aplodontia rufa*) emerging from its burrow. (Photo by Joseph Van Wormer. Bruce Coleman, Inc. Reproduced by permission.)

Behavior

Mountain beavers do not hibernate and so are active throughout winter. They are primarily nocturnal but are frequently active for short periods during the day. They occur in concentrations sometimes referred to as colonies. However, they are not colonial but rather solitary, and the concentrations are likely simply sites of suitable habitat that form population foci. Mountain beaver have small home ranges (average males 0.7 ac [0.3 ha]; females 0.5 ac [0.2 ha]) and, within them, the animal excavates a burrow system with extensive runways. Generally, the burrow system is associated with structures like fallen logs, root wads, or large rocks. A log can act as the main route for an arm of the tunnel system. From this main arm, accessory tunnels extend to favored feeding sites or other structures. These traveling tunnels are generally near the surface and occasionally the roof collapses, exposing the subterranean runway. The burrow system leads deeper to separate underground chambers containing the nest, food larders, and refuse piles. The 1.6-ft (0.5-m) diameter nest chamber contains dry vegetation for insulation. Nearby are smaller feeding chambers where mountain beaver store food plants collected during forays aboveground. Smaller refuse chambers contain decaying vegetation left over from feeding. Other small chambers contain fecal pellets. Besides these, an earth ball chamber can occur containing stones or balls fashioned from soil, thought to be used to seal portions of the living quarters.

Feeding ecology and diet

Mountain beavers are herbivores with a large cecum, a diverticulum from the junction of the small and large intestine, in which microbes digest much of the vegetation. They are

Mountain beaver (*Aplodontia rufa*) burrows are built around the nest. (Photo by © Erwin & Peggy Bauer/Animals Animals. Reproduced by permission.)

A young mountain beaver (*Aplodontia rufa*) playing dead on the lawn of the Olympic Penninsula, Washington, USA. (Photo by Janis Burger. Bruce Coleman, Inc. Reproduced by permission.)

also copraphagic, consuming their excreted soft pellets, a type of feces. This behavior allows digestion of microbial protein and other nutrients remaining in the soft pellets. Mountain beavers travel along their tunnels where they exit and gather food on the surface. During spring and summer, various ferns, grasses, and herbs are eaten along with some leaves and shoots of shrubs. During winter, their diet shifts to ferns, shrubs, and conifers. Mountain beaver readily climb 6.5 ft (2 m) or higher in trees to clip small branches; some saplings appear as if they have been severely pruned. Also during winter, mountain beavers will feed on the bark of young conifers, sometimes girdling trees. Most of their moisture is supplied in their food, but additional water is generally required because mountain beaver have inefficient kidneys and cannot concentrate urine to the extent as other rodents. The tunnels are strategically located so the foraging animal need move only short distances from the safety of their burrows. They cut vegetation and place it at their burrow entrances. Although sometimes food is eaten on the surface, more often it is transported underground for later consumption.

Reproductive biology

In the central portion of the mountain beaver's range, males are in breeding condition from January through March, whereas most females are in estrus during mid-February. Only females two years or older breed and, after a 28- to 30-day gestation period, parturition occurs in the nest chamber from late March through early April. Only one litter is produced per year and, although females have three pairs of mammae, typically between two to three young are born, though litter size can vary up to six. Young are weaned at 6–8 weeks old and, a week or two later, they leave the nest chamber to begin surface activities.

Conservation status

The mountain beaver is listed as Lower Risk/Near Threatened as a species. However, two of its seven subspecies (*A. r. phaea* and *A. r. nigra*) are listed as Vulnerable by IUCN, in part because of habitat loss and also because these are small isolated populations in California disjunct from the principal range of the species. The U. S. Fish and Wildlife Service lists *A. r. nigra* as Endangered. Elsewhere, the mountain beaver is secure, but local extirpations can occur. From a jurisdictional perspective in Canada, *A. r. rufa* could be considered threatened because it has been lost from most of its range in British Columbia due to urbanization and agriculture. However, from a broader geographic perspective, this could be regarded as little more than an emargination of its range in the Pacific Northwest.

Significance to humans

The mountain beaver is significant because it is the most ancient living rodent. Its peculiar kidney is physiologically interesting because of its inability to concentrate urine. At times, the mountain beaver can be a garden pest, but they are more commonly forest pests. They cut newly planted conifer seedlings and remove bark, thus girdling stems and causing root damage on trees up to 20 years old. Such damage can be economically substantial and can diminish forest productivity for timber values.

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Alton S. Harestad, PhD
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Squirrels and relatives I

Flying squirrels (Pteromyinae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Sciuridae
Subfamily Pteromyinae

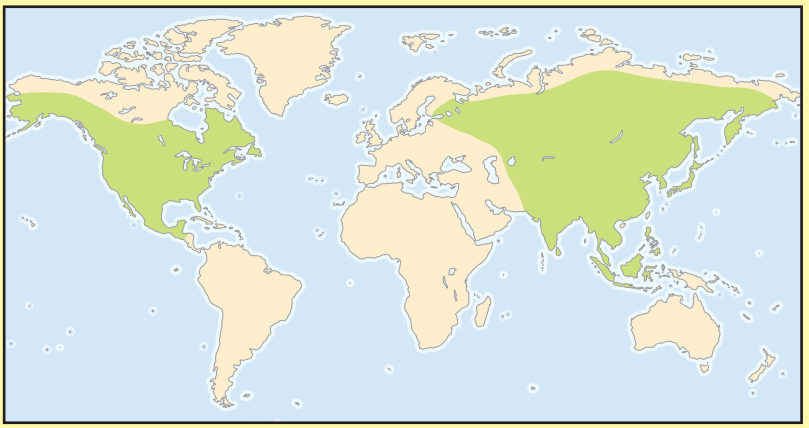
Thumbnail description
Small to medium rodents with large bushy tails often dorso-ventrally flattened; all species possess furred gliding membranes connecting the fore and hind limbs

Size
5–48 in (13–122 cm); 0.7–5 lb 8 oz (20–2,500g)

Number of genera, species
14 genera; 43 species

Habitat
Forest, woodlands, plantations, parkland, and cliffs

Conservation status
Critically Endangered: 2 species; Endangered: 4 species; Vulnerable: 1 species; Lower Risk/Near Threatened: 11 species



Distribution
Northern Europe, north, south, and southeast Asia, and North America

Evolution and systematics

The subfamily Pteromyinae is generally considered to be one of the two subfamilies of squirrels (Sciuridae). It has been considered by some authors to be a monophyletic sister family, the Pteromyidae to the Sciuridae, while others have questioned its monophyly and subfamily status. There is a uniformity of characters among all its members, which are adapted for a nocturnal, gliding lifestyle. All squirrels are thought to be derived from a common arboreal rodent ancestor, *Protosciurus*, rather similar in structure to modern-day tree squirrels such as *Sciurus*.

There are 43 species of flying squirrel grouped into 14 genera. Some of these species are still very poorly known and three species are known only from their type localities; a further nine have very restricted mainland or small island endemic distributions.

Physical characteristics

Flying squirrels are small to medium rodents highly adapted for an arboreal lifestyle. They are generally slim and leggy animals with large bushy tails, which often makes them appear larger than they actually are. All species are adapted for gliding with membranes of muscle running along the sides of the body between the front and hind legs, in some genera, such as the giant flying squirrels (*Petaurista*), these extend up the neck and right down to the base of the tail. A rod of cartilage connected to the wrist is used to extend the gliding membrane. In most species the tail is flattened dorso-ventrally to assist in gliding and directional control.

They have large eyes and generally small but obvious ears. The fur is very soft and dense in all species. They are paler below with generally brown, gray, or blackish upper parts, although the giant flying squirrels are highly variable with some populations being brightly colored—vivid orange above and yellow below.

Distribution

Flying squirrels are most diverse in south and southeast Asia especially in tropical forest. Fifteen species are island endemics, 11 endemic to Indonesian islands, two to the Philippines, and a further two to Japan. Three species occur in northern temperate regions—the distribution of two of which extends right up to the Arctic Circle, northern flying squirrel (*Glaucomys sabrinus*) and Siberian flying squirrel (*Pteromys volans*). Northern flying squirrel and southern flying squirrel (*Glaucomys volans*) are the sole representatives of the group in the New World.

Habitat

Flying squirrels are arboreal and found in a variety of forested or wooded areas including northern boreal forest, temperate deciduous forest, and tropical rainforest. Some species also occur within plantations and parkland. Two

A red giant flying squirrel (*Petaurista petaurista*) about to leap off a branch. (Photo by Chicago Zoological Park/Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

species, the woolly flying squirrel (*Eupetaurus cinereus*) and complex-toothed flying squirrel (*Trogopterus xanthipes*), live at high altitudes on rocky cliffs and outcrops. All species are nocturnal and many very seldom come down to the ground. They nest in a variety of tree holes, crevices or nests that they either construct themselves or occupy built by other species.

Behavior

All species of flying squirrel are totally nocturnal. They display a variety of social systems. Giant flying squirrels are believed to be largely monogamous, occurring in pairs both in and outside the breeding season. Most species though are largely territorial, although this territoriality may breakdown in the temperate species outside of the breeding season, when large groups communally nest in winter dens.

Home ranges of up to 12 acres (5 ha) have been reported in giant flying squirrels and 6 acres (2.5 ha) in southern flying squirrel. Information on the small tropical species is sparse despite some of them being fairly numerous. Their gliding ability is very precise and individuals can change direction in mid-flight, the giant flying squirrels have been reported as gliding up to 1,475 ft (450 m). Many species are naturally very docile and do not attempt to bite when handled. Flying squirrels have a variety of vocalizations including loud high-pitched bird-like trills and soft twittering calls.

Feeding ecology and diet

Flying squirrels feed on a variety of plant and animal matter. Many of the larger tropical species are mainly herbivorous; some specializing on the feeding of young shoots and fruits. The temperate species tend to feed largely upon tree seeds, some fruits and fungi, and animal matter. Smaller tropical species tend to be much more carnivorous, feeding upon insects, spiders, and even small vertebrates. The montane woolly flying squirrel feeds upon mosses and lichens on rocks and conifer needles.

They are known to glide large distances to particular trees in order to feed on seasonal fruits or tender growing leaves. Some species show considerable seasonal variation within their diet, exploiting food resources as they become available.

Reproductive biology

The breeding biology of most species is poorly known or totally undescribed. The tropical species of flying squirrel breed aseasonally while those from temperate regions have short and clearly defined summer breeding seasons. One litter per year is normal for most species; although *Glaucomys* has been reported to have two litters, while the aseasonal *Hylopetes* is highly variable with as long as 17 months between litters.

Most species give birth to small litters, typically only one or two young. A few of the smaller species have larger litters and southern flying squirrel can produce up to seven young. The young are generally small at birth and all but one genus produces offspring that are blind and naked or very sparsely furred at birth. The exception is the dwarf flying squirrels (*Petinomys*) that give birth to comparatively large, fully furred offspring with their eyes open. These infants can climb and start to eat solids when only one day old. In *Glaucomys*, ges-

A southern flying squirrel (*Glaucomys volans*) leaping from a branch. (Photo by Nick Bergkessel/Photo Researchers, Inc. Reproduced by permission.)

A dwarf flying squirrel (*Petinomys* sp.) in Bang Lamung, Thailand. (Photo by Terry Whittaker/Photo Researchers, Inc. Reproduced by permission.)

tation is around 40 days and weaning occurs around eight weeks of age, but young will stay with the mother longer if a second litter is not produced.

Conservation status

Flying squirrels suffer heavily from habitat loss due to deforestation for development and agriculture. The larger species are also hunted locally for food and some species are hunted for their fur or as pests of plantations. In 2002, 18 species are considered threatened or Near Threatened by the World Conservation Union (IUCN), and a further four subspecies are also considered to be at risk.

Significance to humans

Most species of flying squirrel are highly cryptic and even when living in populated areas often go completely unnoticed by humans. Giant flying squirrels are hunted for food across parts of their range and can become pests of fruit crops in some plantations.

1. Southern flying squirrel (*Glaucomys volans*); 2. Siberian flying squirrel (*Pteromys volans*); 3. Hose's pygmy flying squirrel (*Petaurillus hosei*); 4. Red giant flying squirrel (*Petaurista petaurista*). (Illustration by Brian Cressman)

Species accounts

Red giant flying squirrel
Petaurista petaurista

TAXONOMY
Petaurista petaurista (Pallas, 1766), no locality stated, likely western Java, Indonesia. The number of subspecies is uncertain; it is highly variable in color and size across its range.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and tail length 35–48 in (89–122 cm); weight 2.3–5.5 lb (1,050–2,500 g). Fur has a mahogany-red coloring, and the gliding membrane is thickly haired.

DISTRIBUTION
Afghanistan east through south and Southeast Asia down to Sumatra, Java, and Borneo.

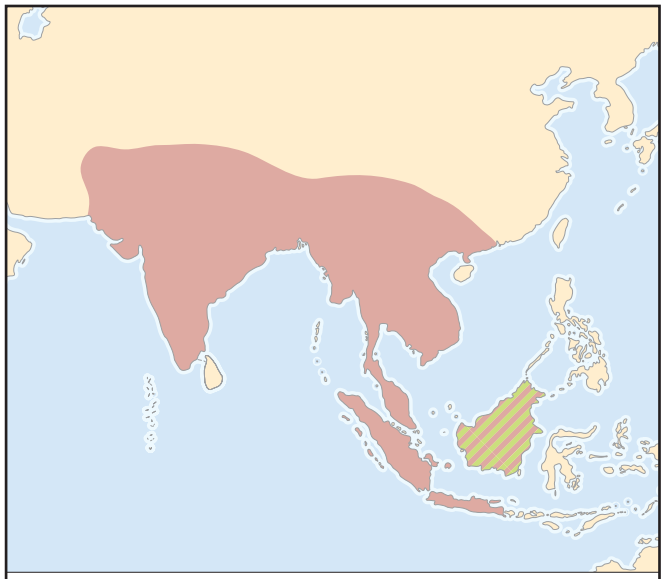
HABITAT
Forest and plantations often at altitudes above 2,250 ft (750 m).

BEHAVIOR
Nocturnal, seldom coming to the ground and gliding large distances between trees for feeding.

FEEDING ECOLOGY AND DIET
Shoots, leaves, and fruits.

REPRODUCTIVE BIOLOGY
Generally monogamous and giving birth to one or two young. Young develop slowly and are not weaned until about 3 months old.

CONSERVATION STATUS
A widespread species, although some highly distinctive populations are locally threatened.



SIGNIFICANCE TO HUMANS
Hunted for food and fur across parts of its range. ◆

Southern flying squirrel
Glaucomys volans

TAXONOMY
Glaucomys volans (Linnaeus, 1758), Virginia, United States. Ten subspecies are recognized.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and tail length is 8–10 in (20–25 cm); weight 1.5–3.5 oz (45–100 g). Upperparts are gray and underparts are white.

DISTRIBUTION
Eastern Canada south through the eastern United States, fragmented populations stretching down to Honduras.

HABITAT
Predominantely deciduous forest.

BEHAVIOR
Nocturnal, normally territorial when breeding but nests communally during the winter.

FEEDING ECOLOGY AND DIET
Nuts, seeds, and insects.

REPRODUCTIVE BIOLOGY
Serially monogamous. Breeds in spring and early summer, up to two litters of 2–7 young produced following a 40 day gestation period.

CONSERVATION STATUS
Generally common but some smaller fragmented populations threatened by habitat loss.

SIGNIFICANCE TO HUMANS
Sometimes encouraged to feeding tables and also kept as a pet. ◆

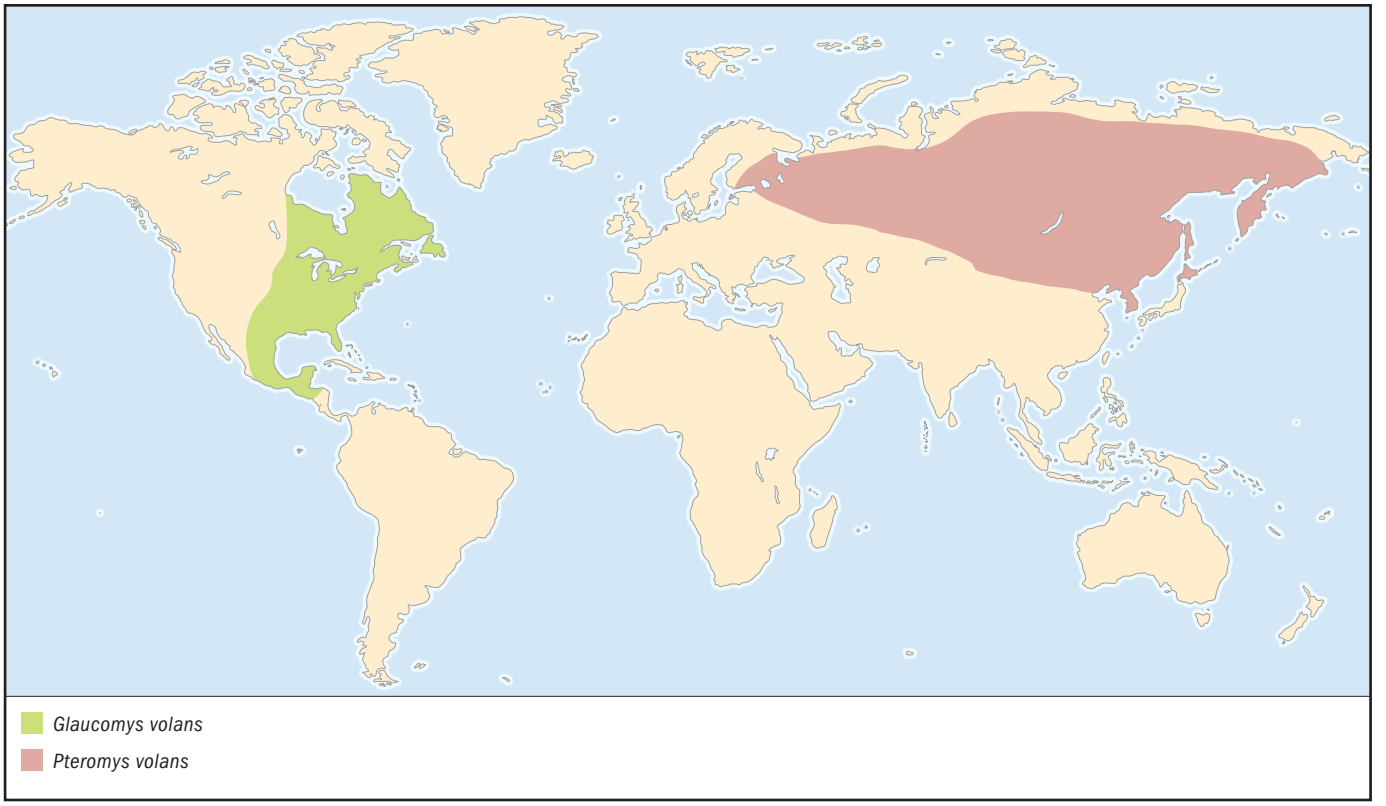
Siberian flying squirrel
Pteromys volans

TAXONOMY
Pteromys volans Linnaeus, 1758, "in borealibus Europae, Asiae, et Americae." Seven subspecies are recognized.

OTHER COMMON NAMES
English: Russian flying squirrel.

PHYSICAL CHARACTERISTICS
Head and tail length is 9–13.5 in (23–35 cm); weight 3–5 oz (80–150 g). Upperparts are yellow-gray to blackish gray in summer and silvery gray in winter. Underparts are white.

DISTRIBUTION
Northern Palaearctic, from Finland east through Siberia and south to Mongolia, northern China and Korea, also Hokkaido.



HABITAT
Mature mixed deciduous and coniferous forest.

BEHAVIOR
Nocturnal and highly arboreal. Nests communally during the winter.

FEEDING ECOLOGY AND DIET
Seeds, nuts, leaves, catkins, invertebrates and possibly even nestlings.

REPRODUCTIVE BIOLOGY
Information on mating behavior is incomplete. One or two litters produced each year of normally 2–3 young.

CONSERVATION STATUS
Declining across much of its range and protected within Europe. Considered Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes nests within buildings, hunted for fur in some parts of Russia. ◆

Hose's pygmy flying squirrel
Petaurillus hosei

TAXONOMY
Petaurillus hosei (Thomas, 1900), eastern Sarawak, Malaysia. No subspecies recognized.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length is 6.5 in (17 cm); weight 0.9 oz (25 g). Upperparts are fawn to pale rufous, cheeks are pale buff, and underparts are white.

DISTRIBUTION
Borneo.

HABITAT
Lowland tropical forest and forest edge.

BEHAVIOR
Nocturnal, several reported to nest together.

FEEDING ECOLOGY AND DIET
Unknown, but probably insectivorous.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
North Chinese flying squirrel *Aeretes melanopterus*	Short, dense, soft fur, dull brownish in color with a slate base. Hairs on side of body have yellowish tips. Underparts are gray to buff, throat and ventral surface are whitish. Gliding membrane is dark brown, head is pale and grayer than back. Tail is bushy with black tip.	Species inhabits forests. Other information is unknown.	Hebei and Sichuan, China.	Diet unknown, but most likely fruits, nuts, and leaves.	Lower Risk/Near Threatened
Black flying squirrel *Aeromys tephromelas*	Coloration of upperparts is dark brown to black, underparts are grayish brown. Long, slender, round tail is same color as back. Cheeks lack whiskers, ears are moderate in size. Head and body length 10–16.8 in (25.5–42.6 cm), tail length 11–20.7 in (28–52.7 cm), weight 39.8–44.1 oz (1,128–1,250 g).	Mature forests or clearings with a few large trees. They are chiefly nocturnal and spend days curled up in high holes.	Malaysian region, except Java and south-western Philippines.	Fruits, nuts, leaves, and probably some insects.	Not threatened
Thomas's flying squirrel *Aeromys thomasi*	Coloration of upperparts is dark brown to black, underparts are grayish brown. Long, slender, round tail is same color as back. Cheeks lack whiskers, ears are moderate in size. Head and body length 10–16.8 in (25.5–42.6 cm), tail length 11–20.7 in (28–52.7 cm), weight 48.7–52.5 oz (1,380–1,490 g).	Mature forests or clearings with a few large trees. They are chiefly nocturnal and spend days curled up in high holes.	Borneo, except the southeastern region.	Fruits, nuts, leaves, and probably some insects.	Not threatened
Hairy-footed flying squirrel *Belomys pearsonii*	Top of head and back are glossy reddish brown. Fur is fine, soft, and fairly long. Gliding membrane is dark brown, sparsely washed with red. Hands are reddish brown, underparts are light red to white. No cheek whiskers, feet are covered with long hair, small ears. Head and body length 7–10.2 in (17.8–26 cm), tail length 4–22.8 in (10.2–58 cm).	Dense, temperate, broad-leaved forests from 4,920 to 7,870 ft (1,500–2,400 m) in elevation. Not a particularly good glider.	Sikkim and Assam , India, to Hunan, Sichuan, Yunnan, Guizhou, Guangxi, and Hainan, China; Bhutan; Taiwan, Indochina, and northern Myanmar.	Fruits, nuts, leaves, and probably some insects.	Lower Risk/Near Threatened
Namdapha flying squirrel *Biswamoyopterus biswasi*	Upperparts are red grizzled with white, hands and feet are darker, underparts are white. Tail is pale smoky gray, changing into russet. Tail is cylindrical. Head and body length 15.96 in (40.5 cm), tail length 23.8 in (60.5 cm).	Single species was found at an elevation of 1,150 ft (350 m). Nothing known of reproductive or behavioral patterns.	Known only from type locality, western slope, Patkai Range in India.	Unknown, most likely fruits, nuts, and leaves.	Critically Endangered
Woolly flying squirrel *Eupetaurus cinereus*	Body is covered with thick, soft, woolly fur that is dark gray above and paler underneath. Long, trumpet-shaped muzzle. Claws are blunt. Head and body length 20.3–24 in (51.5–61.0 cm), tail length 15–18.9 in (38–48 cm).	Rocky terrain in mountainous regions. Little known of reproductive and behavioral patterns.	High elevations from northern Pakistan and Kashmir to Sikkim.	Unknown, most likely fruits, nuts, and leaves.	Endangered
Gray-cheeked flying squirrel *Hylopetes lepidus*	Fur is soft, dense, moderately long. Upperparts are grayish with a tinge of brown or yellow. Bright reddish brown, glossy brownish to black across hips and tail. Underparts are white, gray, or yellow. Ears are large and bluntly pointed, claws are short and blunt, tail is flat and tapers at tip. Head and body length 4.3–13 in (11–33 cm), tail length 3.1–11.5 in (8–29.2 cm).	Various kinds of forest, as well as clearings and cultivated areas, from about 490 to 11,480 ft (150–3,500 m) in elevation. Arboreal and nocturnal.	Southern Vietnam, Thailand to Java; and Borneo.	Mainly fruits, but also nuts, tender shoots, leaves, and, apparently, insects and small snakes.	Not threatened
Javanese flying squirrel *Iomys horsfieldii*	Upper surface of gliding membrane is bright russet, underparts are grayish to pale orange. Tail is brownish above and chestnut underneath. Large, broad, naked ears. Head and body length 5.7–9.1 in (14.6–23.1 cm), tail length 6.3–8.3 in (15.9–21 cm), weight 4.2–8.1 oz 120–231 g).	Forests and plantations at all elevations. Build leaf nests. Litter size ranges from one to four offspring	Malay Peninsula to Java; and Borneo.	Unknown, most likely fruits, nuts, and leaves.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Whiskered flying squirrel *Petinomys genibarbis*	Broad, low head with short muzzle. Fur is dense and soft above, thin on lower parts. Coloration of upperparts varies from brown to black, underparts range from white to dark slate. Tail may be buff, darker towards tip. Head and body length 3.6–16 in (9.2–40.6 cm), tail length 3.3–11.5 in (8.5–29.2 cm), weight 3.9 oz (110 g).	Tropical forests up to 3,970 ft (1,210 m) in elevation. Nocturnal, good climbers.	Malaya to Sumatra, Java, and Borneo.	Nuts, fruits, young twigs, tender shoots and leaves, possibly the bark of certain trees, and perhaps some insects.	Not threatened

Resources

Books

Corbet, G. B., and J. E. Hill. *The Mammals of the Indomalayan Region: A Systematic Review*. Oxford and New York: Oxford University Press, 1992.

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Mike J. R. Jordan, PhD

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Squirrels and relatives II

Ground squirrels

Class Mammalia
Order Rodentia
Suborder Sciuragnathi
Family Sciuridae
Subfamily Sciurinae

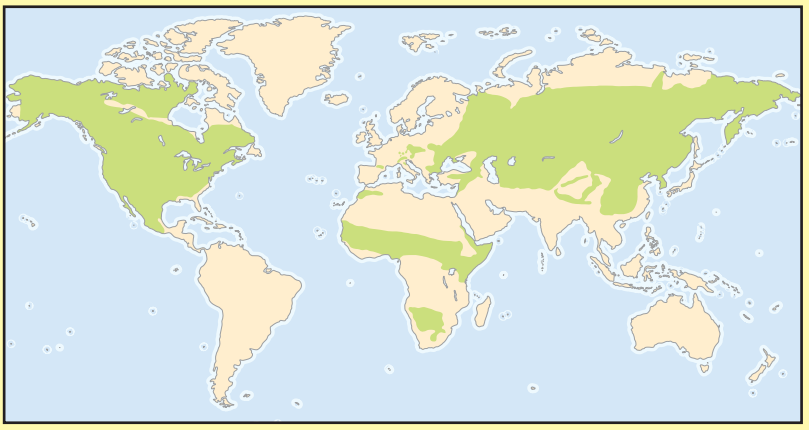
Thumbnail description
Short and stout short-haired rodent with a slender or bushy tail that is one quarter to one half the total squirrel's length; coloration varies between species from uniform to distinctive contrasting patches, dark and light stripes, or speckled with small light spots

Size
7.2–30 in (18.3–75 cm); 0.09–24 lb (0.04–11 kg)

Number of genera, species
9 genera; 95 species

Habitat
Desert, prairie, savanna, shrub, temperate forests, subalpine forests, rocky slopes, alpine meadows, and arctic tundra

Conservation status
Endangered: 4 species; Vulnerable: 6 species; Lower Risk/Near Threatened: 6 species; Lower Risk/Conservation Dependent: 2 species; Data Deficient: 1 species



Distribution
North America, north Africa, sub-Saharan Africa, central to eastern Europe, west and central Asia, north Asia, and east Asia

Evolution and systematics

The ground-dwelling squirrels are grouped into three tribes: 1. Xerini—the African ground squirrels (*Xerus* and *Atlantoxerus*) and a central-Asian ground squirrel (*Spermophilopsis*); 2. Marmotini—the marmots (*Marmota*), antelope squirrels (*Ammospermophilus*), prairie dogs (*Cynomys*), ground squirrels (*Spermophilus*), and Chinese rock squirrels (*Sciurotamias*); and 3. Tamiini—the chipmunks (*Tamias*). The classification of the 25 species of chipmunks has a long history of debate over whether the group should be one, two, or three genera. Jameson, in 1999, recommended that the single genera *Tamias* is incorrect and that the group should be split into three genera (*Tamias*, *Eutamias*, and *Neotamias*) based on the evolutionary relationships of chipmunk ectoparasites. The molecular work of Piaggio and Spicer in 2001 support Jameson's recommendation.

Climate change, plate tectonics and fluctuations in sea level produced pulses of rapid evolution in the Sciuridae beginning with the initial divergence of the Sciuridae in the late Eocene to early Oligocene. Global cooling and the expansion of grasslands during the late Oligocene gave rise to the evolution of the early ground squirrels. According to Mercer and Roth in 2003, African ground squirrels arose from a single colonization by an Eurasian ancestor after the joining of Africa with Asia approximately 18 to 20 million years ago (mya). Asia and North America were joined across the Bering land bridge allowing the exchange and radiation of tree squirrels, however forests followed by the formation of a marine barrier (7.4 to 4.8 mya) prevented the movement of North American *Marmota* sp. and *Spermophilus* sp. into Asia until after an unforested land bridge was established as glaciers expanded and sea level declined. *Tamias* crossed the land bridge at this time as well but a North American or Eurasian origin of this group is still debated.

Physical characteristics

Ground squirrels are diverse in size with the largest (*Marmota*) being more than 100 times the mass of the smallest (*Tamias*). All ground squirrels are generally short legged with stout bodies and a tail that is generally one third to one half the length of the body.

Fur is typically short and coloration varies among species and groups. Chipmunks have alternating dark and light stripes on both sides of their face and along their backs. The stripes vary in contrast among the species. All the Antelope squirrels and African squirrels, except for one from each group, have a single white stripe down either side of their bodies. Striping is not as common in the *Spermophilus* sp. except in golden mantled ground squirrels *S. lateralis* and *S. saturatus*, which is why they are often confused for chipmunks. However, they lack facial striping that distinguishes them from the chipmunks. One of the most striking patterns for a mammal

Black-tailed prairie dogs (*Cynomys ludovicianus*) basking in the sunshine. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

belongs to the thirteen-lined ground squirrel (*S. tridecemlineatus*), which has 13 alternating dark and light stripes along the back and a row of spots that runs down each dark stripe.

Distribution

The ground-dwelling squirrels are widespread throughout North America, Africa, and Eurasia except for Southeast Asia. Ground squirrels have not invaded South America unlike tree squirrels. More than 70% of the world's ground-dwelling squirrels are endemic to North America, including two genera *Cynomys* and *Ammospermophilus*. Only one species, the arctic ground squirrel *Spermophilus parryii*, is found in North America and Asia. All except one of the 25 species of chipmunks (*Tamias sibericus*) are found in North America.

The Chinese rock squirrels *Sciurotamias* and the long-clawed squirrel *Spermophilopsis* are the only genera endemic to Asia. *Xerus* and *Atlantoxerus* are endemic to Africa. There are no ground squirrel genera endemic to Europe.

An alpine marmot (*Marmota marmota*) showing its teeth, used to eat berries, nuts, grass, and roots. (Photo by Frank Krahmer. Bruce Coleman, Inc. Reproduced by permission.)

A hoary marmot (*Marmota caligata*) carrying nesting material in Glacier National Park, Montana, USA. (Photo by Erwin & Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Habitat

The ground-dwelling squirrels occupy a wide variety of habitat types including desert, prairie, savanna, shrub, temperate forests, subalpine forests, rocky slopes, alpine meadows, and arctic tundra. Chipmunks are most often associated with forests and some will nest in trees. The rest of the ground-dwelling squirrels are mostly terrestrial but are capable of climbing trees or shrubs for access to food or fleeing predators. Nearly all ground-dwelling squirrels construct underground burrows and therefore prefer well-drained sandy or gravelly soils that are not compacted. In cold alpine or arctic climates, permafrost limits the extent of burrowing habitat.

Except for the chipmunks, dense shrubs or closed forests are typically avoided. Ground-dwelling squirrels largely rely on visual detection of their predators and dense vegetation obscures their vision putting them at risk of attack by predators. Stumps, boulders, and other climbable objects provide perches for ground squirrels to survey their surroundings for predators.

Behavior

All of the ground-dwelling squirrels are diurnal. Temperate ground squirrels tend to have bimodal daily activity pat-

Young black-tailed prairie dogs (*Cynomys ludovicianus*) play in Tucson, Arizona, USA. (Photo by © George D. Lepp/Corbis. Reproduced by permission.)

terns during the hot summer months. During the hot periods above-ground activities tend to be concentrated in the mornings and late afternoons to early evening. The animals avoid the heat of the day by escaping below ground to their cool burrows.

The degree of sociality varies widely in the ground-dwelling squirrels from the solitary chipmunks to the highly social marmots. Although there are exceptions, the degree of sociality tends to increase with body size and shortness of the growing season where they live. Large-bodied squirrels, such as the marmots, living at high elevations with short growing seasons tend to be highly social. For example, the hoary marmot (*Marmota caligata*) lives in large family groups of up to 35 animals that include an adult male, several females, and several offspring cohorts. The short growing season prevents large-bodied squirrels from reaching adult size for several years and therefore they tend to delay the age at which they disperse until they reach a sufficient size that improves their success. Other factors influence grouping behavior in squirrels as well. The Cape ground squirrels (*Xerus inauris*) of Africa are unusual among the ground-dwelling squirrels in that the males form groups despite the increase in competition for females. Waterman in 1997 suggested that males live in groups to increase their safety from predators.

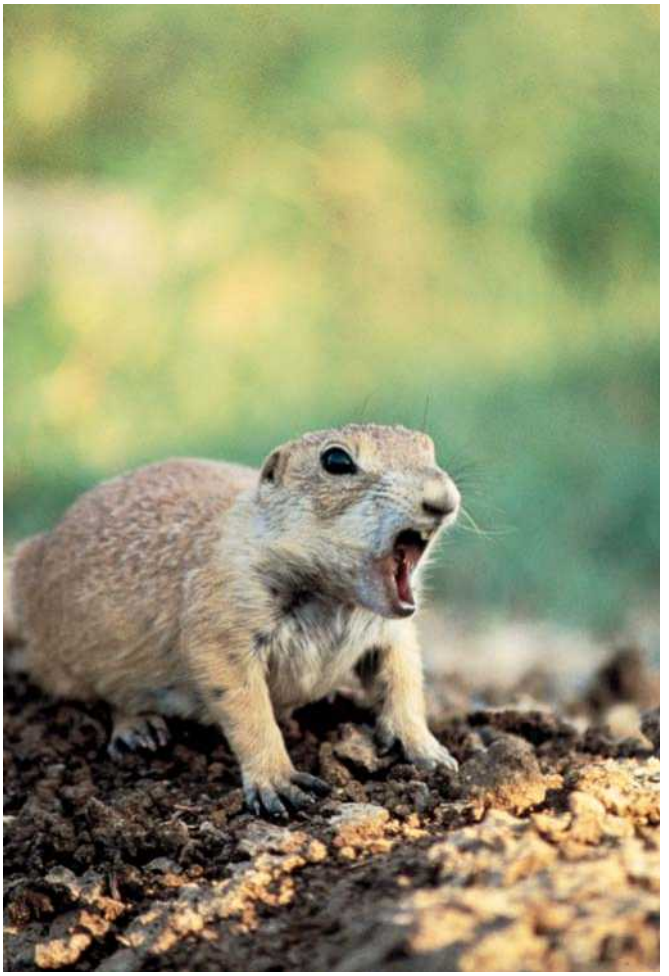
Hibernation is a feature that is prominent in many of the ground-dwelling squirrels. However, the degree of hibernation varies from those that do not hibernate at all such as the Cape ground squirrel (*Xerus inauris*), those that undergo estivation in summer such as Nelson's antelope squirrel, to the majority of ground-dwelling squirrels that hibernate for up to nine months. Although marmots are the largest true hibernating mammal, the arctic ground squirrel is the most extreme. According to Barnes in 1989, the arctic ground squirrel can survive a core body temperature as low as 26.8°F (−2.9°C).

Feeding ecology and diet

Morphologically, the ground-dwelling squirrels are herbivores, however, nearly all of the ground-dwelling squirrels have omnivorous diets to a degree. The diet of some squirrels, such as the chipmunks, are composed primarily of seeds and nuts while the diet of *Spermophilus* and *Marmota* species tend to be composed of mainly grasses and forbs. However, fungi, berries, shrub, and tree buds are important items in the diet of many species. Several species will raid bird's nests for eggs or chicks, and kill and eat small mammals, amphibians, and reptiles. Insects are a small supplement for many species but the Nelson's antelope squirrel will eat primarily insects during the dry season.

Himalayan marmots (*Marmota caudata*) watch for predators. (Photo by Harald Schütz. Reproduced by permission.)

Black-capped marmot (*Marmota camtschatica*) with a cub near its den in the Lena Reserve, Russia. (Photo by L. Veisman. Bruce Coleman, Inc. Reproduced by permission.)



A black-tailed prairie dog (*Cynomys ludovicianus*) threatens an intruder. (Photo by Karen McGougan. Bruce Coleman, Inc. Reproduced by permission.)

Townsend's chipmunk (*Tamias townsendii*) nibbles on a wildflower in Olympic National Park, Washington, USA. (Photo by © Darrell/Corbis. Reproduced by permission.)

Yellow-bellied marmots (*Marmota flaviventris*) exploring abondonded farm equipment, Montana, USA. (Photo by E & P Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Many of the hibernating species, such as *Spermophilus* and *Marmota*, forage intensively during the summer to store fat, sometimes doubling their mass before entering hibernation. Chipmunks hibernate, but most tend not to store fat; instead they cache nuts and seeds that they will access periodically throughout the winter.

Reproductive biology

Hibernation imposes a constraint on reproduction. The preparation and duration of hibernation allow for only a single litter per year. For some species of marmots, many females will skip a year in order to build the necessary energy reserves for reproduction. Remaining spring seed caches allow chipmunks to initiate mating early in the season relative to non-caching hibernating ground squirrels. This early start ensures chipmunks have the opportunity to reproduce again if the first litter fails, or they may successfully raise more than one litter in a good year. Non-hibernating ground squirrels can reproduce more than once per year in good years as they are not constrained by hibernation.

A Belding's ground squirrel (*Spermophilus beldingi*) family emerging from burrow. (Photo by J. VanWormer. Bruce Coleman, Inc. Reproduced by permission.)

Litters tend to be born in underground chambers. The pups are born naked and helpless and remain in the natal nest for 3–5 weeks depending on the species. Weaning usually occurs shortly after pups emerge from the natal chamber and begin foraging for themselves. Mating systems are not well-known.

Conservation status

Ten species of ground-dwelling squirrels are considered threatened, four of which are Endangered. The most critical case is the Vancouver Island marmot (*Marmota vancouverensis*), which has declined severely from the late 1980s possibly owing to changes in landscape from climate and forestry practices. Predation is considered a significant threat to the remaining small colonies. In 2002, only 25 animals were known to live in the wild on Vancouver Island, Canada. Another 63 marmots are in captive breeding facilities with the goal to reintroduce marmots in the near future. The other three endangered species are also in North America and have declined mainly owing to habitat loss from agriculture (*Ammospermophilus nelsoni* and *Cynomys mexicanus*) or fire suppression (*Spermophilus brunneus*). One of the six Vulnerable species is in Europe (*S. citellus*), two are in Asia (*Marmota menzbieri* and *Sci-*

A group of black-tailed prairie dogs (*Cynomys ludovicianus*). (Photo by Scott Nielsen. Bruce Coleman, Inc. Reproduced by permission.)

An eastern chipmunk (*Tamias striatus*) with cheek pouches filled. (Photo by Leoard Lee Rue III. Bruce Coleman, Inc. Reproduced by permission.)

urotamias forresti), and three are in North America (*Spermophilus mohavensis*, *S. washingtoni*, and *Tamias palmeri*). All suffer from habitat loss and fragmentation.

Six species are Near Threatened, two of which are in Asia and four in North America. Most are threatened from habitat loss primarily from agriculture, however, the sylvatic plague is a major threat to the persistence of the black-tailed prairie dog (*Cynomys ludovicianus*).

Significance to humans

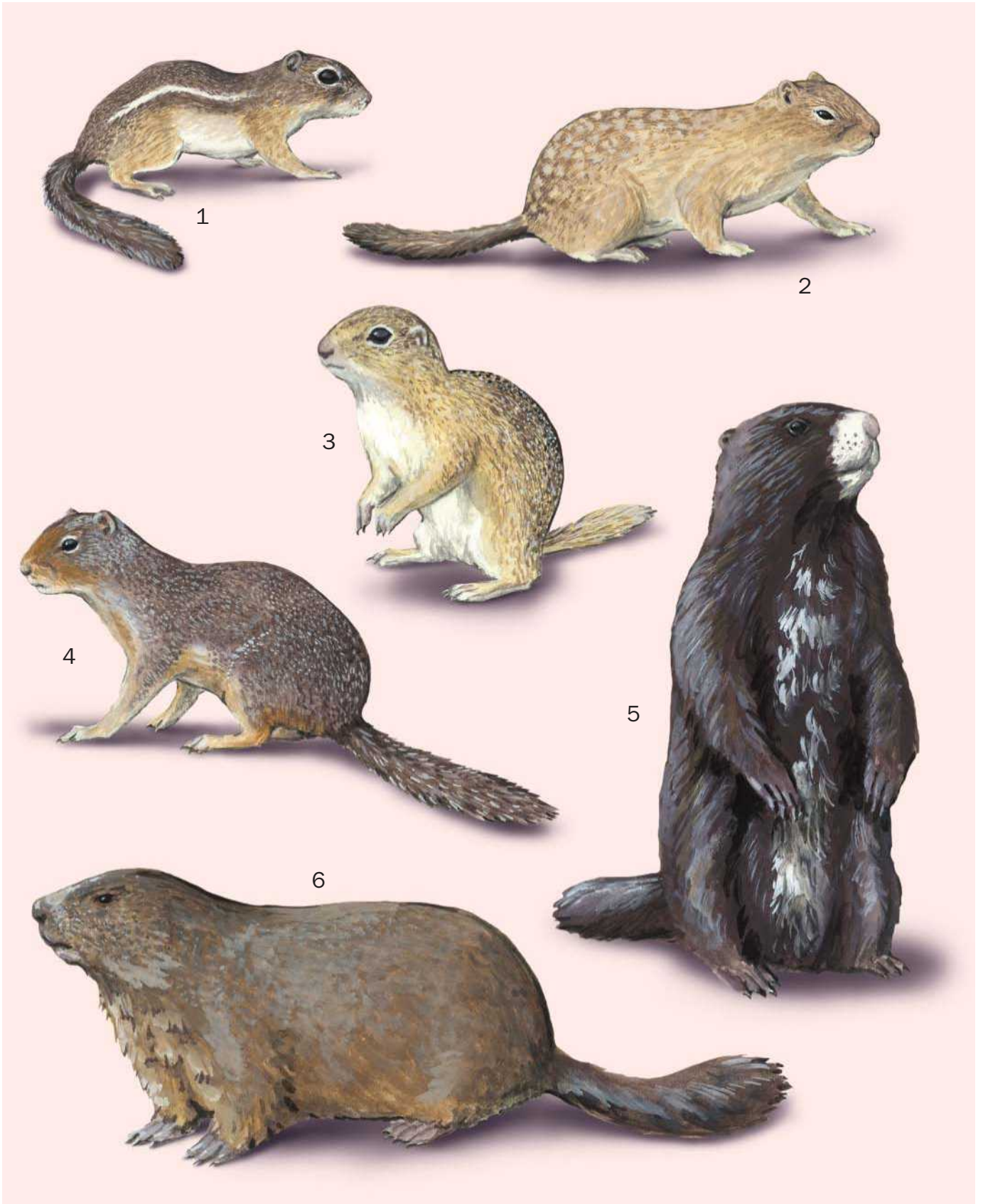
Cave paintings of marmots in France provide evidence that ground-dwelling squirrels and humans interacted as long ago as the mid to late Pleistocene. Historically, marmots were an important source of fat, fur, and meat for early Europeans and an important source of food in Asia. Mongolians did not use marmot skins traditionally but during the twentieth century marmot fur became fashionable in Europe. It is estimated that from 1906 to 1994, Mongolians prepared approximately 132,700 marmot skins per year.

Many of the ground squirrel species are considered agricultural pests. They raid crops, compete with domestic livestock for food, and dig burrows that are hazardous to livestock resulting in government sponsored large scale extermination programs.

Some ground-dwelling squirrels are vectors for human diseases such as Rocky Mountain spotted fever and the bubonic plague. Marmots in central Asia are a significant carrier of the plague and therefore a risk to marmot hunters. In Mongolia, marmot hunting is banned in areas known to have plague, yet, without hunting, marmot populations and the area of plague increase. At the same time, plague-free marmot populations are hunted and decreasing—therefore new management policies are required to reduce plague while conserving marmot populations.

An Olympic marmot (*Marmota olympus*) basking in the sun in Grand Valley, Idaho, USA. (Photo by Lee Rentz. Bruce Coleman, Inc. Reproduced by permission.)

1. Eastern chipmunk (*Tamias striatus*); 2. Least chipmunk (*Tamias minimus*); 3. Woodchuck (*Marmota monax*); 4. Arctic ground squirrel (*Spermophilus parryii*); 5. Black-tailed prairie dog (*Cynomys ludovicianus*); 6. South African ground squirrel (*Xerus inauris*). (Illustration by Brian Cressman)



1. Harris's antelope squirrel (*Ammospermophilus harrisii*); 2. Idaho ground squirrel (*Spermophilus brunneus*); 3. European ground squirrel (*Spermophilus citellus*); 4. Columbian ground squirrel (*Spermophilus columbianus*); 5. Vancouver Island marmot (*Marmota vancouverensis*); 6. Alpine marmot (*Marmota marmota*). (Illustration by Brian Cressman)

Species accounts

Arctic ground squirrel
Spermophilus parryii

TAXONOMY
Arctomys parryii (Richardson, 1825), Hudson Bay, Canada. Seventeen subspecies.

OTHER COMMON NAMES
English: Parka squirrel, Arctic souslik; French: Spermophile arctique; German: Arktisches Erdhörnchen; Spanish: Ardilla terrestre ártica.

PHYSICAL CHARACTERISTICS
Females: 13.7–16.7 in (34.8–42.5 cm), 17.8–35.6 oz (506–1,010 g). Males: 14.8–17.1 in (37.7–43.5 cm), 26.1–36.2 oz (740–1,026 g). Head and shoulders cinnamon or tawny colored; back is grayish or buffy brown with white spots. Melanistic forms that are completely black occur in high frequency in the south central Yukon Territory, Canada.

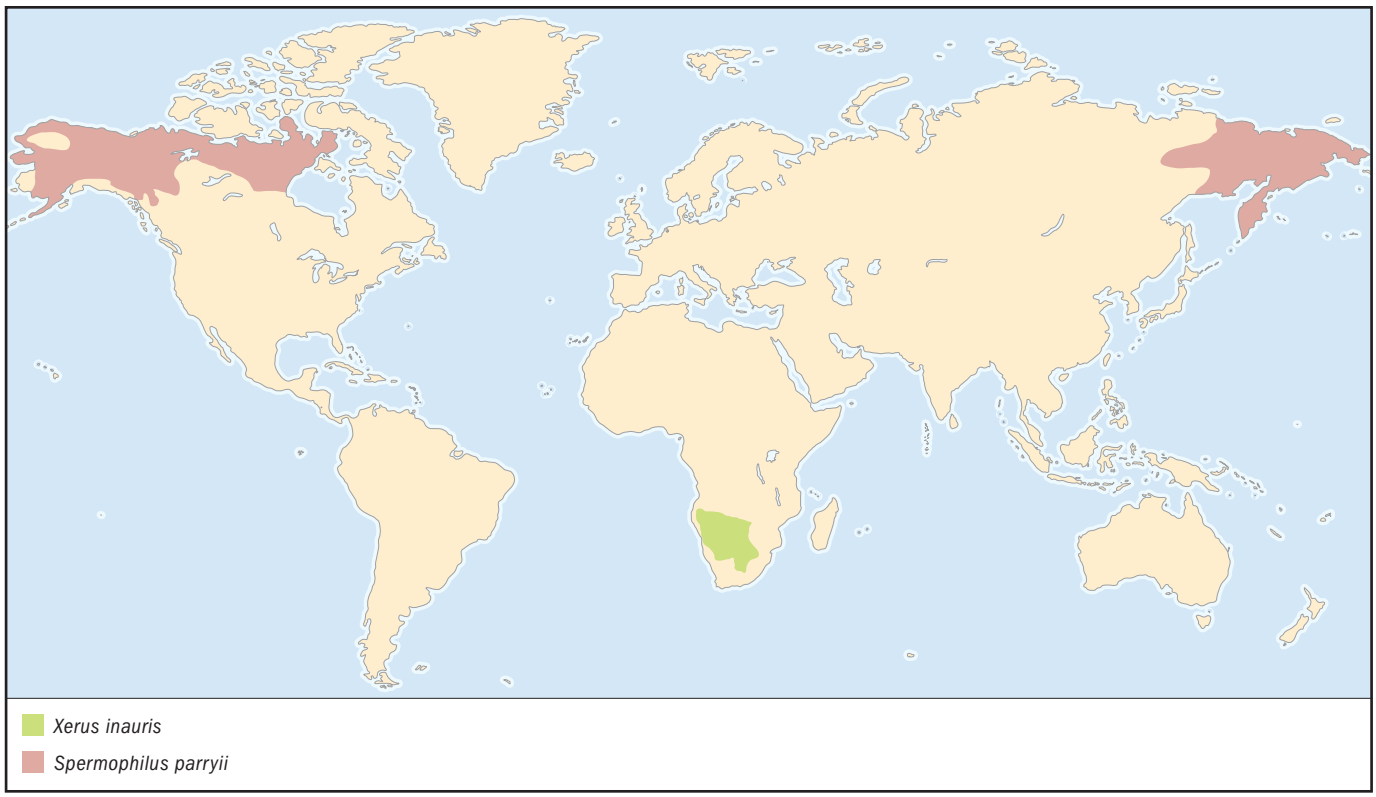
DISTRIBUTION
Eastern Siberia including the Kamtchatka peninsula; northwest North America from Alaska to Hudson Bay, Canada. In Canada, occurs as far south as northwest British Columbia.

HABITAT
Restricted to gravel and sandy areas with good drainage. In arctic habitats burrows are constructed along river banks, lake shores and on moraines and eskers; in alpine habitats, burrows are constructed on stream banks, slopes, and the leading faces of solifluction lobes; in the northern boreal forests, habitat preference is similar to that of the arctic and alpine habitats but also lives along forest edges and clearings.

BEHAVIOR
Lives in small clusters of related females that overlap with the home range of at least one territorial male. Males establish breeding territories immediately after emergence from hibernation in mid April and defend them aggressively against other males. Nearly half of the males die during this period. Males that survive disperse to new territories before hibernation. Juvenile dispersal is male biased and occurs before their first winter hibernation. Adult females enter hibernation beginning in August followed by adult males and juveniles through September.

FEEDING ECOLOGY AND DIET
Eats mainly forbs with a preference for legumes. Will prey upon lemmings (*Dicrostonyx torquatus*), newborn snowshoe hares (*Lepus americanus*), and birds' nests. Will consume insects and carrion. Males collect and cache seeds below ground for access during early spring.

REPRODUCTIVE BIOLOGY
Females emerge 2–3 weeks after males. Breeding occurs 3–4 days later during late April to early May. Nearly the entire population breeds, including yearlings. Promiscuous, but first



male sires approximately 90% of pups. Four to ten pups (maximum 12) are born in an underground natal chamber after 25 days gestation. Young appear above ground 27 days after birth.

CONSERVATION STATUS
Three subspecies restricted to a few islands off the coast of Alaska (*S. p. kodiacensis*, *S. p. lyratus*, and *Citellus undulatus nebulicola*) are classified by the IUCN as Data Deficient. Populations of subspecies *S. p. plesius* in the boreal forest cycle in abundance from 0.2 to 6.9 per acre (0.1 to 2.8 per ha) over an 8-year period. Local extinctions may occur when squirrels are at their cyclic low. Persistent organic pollutants and heavy metals have been detected in squirrels from northern Alaska but levels were low compared with other arctic species.

SIGNIFICANCE TO HUMANS
Northern indigenous people hunt squirrels for food and fur for clothing. ◆

Least chipmunk
Tamias minimus

TAXONOMY
Eutamias minimus (Bachman, 1839), Sweetwater County, Wyoming, United States. Twenty-two subspecies.

OTHER COMMON NAMES
English: Western chipmunk, little chipmunk; French: Tamia mineur; German: Kleiner Chipmunk.

PHYSICAL CHARACTERISTICS
Smallest squirrel. 7.2–9.4 in (18.3–23.9 cm); 1.3–1.8 oz (35.9–50.3 g). Varies in color seasonally and regionally. Yellowish gray to brownish gray. Three dark brown stripes on each cheek separated by two narrow white stripes running nose to ear. Dorsally there are five black stripes edged in brown and separated by four narrower gray stripes.

DISTRIBUTION
Throughout the boreal forests of Canada from the western Yukon to east of the Ontario-Quebec border and south through the Rocky Mountains to Arizona and New Mexico.

HABITAT
Primarily associated with open coniferous forests and forest edges but occurs in a wide range of other habitats including deciduous forests, sagebrush, riparian areas, and alpine tundra. Winter nests are constructed below ground for protection from cold. Summer nests can be in hollow logs, stumps, tree cavities, rock piles, under debris, or in excavated burrows. Entrances of excavated burrows are preferentially constructed under a rock or other object for protection.

BEHAVIOR
Active from late April or May to September. Gives a distinctive high pitched "chip-chip" call. While foraging among buried seed caches, these chipmunks will often urinate on the patch before leaving. A study at the University of Oklahoma by Lynn Devenport and others has shown that this behavior acts to deter the marker and other chipmunks from visiting that patch again. They believe that this increases foraging efficiency by advertising seed caches that are already depleted.

FEEDING ECOLOGY AND DIET
Forages primarily for seeds, nuts, berries, and acorns. Fruit and berries are harvested only for their seeds, the rest is discarded. Also will prey upon insects, bird's eggs, and chicks. Instead of storing fat like other hibernating rodents such as marmots, least chipmunks store seeds in their winter chamber. They interrupt torpor throughout the winter to feed from these seed caches.

REPRODUCTIVE BIOLOGY
Breeding occurs soon after emergence from hibernation. Gestation is 28–30 days. Litters with an average of 5 pups (maximum 7) arrive in mid-May. A second litter is attempted if the first one is lost.

CONSERVATION STATUS
Two subspecies are of special conservation concern because of their restricted distributions. *T. m. astristriatus* is classified as Critically Endangered and consists of a small population restricted to a single glacial cirque in New Mexico. *T. m. selkirki* classified as Vulnerable and is restricted to less than 40 mi^2 (100 km^2) within the Purcell Mountains in British Columbia, Canada.

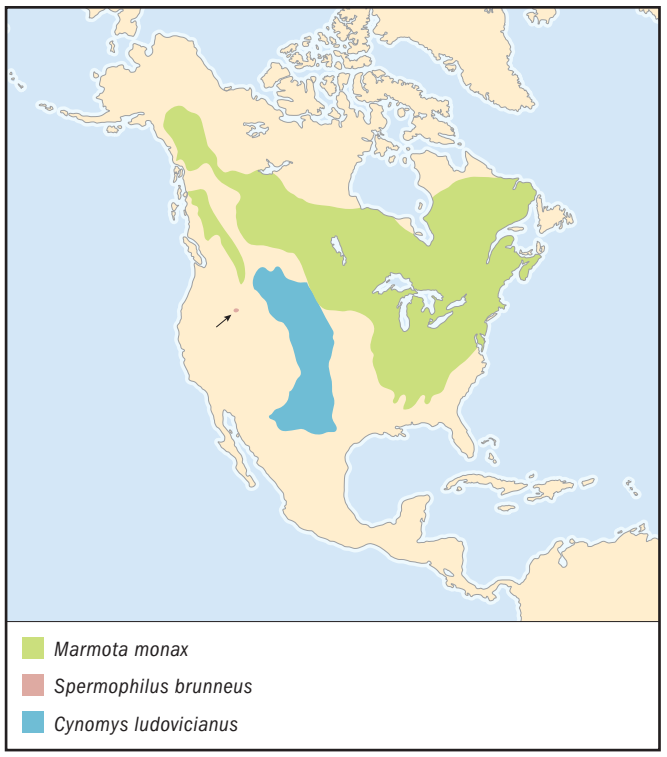
SIGNIFICANCE TO HUMANS
None known. ◆

Woodchuck
Marmota monax

TAXONOMY
Mus monax (Linnaeus, 1758), Maryland, United States. Eleven subspecies.

OTHER COMMON NAMES
English: Groundhog, forest marmot, whistle pig; French: Marmotte commune; German: Waldmurmeltier; Spanish: Marmota canadiense.

PHYSICAL CHARACTERISTICS
16.5–26.2 in (41.8–66.5 cm), females 6.8–10.6 lb (3.1–4.8 kg); males 6.8–11.2 lb (3.1–5.1 kg). The underfur is gray with yel-



low tips, and the guard hairs are banded yellowish to reddish brown with white tips.

DISTRIBUTION
Central Alaska through Yukon and below Great Slave Lake, Northwest Territories to Labrador. The eastern range extends south to Georgia, Alabama, northwestern Louisiana, and Arkansas. The western range extends south through central British Columbia into northern Idaho.

HABITAT
Generally found in low elevation woodland-field ecotones, foraging in meadows, orchards, and pastures. Hibernacula preferentially constructed in soils with good drainage in hedgerows, woods, south-facing inclines, rocky areas, and even haystacks.

BEHAVIOR
The Latin word *monax* means solitary and is appropriately assigned to the woodchuck because it is the only asocial marmot except during breeding and raising of pups. Dominant males aggressively defend hibernacula of females while subordinate males are transient. Approximately 65% of juvenile females and 90% of juvenile males disperse before their first hibernation, the rest remain within the natal home range and disperse the following year. Activity peaks in mid-day during spring and late summer. Although the woodchuck can facilitate heat loss through their feet and nose they will avoid the afternoon heat during mid-summer by seeking refuge in their burrows.

FEEDING ECOLOGY AND DIET
Alfalfa, clover, and dandelions are highly preferred but also forage on a wide variety of other plants and grasses. They have also been observed foraging for bark, twigs, and leaves in various shrubs and trees. Invertebrates and birds' eggs are also eaten.

REPRODUCTIVE BIOLOGY
Breeding occurs shortly after emergence from hibernation, which varies from February to March in southern areas of its range (New York and Pennsylvania) and March to April in more northern areas (Ontario). Pregnancy rates are lower for yearling females (10–25%) than for adult females (56–80%). Gestation is 31–32 days. Only a single litter of 3.4 to 4.6 pups are born per year per female. Litters up to nine pups have been observed. Young are weaned at 44 days.

CONSERVATION STATUS
Not threatened. Populations have proliferated in response to agriculture.

SIGNIFICANCE TO HUMANS
The woodchuck is celebrated annually in North America on Groundhog Day, February 2, for its spring prophecy. The folklore is that if the woodchuck sees its shadow on that day then the woodchuck will stay above ground because spring is close. If the woodchuck see its shadow, it will return to its den since there will be another six weeks of winter. Woodchucks are used as an animal model in studies of many human medical concerns in metabolism, endocrinology, reproduction, and neurology. They are used extensively in research on the hepatitis B virus (HBV) that can cause chronic liver damage in humans. A related virus known as woodchuck hepatitis virus causes a similar disease in woodchucks as HBV does in humans and therefore serves as a good animal model for studying infection and treatments of HBV in humans. Woodchucks are considered an agricultural pest. ◆

Eastern chipmunk
Tamias striatus

TAXONOMY
Sciuris striatus (Linnaeus, 1758), Upper Savannah River, South Carolina, United States. Eleven subspecies.

OTHER COMMON NAMES
English: Chipping squirrel; French: Suisse, tamia rayé, tamia strié; German: Östliches Chipmunk.

PHYSICAL CHARACTERISTICS
Largest chipmunk. 8.9–10.6 in (22.5–26.8 cm); 2.8–4.4 oz (80–125 g). Grayish to reddish brown with five black stripes from neck to base of tail. Two lateral black stripes are separated by a cream-colored stripe while the median stripe is bordered on each side by a grayish to reddish orange stripe.

DISTRIBUTION
Ranges from southern Manitoba east to Nova Scotia and from James Bay south to the states bordering on the gulf of Mexico.

HABITAT
Mainly lives in deciduous forests with cover provided by rocks, stumps, logs, banks, bushes, and brush piles, but will live in more open bushy areas. Extensive burrow systems are constructed below ground.

BEHAVIOR
A solitary chipmunk with only one individual in a burrow system except when offspring are present. Home ranges, 0.07 to 1.0 acre (0.03–0.40 ha), overlap but core areas are defended by their owner with short chases of the intruder. Natal dispersal is male biased such that only 15% of juvenile males settle near their mothers while 26% of females settle within one home range of their mothers.

FEEDING ECOLOGY AND DIET
Diet consists mainly of seeds, nuts, and vegetation but will also eat fungi, invertebrates, amphibians, snakes, birds, and other small mammals. Although chipmunks hibernate, they do not store energy for hibernation as fat, but instead they hoard large quantities of seeds and nuts from oak, beech, and maple from which they will forage from intermittently during the winter. Chipmunks can accumulate up to 165 acorns per day and they store far more acorns then is required for hibernation. At peak hoarding periods during late September to early October, the entire hibernation energy budget equivalent in acorns can be accumulated in only one to two days. This surplus food may be important for many reasons, such as insurance against spoilage or pilfering, or as a supplemental source of food during reproduction or possibly a subsequent hibernation period.

REPRODUCTIVE BIOLOGY
Breeding occurs between late February and April and again from late June to early July. Gestation is 31–32 days with litter size averages of four to five. Juveniles emerge from their natal burrows 5–7 weeks after birth. Adult size is reached within three months. Reproductive maturity is usually not obtained until after their first winter hibernation, however, some early born females can breed in the same year.

CONSERVATION STATUS
Not threatened. Responses of chipmunks to forest fragmentation are mixed however, studies showing negative responses point out the importance of maintaining or creating movement corridors.

SIGNIFICANCE TO HUMANS
None known. ◆

South African ground squirrel
Xerus inauris

TAXONOMY
Xerus inauris Zimmermann, 1780, 100 mi (160 km) north of Cape of Good Hope, South Africa. Seven subspecies.

OTHER COMMON NAMES
English: Cape ground squirrel; French: Écureuil foisseur de cap; German: Kap-erdhornchen.

PHYSICAL CHARACTERISTICS
11–15 in (28–38 cm); 1.1–2.4 lb (500–1,100 g). Tawny-yellow with a lateral white stripe on either side. Tail hairs have two dark bands.

DISTRIBUTION
Range includes Namibia, Botswana, Zimbabwe, and South Africa.

HABITAT
Open arid country with compacted sandy areas for digging communal burrows.

BEHAVIOR
South African ground squirrels do not hibernate. They are highly social, living in kin groups of one to three adult females and usually two to three, but up to nine male and/or female subadults. This species is interesting in that mature males form their own groups, referred to as bands, which can include up to 19 individuals. These bands roam over a home range that is shared with several groups. This is an unusual behavior in mammals because of typical male competition for females. Survival advantages of group living for detection and deterrence of predators outweigh the disadvantages to breeding opportunities from competition.

FEEDING ECOLOGY AND DIET
Diet of grasses, shrubs, roots, bulbs, seeds, and fruit. Also eats insects.

REPRODUCTIVE BIOLOGY
Breeding is asynchronous and can occur at any time of the year although fewer litters appear above ground from July through October. Gestation is 48 days and juveniles are weaned 52 days later. Litter sizes at emergence from the natal burrow range from one to three pups. Females become reproductively mature at age of ten months. Males become reproductive mature earlier at about 8 months. Females are capable of breeding several times during the year but fewer than 10% actually wean more than one litter during a year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Black-tailed prairie dog
Cynomys ludovicianus

TAXONOMY
Arctomys ludoviciana (Ord, 1815), Upper Missouri River. Seven subspecies.

OTHER COMMON NAMES
French: Chien de prairie, cynomys social; German: Schwarzschwanz-Präriehund; Spanish: Perrito de la pradera.

PHYSICAL CHARACTERISTICS
14.0–15.7 in (35.5–39.8 cm); males: 26.5–31.9 oz (750–905 g), females 24.3–28.9 oz (689–819 g). Brown or reddish brown, whitish below.

DISTRIBUTION
In Canada, restricted to southern Saskatchewan. In the United States, exists from Montana east to eastern Nebraska and as far south as Mexico; extirpated from Arizona.

HABITAT
Prefers open, flat, and arid short-grass plains. Can live in tall-grass prairies where grazing by other animals has lowered vegetation height.

BEHAVIOR
Live in family groups called coteries that are typically composed of a single adult male, two or three adult females and several nonbreeding yearlings and juveniles. Black-tailed prairie dogs do not hibernate for the winter but instead enter short one to three day torpor periods when under extreme cold and food deprived conditions.

FEEDING ECOLOGY AND DIET
Diet consists mainly of grasses, but other forbs are also eaten. Dietary preferences vary seasonally with strong preferences for prickly pear (*Opuntia*) during winter possibly because of its high lipid content relative to other plant species during winter.

REPRODUCTIVE BIOLOGY
Breeding is synchronous and occurs from February to March. Gestation is 35 days. Average length of lactation is 43 days but varies with litter size from 37–51 days. Average litter size of emerging pups is 3.1 and varies from one to six. Generally, prairie dogs are not sexually mature until after their second winter, although 9% of females and 2% of males breed as yearlings.

CONSERVATION STATUS
Although estimates of the historical habitat area occupied by black-tailed prairie dogs varies from 99 million to 384 million acres (40–155 million ha), the United States Fish and Wildlife Service in 2002 estimated the occupied habitat in 2001 at 1.4 million acres (0.6 million ha) indicating that less than 1.5% of the historical range is occupied. From 2000 to 2002, the United States Fish and Wildlife Service has identified the black-tailed prairie dog as a candidate for listing as threatened under the U. S. Endangered Species Act. In Canada, the species has been listed as Special Concern from 1978 to 2000 by the Committee on the Status of Wildlife in Canada (COSEWIC). Internationally, the IUCN lists the species as Lower Risk/Near Threatened as of 1998. Prairie dogs were initially threatened from 1880 to 1920 by conversion of grassland to prairie and from 1918 to 1972 by widespread chemical control to reduce competition between prairie dogs and livestock. The greatest threat from the late 1980s to 2001 has been sylvatic plague, an exotic disease first accidentally introduced in the early 1900s.

SIGNIFICANCE TO HUMANS
Viewed as a pest by ranchers and farmers because of threat of burrow to livestock and competition with livestock for food. In prairie dog towns, plant productivity and quality is better and wild ungulates prefer to graze there. ◆

European ground squirrel
Spermophilus citellus

TAXONOMY
Mus citellus (Linnaeus, 1766), Wagram Niederosterrich, Austria. Nine subspecies.

OTHER COMMON NAMES
English: European souslik; French: Souslik d'Europe, souslik tacheté; German: Europäischer Ziesel, Perlziesel; Spanish: Ardilla terrestre, suslik europeo.

PHYSICAL CHARACTERISTICS
8.4–12.0 in (21.4–30.4 cm), 6.3–12.3 oz (180–350 g). Yellow-gray with small dense cream-colored spots on back. Yellow underneath.

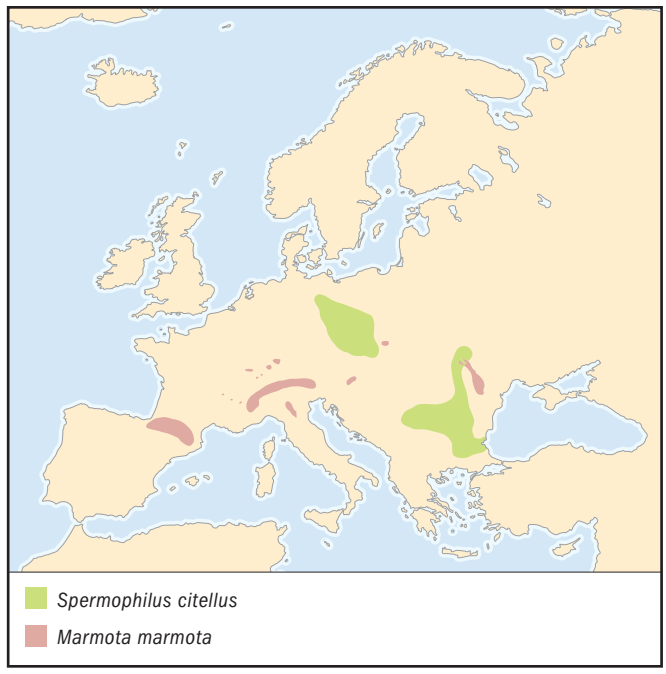
DISTRIBUTION
Central southeast Germany to western Ukraine.

HABITAT
Steppe and open woodland.

BEHAVIOR
A relatively asocial and non-territorial species that lives in loosely structured populations. More than 60% of the population is female because of higher mortality of juvenile and yearling males during hibernation and dispersal. Hibernation begins in late August–September and ends late March–April.

FEEDING ECOLOGY AND DIET
Primarily grasses and other herbs.

REPRODUCTIVE BIOLOGY
A polygynous mating system where males scramble for access to females shortly after the females emerge from hibernation. Females will mate with only one male during the annual 3- to 4-week breeding period. Gestation is 25 days. Litter size at emergence is 4–11. Lactation is approximately 30 days. Sexual maturity is obtained after the first hibernation. All adult males



and 78–90% of yearling males are capable of reproducing during the breeding season. More than 90% of yearling and adult females breed, although only about a third successfully wean their litter.

CONSERVATION STATUS
Assessed as Vulnerable in 1996 by the IUCN. Major threat is the loss of habitat from agricultural practices.

SIGNIFICANCE TO HUMANS
Considered an agricultural pest during second half of twentieth century. ◆

Harris's antelope squirrel
Ammospermophilus harrisii

TAXONOMY
Spermophilus harrisii Audubon and Bachman, 1854, Santa Cruz county, Arizona, United States. Two subspecies.

OTHER COMMON NAMES
English: Yuma antelope squirrel; German: Harris-Antilopen Zeisel.

PHYSICAL CHARACTERISTICS
9.0–9.7 in (22.9–24.6 cm), 4.3–5.3 oz (122–150 g). Brown to dark gray in winter, lighter in summer. White stripe along each side. No white under tail unlike the other *Ammospermophilus* sp.

DISTRIBUTION
Southern Arizona, extreme southwest New Mexico, and northwest Mexico.

HABITAT
Various open and sparsely vegetated desert habitats. Habitats include sandy, gravely, pebbly, and rocky substrates with various desert plant communities of grasses, shrubs, and cacti.

BEHAVIOR
An asocial species that is active all year, although may remain below ground during cold weather feeding on stored seeds. Often seen standing vigilant on top of cacti *Opuntia*.

FEEDING ECOLOGY AND DIET
Feeds on fruit, seeds, and fleshy parts of cacti, and seeds of shrubs. Seeds are transported in cheek pouches to burrows for consuming when environmental conditions are poor.

REPRODUCTIVE BIOLOGY
The mating system has not been described. Breeding period typically February to March but may be as early as December. Gestation is 30 days. Litters of 6–7 young emerge from natal burrows at 4–5 weeks and are weaned at 7 weeks. Sexual maturity is reached after first winter. Usually a single litter per year, sometimes two.

CONSERVATION STATUS
Listed as Imperiled in New Mexico by the New Mexico Natural Heritage Program in 1997.

SIGNIFICANCE TO HUMANS
Considered an agricultural pest. ◆

Vancouver Island marmot
Marmota vancouverensis

TAXONOMY
Marmota vancouverensis Swarth, 1911, Mt. Douglas, Vancouver Island, British Columbia.

OTHER COMMON NAMES
French: Marmotte de l'île Vancouver; German: Vancouver-Murmeltier.

PHYSICAL CHARACTERISTICS
Males: 27.4 in (69.5 cm), 7.7–15.0 lb (3.5–6.8 kg); females: 26.0 in (66.1 cm), 6.6–14.3 kg (3.0–6.5 kg). Dark brown fur fades during summer to a cinnamon color. Adults have dark and lighter brown patchy appearance during molt. White patches on chest, nose, and chin, and white streak on top of head.

DISTRIBUTION
Restricted to Vancouver Island, British Columbia, Canada.

HABITAT
Meadows and open forests from 3,600–3,750 ft (1,100–1,140 m) but will live at lower elevations above 2,300 ft (700 m) in clearings created by forests harvesting.

BEHAVIOR
The social structure of the Vancouver Island marmot is not well known. It is a highly social marmot that lives in colonies in natural subalpine and clearcut areas. A colony may be composed of one or more family groups. Colonies of adults, subadults, yearlings and juveniles in natural subalpine areas can have up to 15 individuals and in clearcut areas up to 27. A particular vocalization "kee-aw" is unique among the marmots.

FEEDING ECOLOGY AND DIET
Diet is mostly forbs and grasses, but will also eat ferns and some berries. Diet varies seasonally with grasses being dominant in early spring and forbs dominant during summer.

REPRODUCTIVE BIOLOGY
Litter size averages 3.4 with a range of 2–5. Average age of first reproduction is four years but can reproduce at age three. Although females are capable or producing litters in subsequent years, most females produce litters in alternate years.

CONSERVATION STATUS
Classified as Endangered by the IUCN and Committee on the Status of Endangered Wildlife in Canada (COSEWIC). According to the Vancouver Island Marmot Recovery Foundation only 25 marmots were known to exist in the wild in fall of 2002. Captive breeding programs began in 1997 for future reintroduction. As of fall 2002, 63 marmots were distributed among facilities in Toronto, Calgary, Vancouver, and on Mt. Washington on Vancouver Island for future reintroduction. The reason for the decline is not certain but may involve one or more factors including the gradual reduction of alpine habitat with climate change, landscape change from forestry practices, and changes in number or behavior of predators.

SIGNIFICANCE TO HUMANS
None known. ◆

Alpine marmot
Marmota marmota

TAXONOMY
Mus marmota (Linnaeus, 1758), Swiss Alps. Six subspecies.

OTHER COMMON NAMES
French: Marmotte des Alpes; German: Alpenmurmeltier; Spanish: Marmotta alpina.

PHYSICAL CHARACTERISTICS
Males: 26 in (67 cm); Males 5.1–12.6 lb (2.3–5.6 kg); females: 5.2–11 lb (2.3–4.9 kg). Fur color varies among populations from gray to red and sometimes blond. A white bridge occurs on the nose.

DISTRIBUTION
Swiss, Italian, and French Alps; western Austria and southern Germany; and Carpathian and Tatra Mountains. Has been introduced into French Pyrennes, eastern Austria, and former Yugoslavia.

HABITAT
Lives in subalpine clearings and alpine from 4,300 to 9,800 ft (1300–3000 m). Prefers southern exposures.

BEHAVIOR
Lives as family groups typically composed of an adult pair and their offspring, which can include newborn to up to 4-year old offspring. Hibernates from September to mid-April or May as a family group. Juveniles benefit from hibernating in a group especially in the presence of older male siblings. Closely related subordinate males assist in thermoregulating their younger offspring. Groups with only the adult pair and a litter of juveniles have a greater probability of dying out over winter.

FEEDING ECOLOGY AND DIET
Feeds on a wide variety of leaves and flowers of herbaceous plants and grasses.

REPRODUCTIVE BIOLOGY
Breeding occurs once a year a few days after emergence from hibernation. Gestation is 33–34 days. Average litter size of 3–4 with range of 1–7. Weaned at 40 days. Reproductively mature at two years old but reproduction in mature offspring of both sexes is suppressed by the parent of the same sex as long as the offspring remains in the family group. Monogamy is the dominant mating system for Alpine marmots in the French Alps, dominant males sire only two thirds of litters, the other litters are likely sired by lone males living outside of the family group.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Evidence of the use of Alpine marmots by humans dates to the mid to late Pleistocene. In Europe they have been a source of fur, meat, and fat during most of the last millenium. However, as agriculture increased over the last 500 years marmots were less relied on as a source of food for people. Instead, they were considered agricultural pests and a source of food for shepherd's dogs. In an age of ecotourism, the Alpine marmot is a symbol of the Alps. Nowhere is this more evident then on Mount Roches de Nayes, near Montreux, Switzerland, where you will find an education facility built in 2001 that showcases the Alpine marmot and other marmots of the world. ◆

Columbian ground squirrel
Spermophilus columbianus

TAXONOMY
Arctomys columbianus (Ord, 1815), between the forks of the Clearwater and Kooskooskie Rivers, Idaho County, Idaho, United States. Four subspecies.

OTHER COMMON NAMES
French: Spermophile du Columbia; German: Columbia Ziesel.

PHYSICAL CHARACTERISTICS
12.8–16.1 in (32.5–41.0 cm), males: 14.3–24.7 oz (405–699 g); females: 12.2–18.7 oz (347–529 g). Nose and face are tawny and body is grayish to tawny, belly and feet are cinnamon.

DISTRIBUTION
Rocky Mountains of eastern British Columbia and western Alberta. South along the Rocky Mountains into western Montana and central Idaho. Lives as far west as south central British Columbia, eastern Washington, and northeastern Oregon.

HABITAT
Subalpine to alpine meadows with sandy to coarse substrates for burrowing. Prefers to hibernate in areas where snow accumulates, such as in shallow depressions, or under shrubs.

BEHAVIOR
Lives in clusters of related females that overlap in range with an adult male. Male home ranges overlap some but during the breeding season they defend a core territory that includes several reproductively mature females. Females will defend the natal burrow of pre-weaned young from all other squirrels, including the adult male. Dispersal is male-biased and occurs after a squirrel's first hibernation. Hibernation is from August–October to April. Adults are active above ground for approximately 100 days.

FEEDING ECOLOGY AND DIET
Polygymous. Consume a variety of forbs and grasses with preference for forbs. Will consume invertebrates and carrion. Males will cache seeds in the fall for consumption in early spring.

REPRODUCTIVE BIOLOGY
Breeding commences a few days after females emerge from hibernation. Gestation is 24 days and lactation lasts for about 30 days. A single litter per year averages 2.3–4.6 pups with a maximum of 7. Only about 15% of yearling females breed on average but more can breed if spring conditions are good.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Considered an agricultural pest that competes with livestock for food. Intermediate host for the Rocky Mountain wood tick (*Dermacentor andersoni*), which can carry Rocky Mountain spotted fever in the United States. Can also carry the bubonic plague *Yersinia pestis*, which can be transmitted to humans through flea bites. ◆

Idaho ground squirrel
Spermophilus brunneus

TAXONOMY
Spermophilus brunneus Howell, 1928, Adams County, New Meadows, Idaho. Two subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
8.2–10.2 in (20.9–25.8 cm), 3.5–4.6 oz (99–131 g). Brown with small white spots. Legs, nose, and underneath of tail are rufous. Has prominent whitish eye ring.

DISTRIBUTION
Endemic to west central Idaho, United States.

HABITAT
Northern population lives in xeric meadows at 3,800–5,100 ft (1,150–1,550 m) surrounded by forest of Ponderosa pine and Douglas fir. Southern population lives in xeric meadows at 2,200–3,200 ft (670–975 m). Digs burrows often under rocks and logs in well-drained soils.

BEHAVIOR
An asocial species in which there is no association between males and females except for breeding. Young of both sexes disperse within several days after emerging from their natal chambers. The southern population at lower elevation is active above ground from late January–early February to late June–early July. The season is approximately 6–8 weeks later at the northern high elevation population.

FEEDING ECOLOGY AND DIET
Preferences for herbaceous leaves, flowers, bulbs and grasses. Diet shifts towards seeds later in the season. Will eat invertebrates and fungi.

REPRODUCTIVE BIOLOGY
Mating occurs shortly after emergence from hibernation. During the breeding season, males over two years old guard sexually receptive females from other males until they are mated, then they may search for other receptive females. Gestation is approximately three weeks and litters are weaned in approximately another three weeks. Average litter size is five but can be as high as 10.

CONSERVATION STATUS
The IUCN has classified the northern population (*S. b. brunneus*) as Critically Endangered, and the southern population (*S. b. endemicus*) as Vulnerable. According to Sherman and Runge in 2002, who studied the northern population from 1987 to 1999, the likely explanation for its collapse is a combination of fire suppression, exotic grasses, drying, and grazing that have reduced native seeds that are a critical component of their diet. The northern subspecies (*S. b. brunneus*) was listed as Threatened under the United States Endangered Species Act in April 2000. The southern subspecies (*S. b. endemicus*) was listed as a candidate for listing by the United States Fish and Wildlife Service in 2001.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Yellow-bellied marmot *Marmota flaviventris* French: Marmotte à ventre fauve; German: Gelbbäuchiges Murmeltier	Yellow-brown to tawny with yellow or orange to russet belly. Cream colored bar across nose. Body length 18.5–27.6 in (47–70 cm), male weight 6.5–11.5 (3.0–5.2 kg), female weight 3.5–8.7 lb (1.6–4.0 kg).	Female kin groups with a dominant territorial male. Half of daughters remain in group, all sons disperse. Lives on 0.5–17.8 acre (0.2–7.2 ha) habitat patches of well drained soils, rocky outcrops, or boulders in open meadows from valley bottoms to alpine.	In Canada only in south-central British Columbia and extreme southern Alberta. In the United States from central Washington east to central Montana and south to mountains of central California and northern New Mexico.	Selectively forage among a variety of forbs and grasses.	Not threatened
Siberian chipmunk *Tamias sibiricus* English: Burunduk; French: Ecureuil rayé de Sibérie Burunduk, Sibirisches; German: Streifenhörnchen; Spanish: Ardilla terrestre de Siberia	Brown-gray to ochre-yellow with five black stripes separated by four lighter stripes running from neck to tail. Body length 4.8–6.8 in (12–17 cm), tail 3.2–4.6 in (8–11.5 cm), weight 1.8–4.3 oz (50–120 g).	Deciduous and coniferous forests. Can climb trees but spends most of time on ground. Nests in lodges constructed on the ground. Hibernate in pairs from October to April in underground burrows under tree roots or stumps.	Forests of northern Europe through Asia to Japan.	Variety of vegetables, seeds, nuts, berries, tree and shrub buds, and mushrooms. Will raid birds' nests for eggs and chicks. Also eats invertebrates, amphibians, and reptiles.	Not threatened
Hoary marmot *Marmota caligata* English: Mountain marmot, whistler; French: Marmotte des Rocheuses, marmotte grise, siffleux; German: Eisgraues Murmeltiere	Color varies widely over its range. Silver gray from shoulder to shoulder. Rump varies from blond, brown, to silver gray. Feet always black. A melanistic subspecies *M. c. vigilis* lives in Glacier Bay Alaska. Body length 26.8–29.6 in (68–75 cm), male weight 9.0–17.6 lb (4.1–8.0 kg), female weight 7.3–15.9 lb (3.3–7.2 kg).	Subalpine to alpine meadows with talus, boulders, or rocky cliffs. Near sea level in south-central Alaska. Lives and hibernates (September–May) as family groups (2–35 marmots) of one to four females with offspring (0–4 years old) and one adult male.	Alaska, United States, Yukon, and Northwest Territories, Canada, south along the Coastal and Rocky Mountains of Canada and the United States to eastern Washington, central Idaho, and western Montana.	Leaves, flowers, and seeds from a variety of forbs and grasses.	Two subspecies, *M. c. sheldoni* and *M. c. vigilis,* are listed as Data Deficient

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Unstriped ground squirrel *Xerus rutilus* French: écureuil foisseur; German: Erdhornchen	Pale tan to brown fur with whitish eye ring. Body length 12.6–17.3 in (32.0–44.0 cm), 9.2–14.8 oz (260–420 g).	Bushland thickets to savanna in arid and semi-arid environments. Isolated burrow systems are occupied by one to six squirrels. Non-hibernating.	East Africa from northeastern Tanzania north to northeastern Sudan and east to Somalia.	Seeds, fruits, herbaceous material, and invertebrates.	Not listed by IUCN
Black-capped marmot *Marmota camtschatica* French: Marmotte du Kamtchatka; German: Kamtschatka Murmeltiere	Brownish fur with black spot from the nape to the head. Body length 17.1–21.4 in (42.7–53.5 cm), tail length 4.8–7.1 in (12–17.7 cm), weight 4.4–8.8 lb (2–4 kg).	Alpine and arctic tundra areas where permafrost is absent. Hibernate as family groups from mid-September to May.	Eastern Siberia.	Variety of plants, some invertebrates, and small mammals.	Not listed by IUCN, though listed as Vulnerable in the Red Book of Yakutia because of declining populations
Red-tailed chipmunk *Tamias ruficaudus* French: Tamia à queue rousse; German: Rotschwanz-Streifenhörnchen, Rotschwanz Chipmunk	Deep orange-brown with five black to fuscous stripes separated by four grayish to tawny and creamy white stripes running from neck to tail along back. Body length 8.8–9.8 in (22.3–24.8 cm), weight 1.9–2.1 oz (55.2–60.4 g).	Dense coniferous forests with shrubby undergrowth. Nest in tree branches up to 60 ft (18.3 m), bushes, in rock crevices, under logs, or underground.	Rocky Mountains of southeastern British Columbia and southwestern Alberta, Canada, and from northeastern Washington to western Montana, United States.	Variety of seeds and fruit from conifers, shrubs, and grasses. Also eats leaves and flowers of some herbaceous plants. Will eat meat.	Not listed by IUCN
Richardson's ground squirrel *Spermophilus richardsonii* English: Flickertail, picket pin; French: Spermophile de Richardson; German: Richardson's Ziesel	Pinkish buff or cinnamon buff shaded with fuscous, light spots on back. Body length 10.9–12.0 in (27.7–30.6 cm), male weight 9.2–23.6 oz (260–670 g), female weight 6.3–18.3 oz (180–520 g).	Open short-grass plains and croplands. Females and daughters will share a home range. Male home ranges only overlap during breeding. Active above ground typically March through September but varies regionally.	Central Alberta, Canada, western Montana to western Minnesota, United States.	Variety of leaves, flowers, and seeds. Also eats invertebrates and carrion.	Not listed by IUCN
Golden-mantled ground squirrel *Spermophilus lateralis* English: Copperhead; French: Spermophile à mante dorée; German: Geldmeantel-Ziesel, Gelgestreiftes Backenhörnchen	Tawny gray with reddish shoulders and russet mantle over the head. A whitish stripe bordered by two black stripes run down each side. Body length 9.3–11.6 in (23.5–29.5 cm), weight 4.2–12.0 oz (120–340 g).	Open coniferous forests, sparsely bushy areas in foothills, mountain slopes, rocky sagebrush country, and alpine tundra. Nests in burrows under rocks, stumps, logs, trees, bushes or in rock crevices. Active from late March–May to late August–November depending on elevation.	Rocky Mountains of Canada and south to New Mexico, United States. West to northern California and east to central Colorado.	Nuts, forbs, and invertebrates. Will raid nests for eggs and chicks.	Not listed by IUCN, though the subspecies *S. l. wortmani* is listed as Data Deficient
Long-clawed ground squirrel *Spermophilopsis leptodactylus* French: Spermophile leptodactyle; German: Langkrallenziesel	Body: 7.9 to 11.8 in (20 to 30 cm); tail: 2.8 to 3.9 in (7 to 10 cm).	Lives and hibernates in small family groups. Desert dwelling on stationary sand dunes.	Southeast Kazakstan, Turkmenistan, Uzbekistan, west Tadzhikistan, northeast Iran, and northwest Afghanistan.	Fruits, seeds, bulbs, and vegetation of desert plants. Also eats invertebrates.	Not listed by IUCN
Barbary ground squirrel *Atlantoxerus getulus* French: Écureuil foisseur de Barbarie, écureuil terrestre nord-Africain; German: Barbarie-Erdhornchen, Atlashörnchen Spanish: Ardilla mora	Body: 8.7 to 17.7 in (22 to 45 cm); tail: 7.9 to 9.8 in (20 to 25 cm), 10.6 to 38.8 oz (300 to 1,100 g). Short, coarse-textured hair; little hair on underside; white stripe down either side of body; whitish eye ring; black and white banded bushy tail.	Colonial in rocky areas with scattered trees and shrubs; lives up to 12,800 ft (4,000 m). Uncertain, but may hibernate at high elevations.	Atlas Mountains in Morocco and western Algeria in northern Africa.	Nuts and seeds.	Not threatened
Gunnison's prairie dog *Cynomys gunnisoni* German: Gunnison's-Präriehund, Weißschwanz-Präriehund	12.2 to 14.7 in (30.9 to 37.3 cm); 8.8 to 38.9 oz (250 to 1,100 g). Yellow buff intermixed with black hairs; white-tipped tail.	Live in clans that average about five individuals (range 1–19) with one or two breeding males, and several breeding females, and one or more non-breeding yearling males. Open habitats or with scattered shrubs and conifers. Active March to October.	The region where Utah, Colorado, New Mexico, and Arizona, United States, meet at elevations of 6,000 to 12,000 ft (1,840 to 3,660 m).	Grasses, forbs, sedges, and shrubs. Also eats invertebrates.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Nelson's antelope squirrel *Ammospermophilus nelsoni* English: San Joaquin antelope squirrel; German: Nelson-Antilopen Zeisel	9.1 to 10.5 in (23.0 to 26.7 cm); 5.4 oz (154 g). Tawny-yellow with a white stripe down either side.	Live in scattered colonies of six to eight individuals. Found on open, rolling hills with gentle slopes, on fine textured soils that allow digging. Prefers to use burrows under shrubs dug by other animals. Adults may estivate during summer.	San Joaquin Valley of California, United States.	Feeds on insects (>90% of diet) from March to December during dry season. Eats grasses, forbs, and seeds at other times.	Endangered
Uinta ground squirrel *Spermophilus armatus*	11.0 to 11.9 in (28.0 to 30.3 cm), 7.4 to 15.2 oz (211 to 430 g). Buff-brown with paler undersides, cinnamon face.	Group together in large open areas such as meadows, pastures, or fields in high valleys to tree line, or shrub-steppe habitats. Individuals intolerant of one another except during breeding. Hibernation from August to April; may estivate in hot and dry areas in summer.	Western Montana to central Idaho, western Wyoming to southeast Idaho, United States.	Grasses, forbs, grass seeds, sagebrush leaves, and earthworms.	Not threatened
Belding's ground squirrel *Spermophilus beldingi* German: Belding Zeisel	9.1 to 11.8 in (23.0 to 30.0 cm), 4.4 to 19.4 oz (126 to 550 g). Gray with cinnamon on underside and reddish-brown on back; black-tipped tail.	Alpine, subalpine meadows, sage-brush flats, mixed brush and grass habitats, fields and pastures. Active from April to May through September. Lives in groups of related females and daughters; all males disperse.	Northeast Oregon south to California, southwest Idaho to central Nevada; and extreme northwest Utah, United States.	Grasses, forbs, and seeds. Also will eat invertebrates, other vertebrates, carrion, and will kill and eat young Belding's ground squirrels.	Not threatened
Allen's chipmunk *Tamias senex* English: Shadow chipmunk	9.0 to 10.3 in (22.9 to 26.1 cm), males: 2.4 to 3.5 oz (67to 99 g); females: 2.6 to 3.8 oz (73 to 108 g). Color varies regionally; grayish to brownish-orange with indistinct stripes except for middle dorsal stripe which is more conspicuous.	Dense coniferous forests. After accumulating 20% of its body mass in fat it hibernates from November through March.	Central Oregon south to east-central California; west to northwest California and east to California-Nevada border, United States.	Fungi, seeds, flowers, and insects.	Not threatened

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Organizations

International Marmot Network. Le Laboratoire de Sociécologie et Conservation, Université Claude Bernard, Lyon, France.

NatureServe. 1101 Wilson Boulevard, 15th Floor, Arlington, VA 22209 USA. Phone: (703) 908-1800. Fax: (703) 908-1917. E-mail: infor@natureserve.org Web site: <http://www.natureserve.org>

Vancouver Island Marmot Recovery Foundation. Box 2332, Station "A", Nanaimo, British Columbia V9R 6X9 Canada. Phone: (250) 753-8080. Fax: (250) 753-8070. E-mail: marmot@islandnet.com Web site: <http://www.marmots.org>

Tim Karels, PhD

Squirrels and relatives III

Tree squirrels

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Sciuridae
Subfamily Sciurinae

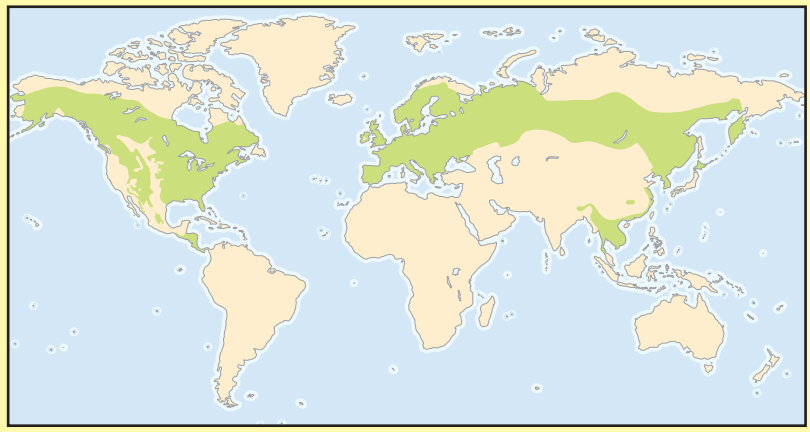
Thumbnail description
Small to medium sized rodents, hind limbs disproportionately long; most species have a prominent tail; fur color extremely variable

Size
Head and body length 2.95–18 in (75–460 mm), tail almost as long again; 0.53 oz–6 lb (15–3,000 g)

Number of genera, species
21 genera; 117 species

Habitat
Forest, woodland, scrub, urban areas, parks, and gardens

Conservation status
Endangered: 1 species; Vulnerable: 14 species; Lower Risk/Near Threatened: 20 species; eight subspecies are considered threatened



Distribution
Found on all continents except Antarctica and Australia

Evolution and systematics

Tree squirrels are fascinating rodents whose arboreal roots are thought to go back to the Eocene (54–38 million years ago [mya]). The first members of the squirrel family which were "tree squirrel like" in their dental morphology appear in the fossil record during the Oligocene (37–25mya). These include specimens from France, *Sciurus dubius*, dated to the early to middle Oligocene and members of the genus *Protosciurus*, which occurred in North America from the early Oligocene to the early Miocene (24–5 mya). The Miocene fossil record also contains a large number of genera of flying and ground squirrels from Europe, Asia, and North America as well as genera of tree squirrels that are still extant today.

The Sciuridae squirrels are divided into ground and tree squirrels in the subfamily Sciurinae and flying squirrels in the subfamily Pteromyinae. The number of recognized genera and species varies among authors. Including arboreal giant and pygmy squirrels, there are 21 described genera with approximately 117 species: Tree squirrels (*Callosciurus*, *Funambulus*, *Funisciurus*, *Glyphotes*, *Heliosciurus*, *Microsciurus*, *Paraxerus*, *Prosciurillus*, *Sciurus*, *Sundasciurus*, *Syntheosciurus*, and *Tamiasciurus*), giant squirrels (*Epixerus*, *Protoxerus*, *Ratufa*, *Reithrosciurus*, and *Rubrisciurus*), pygmy squirrels (*Exilisciurus*, *Myosciurus*, *Nannosciurus*, and *Sciurillus*).

Some genera such as *Sciurus* or *Callosciurus* also contain a significant number of described subspecies. However, the precise status of some of these is in doubt and as new morphological and genetic data become available the number of recognized species may change.

Physical characteristics

The arboreal squirrels range in their size from the incredible pygmy squirrels of tropical forests weighing fractions of an ounce (a few tens of grams) to the giant squirrels of India several pounds (kilograms) in weight. Males and females are similar and there is no sexual dimorphism in either color or size. Their bones are relatively light and their skeleton shows adaptations for climbing. Their hind legs are disproportionately long. They have long toes with curved claws. Their tails, almost as long as their bodies, are used for balance, signaling, and thermoregulation. Their tails gave the genus *Sciurus* its name, stemming from the ancient Greek with *skia* meaning shade or shadow and *oura* meaning tail. They have different sets of sensory hairs, vibrissae, on the head, feet, forelegs, on the underside of their body, and at the base of the tail. These help them orient themselves and move through their three dimensional environment.

Distribution

Tree squirrels are found throughout the world. They are present on all continents with the exception of Australia and Antarctica. A gray squirrel (*Sciurus carolinensis*) population introduced to Australia went extinct in the 1970s. They are ab-

A squirrel caches food items to consume later. (Illustration by Jarrod Erdody)

sent from the polar regions, Madagascar, parts of southern South America, north Africa, and Australasia.

Habitat

Tree squirrels occur in forests, woodlands, gardens, urban areas, and agricultural landscapes. Space and habitat use is extremely flexible and linked to the spatial and temporal distribution of resources. Social organization encompasses individual territoriality and overlapping home ranges with territorial female core areas in habitats where food is sparse and patchily distributed. In contrast, male space use appears to be affected by access to females during the breeding period. There are three known strategies: males adapt their use of space to overlap with as many females as possible; make

Douglas's squirrel (*Tamiasciurus douglasii*) feeds at an aspen sapwell in Eastern Sierras, California. (Photo by Richard R. Hansen/Photo Researchers, Inc. Reproduced by permission.)

A big cypress fox squirrel (*Sciurus niger avicennia*) foraging in the Florida Everglades. (Photo by J. H. Robinson/Photo Researchers, Inc. Reproduced by permission.)

An eastern fox squirrel (*Sciurus niger*) foraging among leaf litter. (Photo by © DigitalVision/PictureQuest. Reproduced by permission.)

Smith's tree squirrels (*Paraxerus cepapi*) are diurnal, arboreal animals, living in small family groups but foraging alone, sometimes on the ground. They eat a wide range of vegetable matter and insects, and cache food. They are easily habituated to people, and sometimes take up residence in the roofs of houses. (Photo by Ann & Steve Toon Wildlife Photography. Reproduced by permission.)

excursions out of their normal home range to visit estrus females; or track female movements. In areas where several species co-occur such as in African rainforest habitats, Emmons in 1980 found that two of nine species were restricted to specific habitats, foraging by the different species occurred at different heights on and above the ground in the trees, and there was a temporal partitioning with differences in the timing of the active period. In addition, the species differed in body size with resulting differences in their diet.

Behavior

Tree squirrels do not hibernate and do not form colonies. Most species are solitary, but some African species such as *Heliosciurus rufobrachium* or *Funisciurus anerythrus* are known to move in pairs or small groups. Tree squirrels use olfactory, vocal, and visual signals to communicate. Chemical signals are important in rodent communication and tree squirrels have a number of scent glands in the facial area around the mouth and cheeks. "Cheek-rubbing" is sometimes linked to biting of the substrate, and urine is used to mark the base of specific trees and the underside of branches. Anal dragging is also reported for some species in which anal glands and perhaps fecal materiel are used to produce a signal. Little is known about the different functions of marking in relation to orientation or inter-individual communication or even the potential for disease transmission.

Vocalizations of squirrels can be linked to several behavioral contexts. These include contact seeking or distress of young, alarm calls, calls associated with mating, and aggressive sounds. In contrast to forest species, estrus females in savanna species such as *Paraxerus cepapi* or *Funisciurus congicus* use vocal calls rather than olfactory clues to attract males. Some rainforest species have been reported to lower the frequency and to increase the length of calls as an adaptation to the dense vegetation around them.

Squirrels also make use of their fluffy tails, and tail waving and shivering is sometimes observed when males approach

The eastern gray squirrel (*Sciurus carolinensis*) can be either gray or black. (Photo by M. H. Sharp/Photo Researchers, Inc. Reproduced by permission.)

The striped tree squirrel (*Funisciurus congicus*) is endemic to Nambia and Angola. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

females during mating. Tail flicking as well as foot stamping, linked to aggressive postures such as piloerection (hair-erection), are seen during agonistic encounters.

Feeding ecology and diet

Fruit, leaves, and bark are important in the diet of tropical giant squirrels, whereas nuts as well as conifer and deciduous tree seeds are a significant component of North American and European squirrels. A large variety of other food items are also consumed including fungi, berries, buds, shoots, tree sap, and insects. Anecdotal evidence also indicates that some species may opportunistically prey on bird eggs in nests. Squirrels are also known to satisfy their calcium demands by gnawing bones.

Squirrels, like many birds, hide food items to consume them at a later time. Two main strategies have been observed: scatter hoarding in which one or several items are cached at different locations throughout the squirrels territory or home range and larder hoarding in which a large amount of food is stored in one or a small number of sites. Caching is thought to be an adaptive strategy and food stores are important in periods of adverse weather conditions and low natural food availability. Its intensity varies with habitat type and the behavior has been linked to increased survival and reproductive success. The "stealing" of European red squirrel, *Sciurus vulgaris*, caches by the larger introduced gray squirrel, *S. carolinensis*, has been suggested as a factor contributing to the decline of the native red squirrel in Italy by Wauters and others in 2002.

Reproductive biology

Tree squirrels have a polygamous mating system in which either sex can have more than one mate. Most knowledge comes from studies in North America and Europe where mating behavior among the different species of tree squirrel is very similar. Females are in estrus for less than one day and males compete for access to the females. During "mating chases" in which a female is often followed by several males, she will try and avoid pursuing males and mate in sheltered locations with reduced risk of attack and injury. Generally, there is a hierarchy among the males pursuing the female with the dominant males closest to the female. Approaches of males towards the female are cautious with withdrawal movements, vocalizations, and flicking actions of the tail to check whether the female will accept the male.

The onset of estrus is not synchronous in females within a population and depends on body condition. Males do not contribute to parental care. Litter size and reproductive suc-

An eastern fox squirrel (*Sciurus niger*) leaps upward from a log. (Photo by Nick Bergkessel/Photo Researchers, Inc. Reproduced by permission.)

Abert's squirrel (*Sciurus aberti*) eating on a branch. (Photo by C. K. Lorenz/Photo Researchers, Inc. Reproduced by permission.)

cess are linked to habitat quality and food availability with some females succeeding in raising more than one litter a year.

Squirrels nest in tree cavities (dens), nests (dreys), or in some cases holes in the ground. Dreys are elaborate circular structures made up of a coarse outer layer of leaves or needles and sticks and a woven inner layer of grass, moss, bark, feathers and other similar materials. Communal nesting, particularly during periods of adverse weather occurs in a number of species.

Conservation status

The IUCN lists 14 species (*Epixerus ebii*, *E. wilsoni*, *Funambulus tristriatus*, *Funisciurus isabella*, *Paraxerus alexandri*, *Prosciurillus weberi*, *Sciurus anomalus*, *S. arizonensis*, *S. richmondi*, *S. sanborni*, *Sundasciurus brookei*, *S. moellendorffi*, *S. steerii*, and *Syntheosciurus brochus*) in the Lower Risk category, 14 species as Vulnerable (*Callosciurus pygerythrus*, *C. quinquestriatus*, *Funisciurus carruthersi*, *Myosciurus pumilio*, *Paraxerus cooperi*, *P. palliatus*, *P. vexillarius*, *P. vincenti*, *Prosciurillus abstrusus*, *Ratufa indica*, *R. macroura*, *Sundasciurus jentinki*, *S. rabori*, and *S. samarensis*), and one species as Endangered (*Sundasciurus juvencus*). The European red squirrel, *Sciurus vulgaris*, is considered endangered in parts of its range, and the United States Endangered Species Act list two subspecies as endangered. This includes the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) of Arizona and the Delmarva fox squirrel (*Sciurus niger cinereus*) of the Delmarva Peninsula to southeastern Pennsylvania.

The main causes for species declines are human induced habitat loss, degradation, and fragmentation as well as persecution and hunting. However, there is insufficient information on the behavior, ecology, population dynamics, and threats to many Asian, South American, and African species and a need for basic ecological studies to allow adequate conservation assessments.

Significance to humans

Squirrels have been hunted for sport, their fur, and their meat. Some species are considered a pest or nuisance due to damage to crops or trees or pose a threat to native species due to introductions outside their natural range. However, many people take pleasure in their presence in parks and gardens and enjoy watching their ingenious ability to overcome obstacles in search of food. Squirrels are also notably present in the folklore of all countries where they are found, included in children's tales, sayings, and weatherlore: "Squirrels gathering nuts in a flurry, will cause snow to gather in a hurry."

A Eurasian red squirrel (*Sciurus vulgaris*) leaps to a lower branch. (Photo by Stephen Dalton/Photo Researchers, Inc. Reproduced by permission.)

1. Peters's squirrel (*Sciurus oculatus*); 2. Pallas's squirrel (*Callosciurus erythraeus*); 3. Variegated squirrel (*Sciurus variegatoides*); 4. Red squirrel (*Sciurus vulgaris*); 5. Arizona gray squirrel (*Sciurus arizonensis*); 6. Gray squirrel (*Sciurus carolinensis*); 7. Abert squirrel (*Sciurus aberti*); 8. North American red squirrel (*Tamiasciurus hudsonicus*); 9. Eastern fox squirrel (*Sciurus niger*). (Illustration by Bruce Worden)

Species accounts

Red squirrel
Sciurus vulgaris

TAXONOMY
Sciurus vulgaris Linnaeus, 1758, Uppsala, Sweden.

OTHER COMMON NAMES
French: Ecureuil roux; German: Eichhörnchen; Spanish: Ardilla roja.

PHYSICAL CHARACTERISTICS
Head and body length 7–9.5 in (180–240 mm), tail 5.5–7.6 in (140–195 mm); weight 7.8–15.4 oz (220–435 g); sexes similar, large variation in coat color across range. Upper fur varies from red-brown or chestnut to very dark in appearance. Fur of some subspecies in winter, such as the Yenisei squirrel (*S. v. jenissejensis*), Siberia, is an intense bluish gray with dark gray mottling. Ear tufts grow in autumn and are prominent during the winter but are absent during the summer.

DISTRIBUTION
From Ireland and Britain in the west, across the Palaearctic to Hokkaido in Japan.

HABITAT
Deciduous, mixed, and coniferous woodlands, also occurs in suburban areas, gardens, and parks.

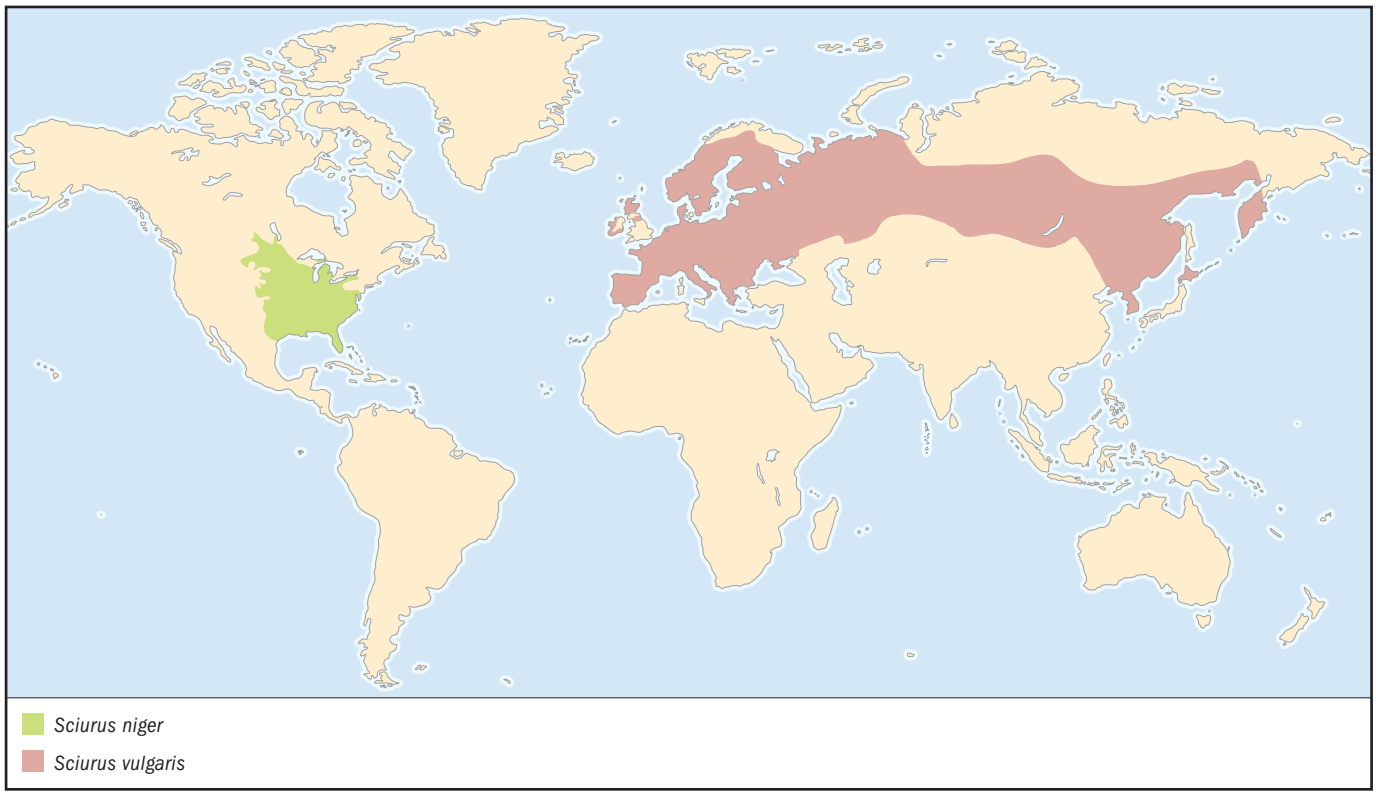
BEHAVIOR
The species is not territorial but occupies home ranges which overlap with other conspecifics. Core areas of females within the home range are thought to be exclusive in some habitats. Habitat use flexible in large conifer forests with frequent home range shifts by individuals tracking seed crops in different conifer species. Red squirrels are diurnal and active all year.

FEEDING ECOLOGY AND DIET
Main diet is tree seeds and fungi. In poor seed years red squirrels will also feed on buds, shoots, and berries

REPRODUCTIVE BIOLOGY
Promiscuous mating system, males and females do not form pair bonds. Breeding starts December–January and continues until early October when the last litters are weaned. There are two breeding peaks within a year; spring (February–April) and summer (May–August) litters respectively. Breeding may be delayed or missed in years with poor food supplies.

CONSERVATION STATUS
Dramatic range and population declines in Britain, Ireland, and parts of Italy due to competition by the introduced North American gray squirrel. Habitat fragmentation and disease outbreaks such as the parapox virus in England have also contributed to population declines. The species is considered endangered in the United Kingdom.

SIGNIFICANCE TO HUMANS
Traditionally hunted for its fur. The species now is a cherished sight in parks and gardens. Significant animal in folklore, in



Nordic myths the squirrel Ratatosk was the carrier of messages between the eagle at the top of Yggdrasil the ash tree spanning the worlds to the serpent Niddhogg below. ◆

Gray squirrel
Sciurus carolinensis

TAXONOMY
Sciurus carolinensis Gmelin, 1788, "Carolina." United States.

OTHER COMMON NAMES
English: Eastern gray squirrel, migratory squirrel; French: Ecureil gris; German: Grauhörnchen; Spanish: Ardilla gris.

PHYSICAL CHARACTERISTICS
Head and body length 9.4–11.2 in (240–285 mm), tail 7.5–9.5 in (190–240 mm); weight 10.6–26 oz (300–720 g); sexes similar. Grizzled black to pale gray coat color mixed with reddish brown on feet, hips, and head, underpart white to pale gray.

DISTRIBUTION
Eastern United States, with introductions to Montana, Oregon, Washington, and California, also introduced to Quebec, New Brunswick, British Colombia, Manitoba, and Vancouver Island in Canada and Britain, Ireland, and South Africa.

HABITAT
Mature continuous forest and woodland. Highest observed densities in stands of oak, walnut, and hickory, very low densities in conifer dominated plantations colonized by gray squirrels in Britain.

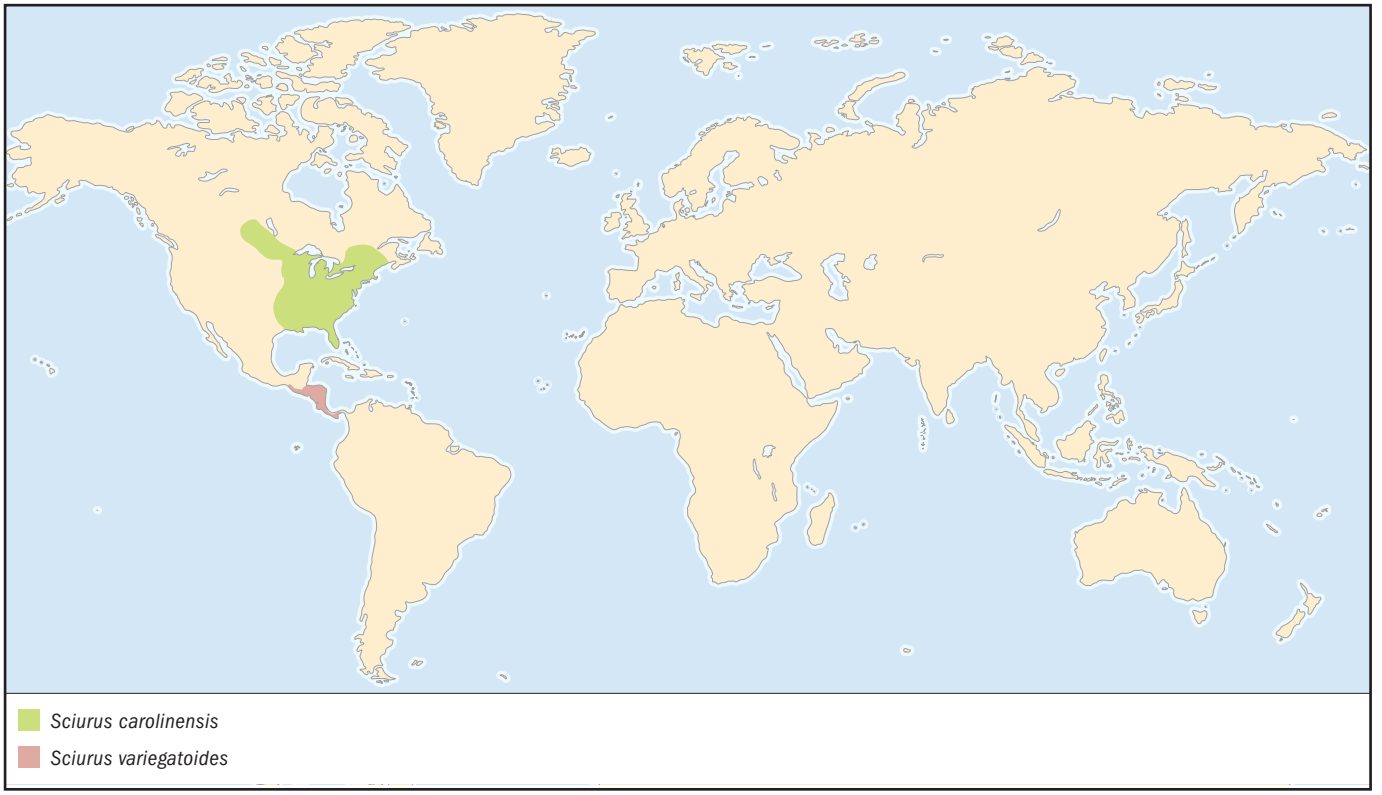
BEHAVIOR
Diurnal activity pattern, active all year. Gray squirrels considered solitary and both sexes disperse. However, female-biased philopatry and the formation of female kin groups observed in high quality parkland in Kansas.

FEEDING ECOLOGY AND DIET
Gray squirrels feed predominantly on nuts as well as tree seeds of both deciduous and coniferous species. Other food items include, flowers, buds, fungi, and fruit. Gray squirrels hoard seeds such as acorns. The squirrels may react to a chemical cue in the shell of the acorns and caching decisions were found to be based on perishability with longer lived items being cached rather than consumed. In addition, gray squirrels increase the longevity of their food stores by preventing germination through embryo excision. This is particularly the case for white oak (*Quercus alba*) acorns.

REPRODUCTIVE BIOLOGY
Polygamous. Females can have young within their first year of age. There are two breeding peaks, December to February and May to June (breeding in South Africa begins in October). Males are attracted to estrus females from considerable distances away and start following the females, sometimes several days before onset of estrus. Gestation period is approximately 44 days, followed by approximately 70 days of lactation. Litter size ranges from 1–7 with an average of about 2.3.

CONSERVATION STATUS
Common; not threatened

SIGNIFICANCE TO HUMANS
Hunted for sport and food. Adored by many in city parks and gardens, although gardeners dislike them for digging up bulbs and competing with birds at feeders. Considered a pest in Britain due to causing significant damage to deciduous and



coniferous trees in woodlands through bark stripping and due to competition with red squirrels. ◆

Eastern fox squirrel
Sciurus niger

TAXONOMY
Sciurus niger Linnaeus, 1758, South Carolina, United States.

OTHER COMMON NAMES
English: Cat squirrel, stump-eared squirrel.

PHYSICAL CHARACTERISTICS
Head and body length 10–14.5 in (260–370 mm), tail 7–13 in (180–330 mm); weight 17.5–49.5 oz (500–1,400 g). Coat color variable.

DISTRIBUTION
Eastern and central United states reaching southern Canada in the north. Introduced to Ontario in Canada and New Mexico, Texas, California, Oregon, Colorado, Idaho, and North Dakota within the United States.

HABITAT
Forests, woodlands, urban areas, and agricultural landscapes.

BEHAVIOR
Diurnal activity pattern, period of greatest activity in winter is in the early morning. Social system characterized by dominance hierarchy. Main factors influencing dominance status of individuals are their sex and age. Fox squirrels will forage in open fields near woodland. The behavior of caching seeds in grassland thought to be important in seed dispersal and habitat succession.

FEEDING ECOLOGY AND DIET
Tree seeds and nuts as well as buds and flowers of trees.

REPRODUCTIVE BIOLOGY
Polygamous. Reproductively active from mid-December onwards. Similar to gray squirrels, there are two breeding peaks within a year but not all females produce two litters. Mean litter size ranges from 2–3.5 young.

CONSERVATION STATUS
Delmarva Peninsula fox squirrel, *S. n. cinereus*, considered endangered. Logging and changes to habitat composition have been suggested as causes for decline. The Big Cypress fox squirrel, *S. n. avicennia*, in Florida is locally regarded as threatened.

SIGNIFICANCE TO HUMANS
Hunted for food and sport. ◆

Abert squirrel
Sciurus aberti

TAXONOMY
Sciurus aberti Woodhouse, 1853, Arizona, United States.

OTHER COMMON NAMES
English: Tassel-eared squirrel; Spanish: Ardilla de Abert.

PHYSICAL CHARACTERISTICS
Head and body length 10–12.5 in (260–320 mm), tail (190–260 mm); weight 16–29 oz (450–820 g). Peppered gray upper fur, underside white. White conspicuous eye ring. Tail is gray fringed in white. Ear tufts or tassels can reach up to 1.5 in (40 mm) in February and March, very reduced or absent during the summer. Some populations in New Mexico and Colorado have a high incidence of melanism. Kaibab race characterized by dark gray to black belly and white tail.

DISTRIBUTION
Northern Mexico, Arizona, New Mexico, Utah, Colorado, and Wyoming.

HABITAT
Ponderosa and yellow pine forests, mixed conifer forests.

BEHAVIOR
Diurnal activity pattern. Home range size reported to vary seasonally linked to the availability of resources, with male home ranges larger than female ranges.

FEEDING ECOLOGY AND DIET
Ponderosa pine seeds, bark, buds, and flowers. Other food items include insects, acorns, mistletoe berries, and fungi. Fungi are an important food source in the summer and Abert squirrels may be important spore dispersal agents.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation approximately 40 days, mean litter size 3.4 young.

CONSERVATION STATUS
There have been suggestions that existing logging and forest management practices may impact negatively on some populations.

SIGNIFICANCE TO HUMANS
None known. ◆

Arizona gray squirrel
Sciurus arizonensis

SUBFAMILY
Sciurinae

TAXONOMY
Sciurus arizonensis Coues, 1867, Arizona, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 9.6–12.6 in (244–321 mm), tail 7.5–11 in (200–285 mm); weight 18–31 oz (520–870 g). Upper body grizzled silver gray, in winter with brownish yellow dorsal stripe. Underside white, tail is black fringed with white; with orange to rusty brown hairs ventrally. White eye ring.

DISTRIBUTION
Arizona, New Mexico, and Sonora, Mexico.

HABITAT
Riparian deciduous forest, mixed broadleaf forests at elevations of 3,600–9,200 ft (1,100–2,800 m).

BEHAVIOR
Diurnal activity pattern. Nests are located in a variety of species including sycamores, walnut trees and Apache pines, most found in oak trees. Recorded vocalizations include chucking and barking alarm calls.

FEEDING ECOLOGY AND DIET
Diet includes corns, walnuts, conifer seeds, berries, tree flowers, and alder buds.

REPRODUCTIVE BIOLOGY
Polygamous. Breeding activity linked to flower emergence and most females in estrus in April and early May. Observed litter size ranges from 2 to 4.

CONSERVATION STATUS
Introduction of Abert squirrels into the Catalina Mountains may adversely affect existing populations. Arizona gray squirrels have been listed as a Category 2 species by the Fish and Wildlife Service. Considered endangered in Mexico due to severe habitat loss through agricultural development and logging.

SIGNIFICANCE TO HUMANS
Visits picnic sites in the mountains. Focus of scientific study. ◆

Peters's squirrel
Sciurus oculatus

TAXONOMY
Sciurus oculatus Peters, 1863, Mexico.

OTHER COMMON NAMES
English: Black-backed or spectacled squirrel.

PHYSICAL CHARACTERISTICS
Head and body length 9.5–11 in (250–280 mm), tail (250–270 mm); weight 14.5–19.5 oz (410–550 g). Upper fur grizzled gray or containing a band of black. Tail is black with suffusion of white. Underparts white or mixed with pale yellow or ochre.

DISTRIBUTION
Mexican plateaus from Morelos to San Luis Potosi.

HABITAT
Oak, pine, and fir forest between 4,900–11,810 (1,500–3,600) m elevation.

BEHAVIOR
Animals are capable of moving swiftly through the trees. Little known about their space use and social organization.

FEEDING ECOLOGY AND DIET
Known to feed on acorns, almonds, and wild figs.

REPRODUCTIVE BIOLOGY
Little known about breeding behavior, females observed to be in breeding condition in July in Veracruz.

CONSERVATION STATUS
Agricultural development caused significant loss of forest habitat and the species is considered fragile.

SIGNIFICANCE TO HUMANS
Occasionally hunted for food in some areas. ◆

Variegated squirrel
Sciurus variegatoides

TAXONOMY
Sciurus variegatoides Ogilby, 1839, El Salvador.

OTHER COMMON NAMES
Spanish: Ardilla chiza.

PHYSICAL CHARACTERISTICS
Head and body length 8.7–10.6 in (240–270 mm), tail 9.4–12.5 in (240–320 mm), 15.5–32 oz (440–900 g). Variable in color, shiny coat of black to grizzled yellowish gray, underside white, feet whitish speckled with black.

DISTRIBUTION
From central Panama, Costa Rica, Nicaragua, Honduras, El Salvador, Guatemala north to the southern Chiapas in Mexico.

HABITAT
Tropical evergreen forests, nut palm forests, as well as deciduous tropical forests.

BEHAVIOR
Arboreal squirrel with diurnal activity pattern. Nest located on stems near the main trunk. Territories may range over 5.9 acres (2.4 ha).

FEEDING ECOLOGY AND DIET
Fruits, nuts, seeds of hard shelled fruits, and fungi. Main components of an observed diet included the seeds of guacimo, mango, and hogplum.

REPRODUCTIVE BIOLOGY
Polygamous. Breeding period thought to be in April or May. Litter size variable, approximately 4–6 young.

CONSERVATION STATUS
Some populations in Mexico considered fragile.

SIGNIFICANCE TO HUMANS
Occasionally hunted. ◆

North American red squirrel
Tamiasciurus hudsonicus

TAXONOMY
Tamiasciurus hudsonicus (Erxleben 1777), Hudson Bay, Canada.

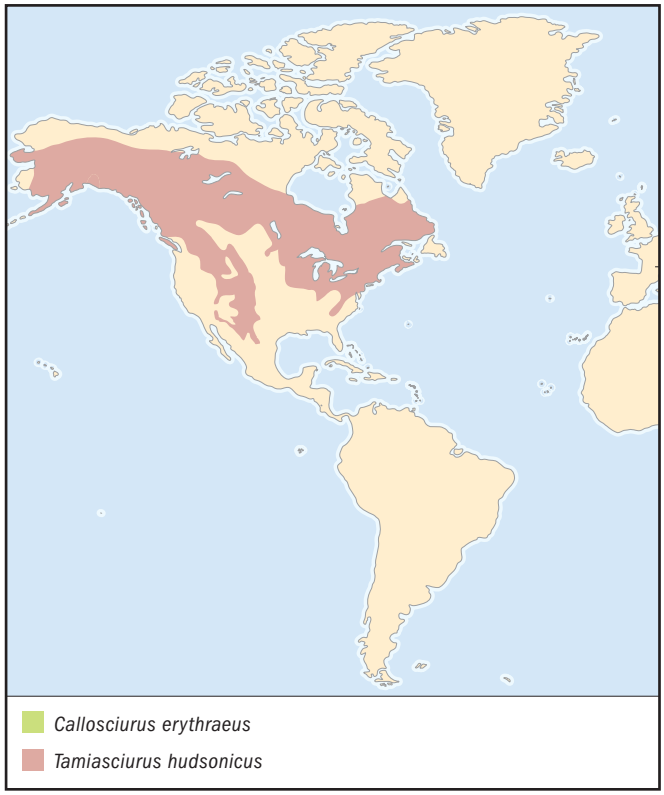
OTHER COMMON NAMES
English: Pine squirrel, chickaree; French: Ecureuil de l'Hudson; Spanish: Ardilla de Douglas.

PHYSICAL CHARACTERISTICS
Head and body length 7–9 in, (178–230), tail 3.5–6.3 in (90–160 mm); 6.4–8.8 oz (180–250 g). Fur reddish brown or olive gray, underside white or faint yellowish. Tail with yellowish to rusty tips with a black band. White eye ring.

DISTRIBUTION
Boreal forests of Canada and the northern United States from Alaska in the west to Quebec and Main in the east. Fragmented populations in the Apalachian mountains and as far southeast as North Carolina, introduced to Newfoundland. Southward in the west, the species occurs in the Cascade and Rocky mountains and on Vancouver island. There are also isolated populations in subalpine "sky-island" habitats in New Mexico and Arizona.

HABITAT
Coniferous forests as well as coniferous-deciduous stands. Other habitats include aspen, red pine and Norway spruce. Red squirrels are territorial and a single individual of either sex occupies and defends a territory.

BEHAVIOR
Diurnal activity pattern. They use vocal calls during courtship and to defend their territory. Four vocalizations and an alarm call were connected with territorial behavior in a study of the species in the Cascade Mountains, British Colombia.



FEEDING ECOLOGY AND DIET
Main diet are conifer and deciduous tree seeds and fungi. Other items include tree buds, flowers and sap, bark and insects. The species larder hoards cones in a central cache site (midden) that typically mark the center of the territory. Scatterhoarding of cones has also been observed. Whitebark pine cones are an important food of grizzly bears in Yellowstone and they are know to excavate red squirrel middens.

REPRODUCTIVE BIOLOGY
Polygamous. Timing of breeding varies throughout the range. Courtship is thought to begin when bare patches of ground appear at the end of winter. During the breeding period males leave their territories more often and females allow males to enter their territories. Females come into estrus for only one day. Litter sizes vary between 3–6 young.

CONSERVATION STATUS
Isolated populations such as the Mt. Graham red squirrel subspecies in Arizona are protected and considered endangered.

SIGNIFICANCE TO HUMANS
Hunted or trapped for fur in some areas. ◆

Pallas's squirrel
Callosciurus erythraeus

TAXONOMY
Callosciurus erythraeus (Pallas, 1779), Assam, India.

OTHER COMMON NAMES
English: Red-bellied squirrel; French: Ecureuil à ventre rouge; Spanish: Ardilla de Pallas.

PHYSICAL CHARACTERISTICS
Head and body length 7.8–10.2 in (200–260 mm), tail 6–7.6 in (160–195 mm); 11–16 oz (310–460 g). Very variable in color, Upper fur olive brown agouti, underside reddish (varying from maroon to creamy buff).

DISTRIBUTION
From Bhutan and Assam in the east through Myanman to southern China, south to Indochina, Thailand, and Malaya. Also occurs on Taiwan, introduced to Japan and Cap d'Antibes in France.

HABITAT
Broadleaf evergreen forest, dipterocarp forest, bamboo-rich forest, tropical rainforest. Overlapping home range system of space use, less overlap among females than males.

BEHAVIOR
Diurnal activity pattern. Observed mobbing snakes in Japan to defend young. Distinct recorded vocalizations for aerial and terrestrial predators leading conspecifics to adopt different escape strategies. Alarm calls also used following mating. This is thought to be a possible strategy by males to delay second matings by the female and increase the probability of paternity.

FEEDING ECOLOGY AND DIET
Fruit, seeds, nuts, and insects.

REPRODUCTIVE BIOLOGY
Promiscuous. Reproductively active throughout the year, peaks March to August. Average litter size 1.4 young.

CONSERVATION STATUS
Common; not threatened.

SIGNIFICANCE TO HUMANS
Introduced population in France causes damage to trees, may compete with native red squirrel. Considered a pest on oil palm plantations. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
West African pygmy squirrel *Myosciurus pumilio*	Upper fur brown, underside olive-white. Weight approximately 0.6 oz (16 g).	Occurs in all types of forests within its distributional range. Observed foraging at all heights of the canopy, but most often seen at heights of 0–16 ft (0–5 m).	Gabon, Equatorial Guinea, and Cameroon.	Feeds continuously; diet includes bark, fungi, and insects.	Vulnerable
Indian giant squirrel *Ratufa indica* English: Malabar squirrel; French: Ecureuil géant de l'Inde; German: Indisches Riesenhörnchen	Upper fur reddish brown to black, red ears, ear tufts present. Underside buff colored. Head and body length approximately 11.5–17.5 in (30–45 cm), tail 23.5 in (60 cm).	Deciduous forest, monsoonal forests, evergreen seasonal cloud forests. Solitary arboreal squirrel.	Forested areas of peninsular India, Ghats, India.	Leaves, bark, flowers, fruit, and seeds.	Vulnerable
Allen's squirrel *Sciurus alleni*	Upper fur grizzled gray with black, sides yellowish brown. White eye ring. Underside white. Tail black mixed with white. Weight 9.8–17.5 oz (280–500 g).	Deciduous and conifer forests. Diurnal activity pattern. Little known about reproductive behavior and space use.	Mexico, found at elevations of 1,970–8,200 ft (600–2,500 m).	Seeds of deciduous and conifer trees, fruit, and insects.	Not listed by IUCN
Persian squirrel *Sciurus anomalus* English: Golden squirrel; French: Ecureuil de Perse; German: Kaukasisches Eichhörnchen; Spanish: Ardilla persa	Upper fur gray mixed with white, yellow head with gray; yellow eye ring, legs and tail amber in color, underside yellow. Weight approximately 10.5 oz (300 g).	Mixed deciduous woodland habitats. Diurnal activity pattern, active all year.	Lebanon, Jordan, Turkey, Iraq, Iran, Transcaucasia; and island of Lesbos, Greece.	Tree seeds, fungi, buds, and shoots.	Lower Risk/Near Threatened
Deppe's squirrel *Sciurus deppei* English: Guanacaste squirrel, Orizaba squirrel; Spanish: Ardilla montañera	Upper fur reddish to yellowish brown, sometimes mixed with gray. Underside white to dull reddish brown. Tail color variable, black fringed with white, with ochre on the underside. Weight 7–10.6 oz (200–300 g).	Tropical forests, pine-oak forests, evergreen, and cloud forests. Diurnal activity pattern, active all year. Arboreal, but will forage on the ground.	Costa Rica and Mexico.	Fruit, tree seeds, nuts, fungi, and foliage.	Not threatened
Western gray squirrel *Sciurus griseus* English: California gray squirrel, Oregon gray squirrel	Silvery gray upper fur, underside white or cream. Tail gray fringed with white. Weight 15.9–35 oz (450–1,000 g).	Solitary, space use characterized by overlapping home ranges. Occurs in both deciduous and conifer forests as well as evergreen hardwood forests.	Washington State, Oregon, and California, United States.	Seeds of deciduous and conifer trees, hypogeous fungi, fruit, conifer cambium, and insect larvae.	Not threatened, though status reviewed by U.S. Fish and Wildlife Service (FWS) in 2002
Mexican fox squirrel *Sciurus nayaritensis* English: Nayarit squirrel, Apache fox squirrel, Chiricahua fox squirrel	Upper fur brown to gray with red or ochre. In southern populations, upper fur mixed with white. Underside reddish to white. Weight approximately 22–29 oz (620–820 g).	Pine-oak, montane, and conifer forests. Little known about social organization, population dynamics, and space use.	Chiricahua mountains, Arizona; and western Sierra Madre, Mexico.	Seeds of deciduous and conifer trees, nuts, and plant material such as buds.	Not listed by IUCN, though listed as Category 2 species by the U.S. FWS
Yucatán squirrel *Sciurus yucatanensis* English: Black-footed squirrel, Campeche squirrel	Color variable. Upper fur black mixed with gray, yellow, and ochre. Underside white to yellowish gray to black. White ear tufts in winter and spring.	Tropical broadleaf forest and pine-oak forests. Little known about population dynamics, social organization, and space use.	Yucatán Peninsula, Mexico; Belize; and northern Guatemala.	Fruit and tree seeds.	Not listed by IUCN
Mountain squirrel *Syntheosciurus brochus*	Upper fur dark reddish olive to black; tail similar to body with reddish tips. Underside orange-red to ochre. Total length approximately 12 in (30 cm).	Montane cloud forest and evergreen deciduous forest.	Known from four locations in Costa Rica and Panama.	Unknown.	Lower Risk/Near Threatened

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Other

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United States Fish and Wildlife Service Endangered Species Programme. [February 12, 2003]. <http://endangered.fws.gov/>

Peter W. W. Lurz, PhD

Beavers
(Castoridae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Castoridae

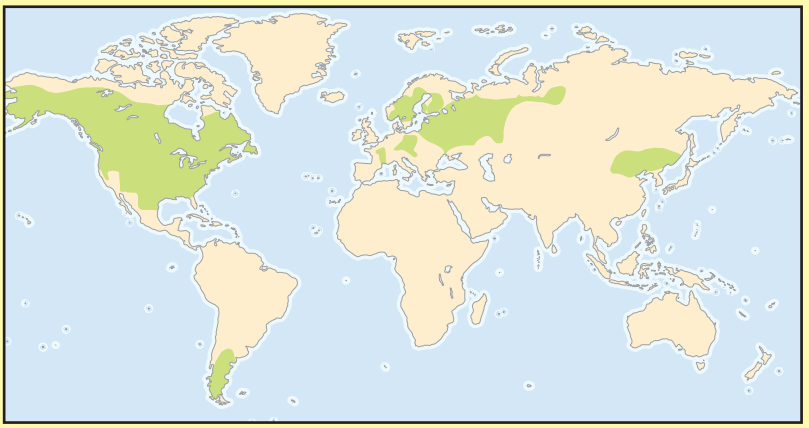
Thumbnail description
Beavers are large, dark brown rodents with a broad, flat mostly hairless tail; they have a compact body design with webbed hind feet, dexterous front feet and long incisors

Size
31–58 in (80–140 cm); tail one-third of length; 33–75 lb (15–33 kg) with records over 100 lb (45 kg)

Number of genera, species
1 genus; 2 species

Habitat
Freshwater wetlands, rivers, streams, lakes, and ponds

Conservation status
Lower Risk/Near Threatened: 1 species



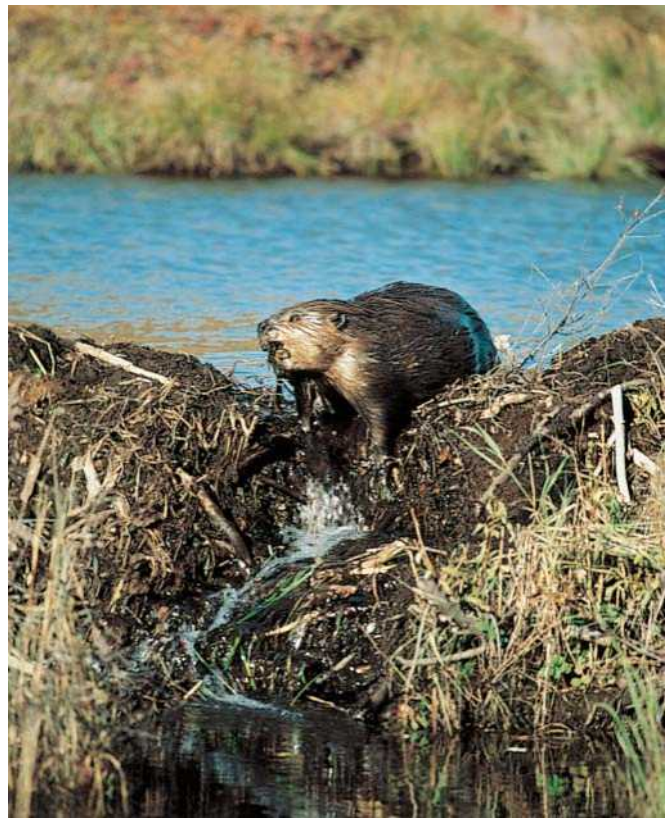
Distribution
North America, Asia, and Europe except desert and tundra regions

Evolution and systematics

The Rodentia is a monophyletic mammalian order. Molecular evidence suggests a close association of Castoridae to the Geomyidae (pocket mice and pocket gophers). The two beaver species differ by eight chromosomes of *Castor* (40 for the North American and 48 for the Eurasian beaver). The genus *Castor* dates to the early Pliocene late Miocene boundary, separating from giant beavers (*Castoroides* in North America, and *Trogontherium* of Eurasia) about this time. The family Castoridae dates to the Oligocene and was once quite diverse. Today it contains two species, *C. canadensis* and *C. fiber*.

Physical characteristics

Beavers are the largest rodents in the Northern Hemisphere. Males and females are similar in size and cannot be distinguished by external appearance except near parturition and during lactation when females have four prominent pectoral mammae. Beavers have yellowish brown to black fur with long guard hairs and short underfur that aid in water shedding and insulation. Their flat tail serves as a fat storage area. The feet have five digits. The hind feet are webbed with a double claw on the second toe of each hind foot that is used for grooming. The front feet are useful for digging and food handling. The orangish incisors are open-rooted, long, curved, and continually growing while the cheek teeth are high crowned (dental formula is (I1/1 C0/0 P1/1 M3/3) × 2 = 20 teeth total). Both the ears and nostrils can be closed by valves when underwater. A skin-fold inside the mouth permits items to be carried by the teeth without water entering



A North American beaver (*Castor canadensis*) hauling willow onto a dam in Alaska, USA. (Photo by Animals Animals ©Johnny Johnson. Reproduced by permission.)

A North American beaver (*Castor canadensis*) den on the upper Mississippi River in Minnesota, USA. (Photo by Animals Animals ©C. C. Lockwood. Reproduced by permission.)

the throat. A nictitating membrane covers the eyes providing protecting and enhancing visual acuity underwater. Their eyesight is not great but smell and hearing are acute. The genus name refers to a pair of castor sacs that release a pungent, musky odor when urine passes through them and out the cloaca (called castoreum). Paired anal glands release secretion through separate anal papillae also in the cloaca. The secretion can distinguish male and female beavers of each species

A North American beaver (*Castor canadensis*) family inside their lodge. (Photo by Wolfgang Bayer. Bruce Coleman, Inc. Reproduced by permission.)

A young North American beaver (*Castor canadensis*) feeding on plants in the Grassmere Wildlife Park in Nashville, Tennesee, USA. (Photo by Byron Jorjorian. Bruce Coleman, Inc. Reproduced by permission.)

A North American beaver (*Castor canadensis*) eating willow on Vermillion Lakes, Banff National Park, Alberta Canada. (Photo by Animals Animals ©Patti Murray. Reproduced by permission.)

and even the two species apart. The reproductive organs are internal. Males have a baculum that is detectable upon palpation. They are hindgut fermenters with an enlarged caecum containing micobiota. They practice coprophagy and possess a cardiac gland in the stomach that secretes digestive chemicals.

Distribution

Beavers were once found throughout Europe, much of Asia, and North America. Hunting by humans for their pelts greatly decreased their range in previous centuries. Recent reintroduction programs successfully restored the beaver to Russia and Scandinavia and *C. canadensis* to Finland. A few pairs of North American beavers were imported some 50 years ago by the Argentinian government to start commercial fur farming, and when the venture failed, they were released in the environment. They have now proliferated to some 100,000 pairs that cause ecological mayhem and are now found in Chile as well.

Habitat

Beavers live in riparian habitats and are semi-aquatic. They build dams that can be quite extensive, reaching over 10 ft (3 m) in height and hundreds of feet (meters) long, although 65–98 ft (20–30 m) is common. If food is readily available, beavers are not impelled to create dams. Beavers may create multiple homes in their territory. The homes can be bank burrows, a bank den, or a wood lodge, each with several entrances.

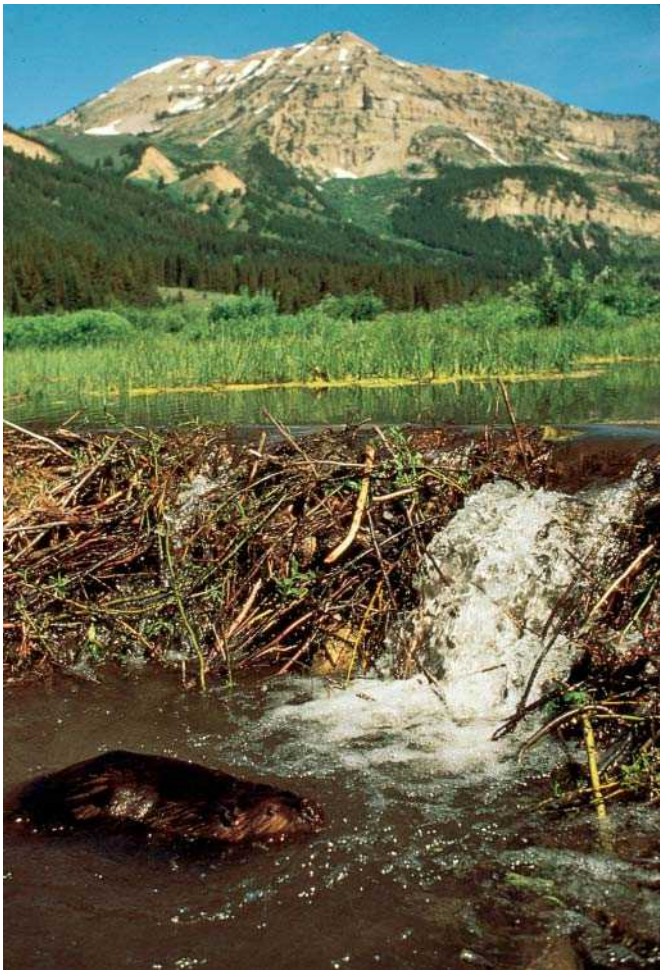
Behavior

Beavers begin their active periods in the evening around 6:00 P.M. Adults spend much of their time traveling, foraging, and being in the lodge. Time budgets do not vary much with season. During ice cover, beavers minimize their energy expenditure by remaining close to their home. Beavers paddle with their webbed hind feet and use the tail as a rudder. The tail is slapped on the water to let an approaching intruder know they have been spotted and to warn family members. Beavers vocalize as well and kits are the most vocal with their cries discernible even through the walls of the lodge. Both sexes are involved in scent marking, but adult males mark most frequently. Castoreum and sometimes anal gland secretion provide a territorial specific odor to the marks. Resident adult beavers will investigate and often mark on top of the mark from nonresident beavers. They can distinguish scents of neighbors from strangers, and recognize their mate, family, kin, and even species. Territorial scent marking is most prevalent in the spring and early summer when beavers, especially two-year-olds, disperse. Body and tail scars are evidence of conflicts between individuals from different families. Scent marking, body postures, splashing of sticks, tail-slapping, tooth sharpening, agitated swimming, and even low growls are indicative of an aroused territory holder. Females tend to disperse further than males but distance can vary greatly from less than 0.6 mi (1 km) to tens of miles (kilometers).

Feeding ecology and diet

The foraging of beavers can have a dramatic impact on community trophic dynamics and forest composition. Beavers can remove stands of small trees and fell trees up to 46 in (117 cm) in diameter. This creates patches in the forest and allows understory vegetation to grow. Beavers are thought to remove a greater proportion of biomass per area foraging than any other herbivore. Beavers are generalist herbivores and central place foragers in that they carry food back to their home site. In northerly climates, beavers often create a cache of woody material near their lodge as a winter food supply.

A North American beaver (*Castor canadensis*) swimming underwater. (Photo by J. & D. Bartlett. Bruce Coleman, Inc. Reproduced by permission.)



A North American beaver (*Castor canadensis*) working on a dam. (Photo by J. T. Wright. Bruce Coleman, Inc. Reproduced by permission.)

Beavers generally prefer soft wood trees but in spring and summer consume a variety of herbaceous material and aquatic plants. The denuded branches are used for dam and lodge construction. Some tree species may be used primarily for building and rarely consumed.

Reproductive biology

Beavers lives in families (average three to eight) composed of an adult monogamous pair and offspring from two successive years. As population density increases, the number of beavers at a single site increases (maximum 18), apparently because viable habitat is not available. Mating takes place once a year from January to March. Beavers usually mate first in their third winter. Gestation is 100–110 days, and births generally occur in April through June. Kits weigh 0.4–1.5 lb (0.2–0.6 kg) at birth, and remain in the lodge for at least the first four weeks of life. Family members will bring forage into the lodge for the kits. Fertility is highest for beavers from 2.5 to seven years of age with one to nine kits born each year. Nursing ends after two to three months. Beavers are long-lived with record ages of 24 years in the wild but typical longevity is generally only seven to eight years.

Conservation status

Populations of each species once ranged in the tens of millions. While nowhere near their former numbers, beavers are recovering throughout their traditional range. If not hunted excessively, beavers should maintain viable populations. The Eurasian beaver is listed as Lower Risk/Near Threatened by the IUCN, and protected under Appendix 3 of the Convention on the Conservation of European Wildlife and Natural Habitats.

Significance to humans

Historically, beavers provided humans with excellent pelts that were used for clothes from hats to coats. This popularity lead to the extirpation of beavers throughout much of Eurasia and North America. Their meat was consumed and the castor sacs used extensively in the perfume industry. By the early twentieth century, beavers lost much of their consumptive economic value, probably saving them from extinction. Beavers are ecosystem engineers, greatly affecting water flow and the cycling of biogeochemicals. Beavers alter the landscape through their construction of

A North American beaver (*Castor canadensis*) fells a tree in Wyoming, USA. (Photo by Wolfgang Bayer. Bruce Coleman, Inc. Reproduced by permission.)

A North American beaver lodge in Alberta, Canada. (Photo by Animals Animals ©Perry D. Slocum. Reproduced by permission.)

A North American beaver (*Castor canadensis*) emerges from its lodge in New Hampshire, USA. (Photo by Animals Animals ©Ted Levin. Reproduced by permission.)

dams, carving of canals, cutting of trees and burrowing into banks. Their actions increase wetland area and overall biological production. Invertebrates, amphibians, fish, waterfowl, and numerous other terrestrial species benefit by these alterations. Beaver activity increases the resistance of ecosystems to disturbance by stabilizing water flow and the water table. By filtering and retaining sediments, beaver dams improve water quality and reduce erosion. However, beavers may be given the label as a nuisance species. Valuable and ornamental timber may be girdled, cut, or flooded. Damming can flood roads, recreation areas, crops, or dwellings. Control is generally performed by harvesting beavers or preventative maintenance. The Clemson beaver leveler is one device that prevents beavers from flooding surrounding land. Feeding damage can be reduced by chemical repellents, fencing, or by using wire around individual trees. Most negative impacts can be reduced through appropriate management. Local human attitudes and education have a huge impact on whether beavers are viewed as positive or negative components of the biological community.

1. North American beaver (*Castor canadensis*); 2. Eurasian beaver (*Castor fiber*). (Illustration by John Megahan)

Species accounts

Eurasian beaver
Castor fiber

TAXONOMY
Castor fiber Linnaeus, 1758, Sweden.

OTHER COMMON NAMES
English: European beaver.

PHYSICAL CHARACTERISTICS
Weight 33–75 lb (15–35 kg). Yellowish brown to black fur and a flat tail. Has longer nasal bones, larger and more massive skull and smaller tail than the North American beaver. The anal gland secretion is a thick paste of a grayish color in females but oily with a whitish or pale straw color in males. It is brown and viscous in male but it is whitish or light yellow and runny in female North American beavers. Eurasian beavers are significantly more resistant to tularemia.

DISTRIBUTION
Formerly distributed continuously across Eurasia from the British Isles to eastern Siberia. Presently, established throughout Europe except for Iberia, Italy, and the southern Balkans. Present also in China, Mongolia, and Khabarovsk.

HABITAT
Common to freshwater wetlands, rivers, streams, lakes, ponds, and even bogs.

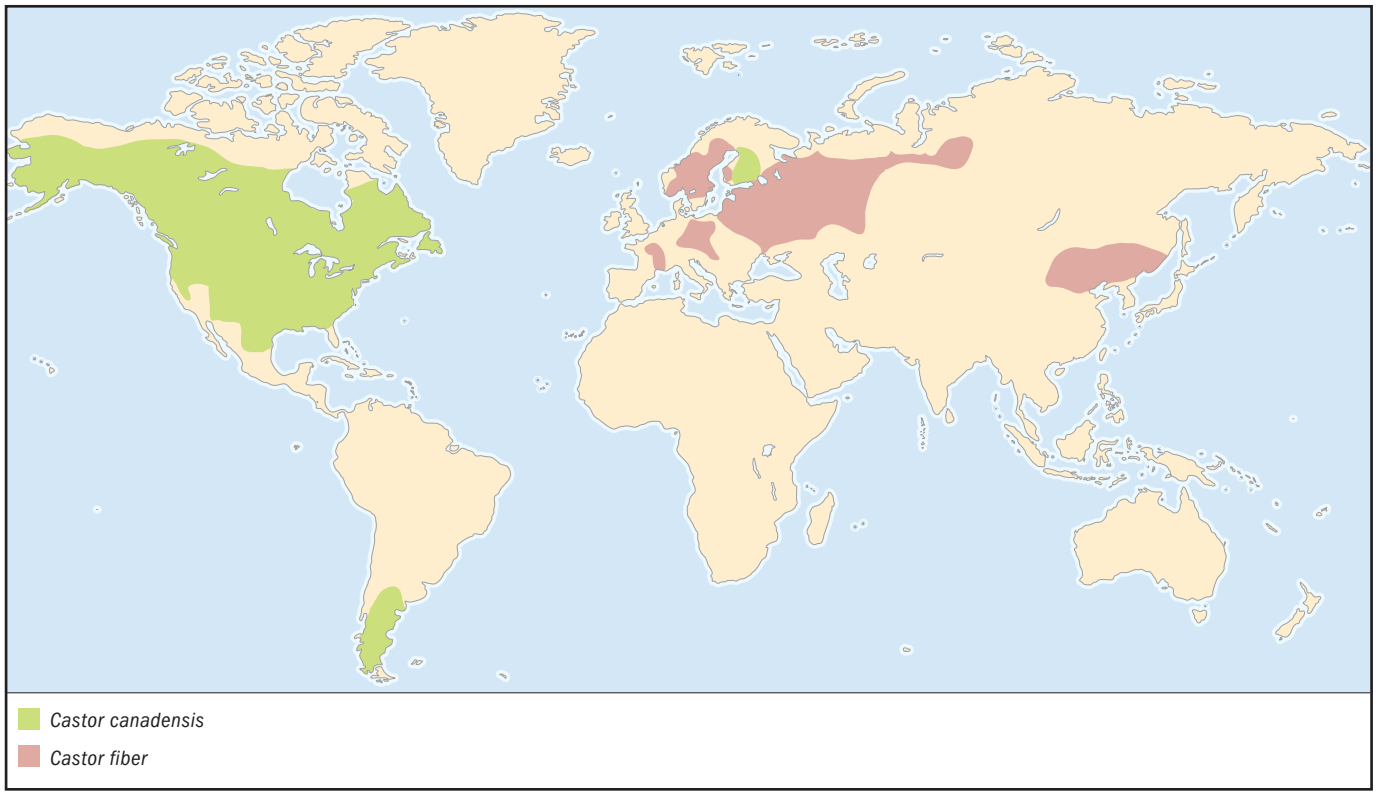
BEHAVIOR
Nocturnal, but more diurnal (especially at dusk) if undisturbed. Territorial throughout the year. Tends to live in burrows and is less likely to construct dams than the North American beaver. Mark tufts of grass, rocks, and logs, as well as directly onto the ground.

FEEDING ECOLOGY AND DIET
In spring and summer, particularly aquatic plants, and a wide range of grasses, forbs, ferns, shrubs, leaves and twigs, crops, bushes and trees in fall, and twigs and bark in winter. Tree preferences are aspen, poplar, and willow.

REPRODUCTIVE BIOLOGY
The Eurasian beaver matures later and has smaller litters (average 2–3 kits; maximum 7) than the North American beaver. Monogamous.

CONSERVATION STATUS
Overhunting reduced Eurasian beaver populations to about 1,200 animals, in eight isolated populations around the end of the nineteenth century. Protection, natural spread, and reintroductions led to a powerful recovery in both range and populations during the twentieth century, which continues at a rapid pace despite considerable loss and degradation of habitat. The minimum population estimate is 593,000 in 2002. The Eurasian beaver is protected under Appendix 3 of the Convention on the Conservation of European Wildlife and Natural Habitats and is listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
In Eurasia nearly all beaver-human conflicts are caused by beavers feeding on cultivated plants, or dam building. They are



keystone species in wetland habitats, and humans increasingly acknowledge their environmental contributions. Hunting and dead-trapping are allowed in the Nordic countries, Russia, and Baltic countries. Presently, beaver safaris are offered to observe beavers in Norway, Sweden, Poland, and France. ◆

North American beaver

Castor canadensis

TAXONOMY
Castor canadensis Kuhl, 1820, Hudson Bay, Canada.

OTHER COMMON NAMES
English: Canadian beaver.

PHYSICAL CHARACTERISTICS
Weight 33–75 lb (15–35 kg). Yellowish brown to black fur and a flat tail.

DISTRIBUTION
Historically located throughout the continental United States, the subarctic of Canada to the tundra and northern Mexico, excluding desert regions and southern Florida. Presently, beavers are found in most of these areas but in lower numbers. Successful introductions in Finland, Russia, and Argentina.

HABITAT
Nocturnal, but more diurnal (especially at dusk) if undisturbed. Territorial throughout the year. Tends to live in burrows and is less likely to construct dams than the North American beaver. Mark tufts of grass, rocks, and logs, as well as directly onto the ground.

BEHAVIOR
Alters the landscape more with extensive dams than the Eurasian beaver. Scent marking occurs almost exclusively by creating mud mounds. Otherwise, behavior is similar to the Eurasian beaver.

FEEDING ECOLOGY AND DIET
Strict herbivores, prefer the cambium and leaves of soft wooded trees like aspen (*Populus*). However, incorporate a wide range of food items into their diet such as aquatic plants, herbs, grass, shrubs, conifers, and deciduous hardwoods.

REPRODUCTIVE BIOLOGY
As for the Eurasian beaver but mature earlier and has larger litters (average 3–4 kits; maximum 12). Monogamous.

CONSERVATION STATUS
In the late twentieth century, population estimates were 6–12 million, probably less than 10% of historical levels. Beavers have no special status although in some regions it is illegal to tamper with their dams.

SIGNIFICANCE TO HUMANS
In past centuries, the Canadian beaver was an important animal for the First Nations and is part of Native American myths and folklore. The Apaches endowed beavers with the magic powers of the medicine men and they are also part of the folklore of European settlers. Much of the exploration of North America was also a result of the search for beavers, highly prized because of the value of their pelts. In the latter half of the twentieth century, the poor economic value of beavers has assisted the recovery of many populations. Beavers provide enormous ecological benefits as well as recreational and aesthetic value. They probably affect their immediate environment as much as humans. The greatest environmental change results from their dam-building activities. The damming of streams raises the level of the water table. Several tree species cannot survive in waterlogged soil and their death allows the spread of species that are adapted to permanently wet soil. These include for example, willows, cottonwoods, and alders. Beaver ponds are a favorable habitat for many forms of life: insects lay eggs in them, fish feed on the insect larvae, and muskrats, mink, shorebirds, and fish thrive. There are over 50 species of animals that live in beaver ponds. ◆

Resources

Books

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Conley, V. A. *The War Against the Beavers.* Minneapolis: University of Minnesota Press, 2003.

Novak, M., J. Baker, M. Obbard, and B. Mallock, eds. *Wildlife Furbearer Management and Conservation in North America.* Toronto: Ashton-Potter Limited, Ontario Ministry of Natural Resources, 1987.

Owl, Grey. *Tales of An Empty Cabin.* Toronto: Key Porter Books, 1999.

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Halley, D., and F. Rosell. "The Beaver's Reconquest of Eurasia: Status, Population Development and Management of a Conservation Success." *Mammal Review* 32 (2002): 153–178.

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Organizations

Arkansas Soil and Water Conservation Commission, Beaver Conservation Program. 101 East Capitol Avenue, Suite 350, Little Rock, Arkansas 72201 USA. Phone: (501) 682-3953. Fax: (501) 682-3991. Web site: <http://www.state.ar.us/aswcc/page6.html/>

Bruce A. Schulte, PhD
Frank Rosell, PhD

Pocket gophers
(Geomyidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Geomyidae

Thumbnail description
Small- to medium-sized herbivores, characterized by a tube-shaped body, small eyes and ears, short tail, short but stout forelimbs, and small hindlimbs

Size
5–14 in (13–36 cm); 0.13–3.1 lb (60–1,400 g)

Number of genera, species
6 genera; 36 species

Habitat
Meadows, prairies, woodlands, and deserts

Conservation status
Critically Endangered: 2 species; Endangered: 1 species; Vulnerable: 2 species; Lower Risk/Near Threatened: 10 species

Distribution
North, central, and northwestern North America

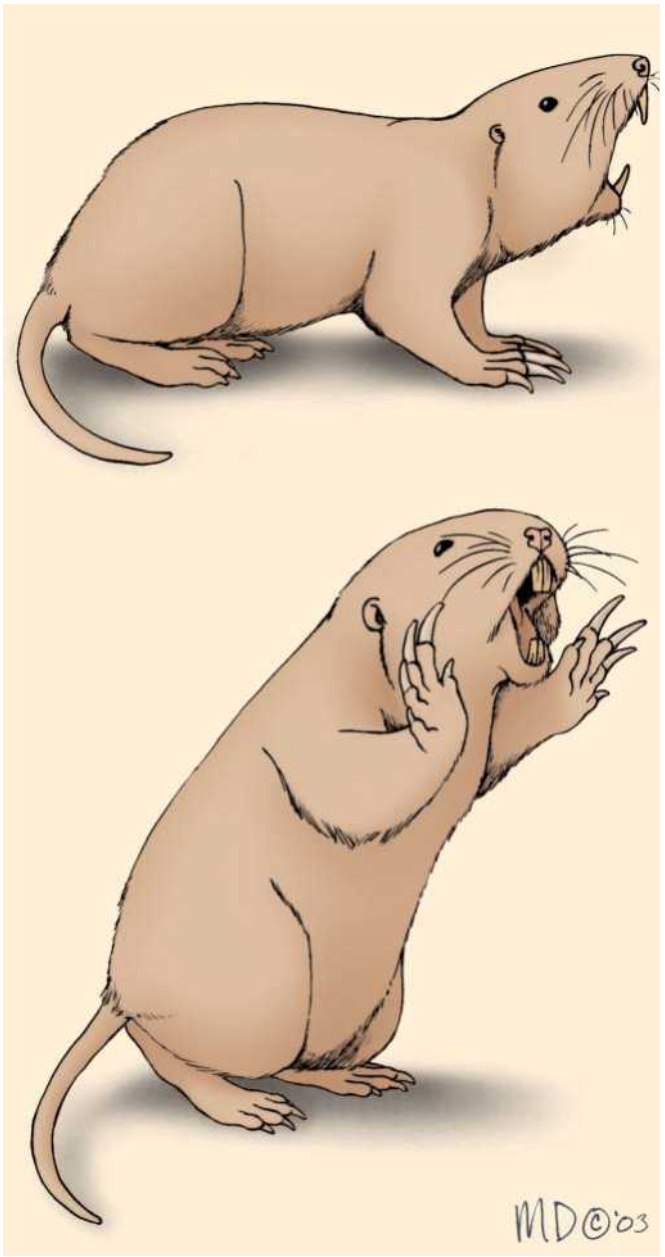
Evolution and systematics

Pocket gophers have an extensive fossil record that dates back to the late Oligocene or early Miocene of North America, approximately 25 million years ago. The closest living relatives to pocket gophers are members of the rodent family Heteromyidae, which includes kangaroo rats (*Dipodomys*) and pocket mice (*Chaetodipus* and *Perognathus*).

Living pocket gophers comprise two major lineages, one of which contains only a single living genus, *Thomomys*, the other containing the living genera *Geomys*, *Cratogeomys*, *Orthogeomys*, *Pappogeomys*, and *Zygogeomys*. Molecular analyses of DNA sequences support this basic subdivision within the family Geomyidae. Pocket gophers are most diverse in Mexico, where representatives of all six genera (and 22 of the 36 species) can be found.

Evolutionary relationships among species of pocket gophers have been compared to the relationships among species of chewing lice that live in the pocket gopher's fur. Surprisingly, the louse relationships almost exactly mirror the relationships among their hosts (a phenomenon known as "cospeciation"), which suggests that lice and pocket gophers have been living together for many millions of years.

A mountain pocket gopher (*Thomomys monticola*) in the East Sierras, California, USA. (Photo by Richard R, Hansen/Photo Researchers, Inc. Reproduced by permission.)



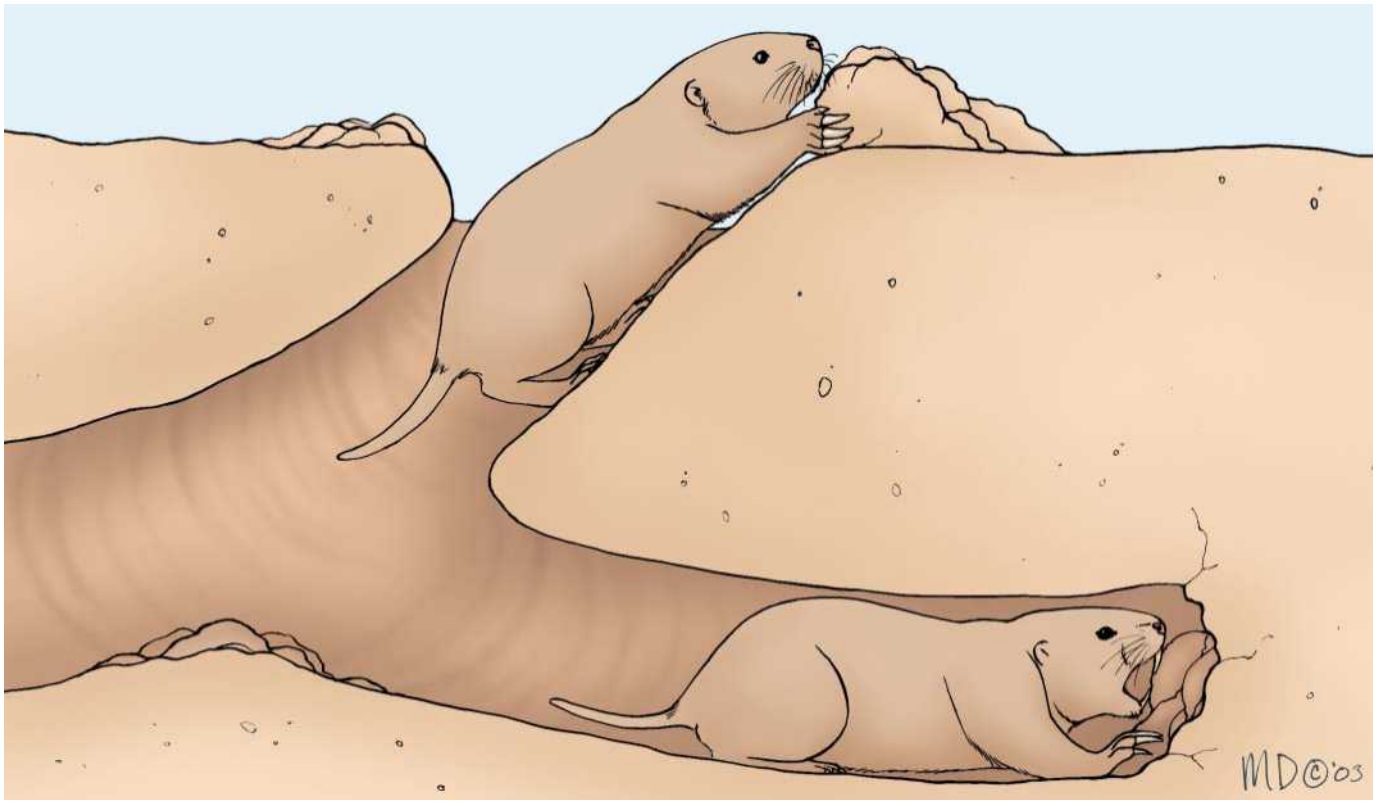
Pocket gopher defense postures display the animal's claws and teeth. (Illustration by Marguette Dongvillo)

A plains pocket gopher (*Geomys bursarius*) removing soil from its tunnel near Geuda Springs, Kansas, USA. (Photo by Kenneth M. Highfill/Photo Researchers, Inc. Reproduced by permission.)

A mountain pocket gopher (*Thomomys monticola*) peers out from its burrow. (Photo by Wardene Weisser. Bruce Coleman, Inc. Reproduced by permission.)

Physical characteristics

Pocket gophers are extraordinarily well adapted for life in subterranean tunnels. Their body is tubular in shape, which permits them to travel rapidly both forwards and backwards in tunnels. Their eyes and external ears (pinnae) are reduced in size, and numerous hairs around the eyes and ears prevent the entry of soil. Pocket gophers have relatively short limbs and a short, almost hairless tail. Most digging is accomplished using the claws of the powerful forefeet, but the large, procumbent, and blade-like incisor teeth also are used on occasion for digging. While digging, the pocket gopher's lips can be closed behind the incisors to prevent soil from entering the mouth. Although short, the forelegs are stout, with



Pocket gophers push the soil from the mouth of a burrow using a "snowplow" approach with their paws, and use their incisors to chew at hard soil. (Illustration by Maguette Dongvillo)

The northern pocket gopher (*Thomomys talpoides*) rarely strays far from its burrow. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

broad hands and long, curved claws. These powerful digging appendages can also be used to push large quantities of earth within the burrow.

Pocket gophers have cheek pouches that open external to the mouth and extend from the mouth region to the animal's shoulders (hence the common name "pocket" gopher). These commodious pouches are lined with fur and are used to transport food and nest material (but not soil) within the burrow system. When full, the pouches make the pocket gopher's head appear almost twice its natural size. The fur of pocket gophers is generally short and may be very sparse in species living in hot, tropical environments. Fur color varies widely, even within a species, and tends to match the color of freshly excavated soil (generally light brown to almost black). This camouflage appears to be an adaptation to hide the animal from aerial predators such as hawks when the pocket gopher is pushing excavated soil onto the surface.

Distribution

Pocket gophers are found only in the Western Hemisphere, where their range extends from southern Canada through western North America, southward to northwestern Colombia in South America. One isolated species, *Geomys*

A valley pocket gopher (*Thomomys bottae*) in its burrow with a nest chamber. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A southern pocket gopher (*Thomomys umbrinus*) peers out from its burrow in southeast Arizona. (Photo by Joe McDonald. Bruce Coleman, Inc. Reproduced by permission.)

pinetis, occurs in the southeastern United States (Alabama, Georgia, and Florida).

Habitat

Pocket gophers live in almost any habitat that contains friable soil and does not flood. They are known from meadows, prairies, woodlands, alpine forests, valleys, deserts, rainforests, and agricultural fields. Neither elevation nor temperature seem to limit pocket gopher distibution—they are known from hot desert habitats at sea level and also from cold, high-elevation habitats near timberline. Pocket gophers live in a wide variety of plant communities where they feed on the roots and tubers of many species of plants. They are especially abundant in agricultural fields and seem to prefer alfalfa, potato, banana, and sugar cane crops.

Behavior

Pocket gophers are extremely asocial mammals that generally live alone in their burrow systems. The population density of pocket gophers tends to vary widely among habitats, depending on the availability of food resources. Numbers of individuals may be fewer than 50 to as many as several hundred individuals per acre (0.4 ha). Their burrow systems are easily recognized by the characteristic mounds of earth (generally five to 20 per burrow system) that have rounded rather

A northern pocket gopher (*Thomomys talpoides*) burrowing in Wyoming, USA. (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

A northern pocket gopher (*Thomomys talpoides*) foraging for grasses. (Photo by J. Foott. Bruce Coleman, Inc. Reproduced by permission.)

A valley pocket gopher (*Thomomys bottae*) acts aggressively after being flooded out of its burrow. (Photo by Gary R. Zahm. Bruce Coleman, Inc. Reproduced by permission.)

than conical tops. Burrow entrances are usually plugged with soil when not in use. Where gophers occur in high numbers, the spacing of individual burrow systems is highly uniform, producing a buffer zone between burrows. This pattern is evident even in areas that differ widely in food availability, which suggests that the buffer zones are related to social interactions among pocket gophers, rather than food availability. Although pocket gophers live in almost continual darkness, they are generally crepuscular (active mainly at dawn and dusk), and some species are nocturnal. Pocket gophers are active all year and do not hibernate.

Pocket gophers display a remarkable amount of burrowing activity, and they, like beavers, have caused numerous changes in the landscape. Estimates of the amount of soil moved by pocket gophers in a single year range from 4.4–74.5 cubic yd (3.4–57 cubic m) per acre (0.4 ha). The disturbance resulting from this burrowing activity alters both physical and biotic processes in the local environment. Although pocket gophers eat voraciously, the net long-term effect of their presence is an increase in plant biomass, probably because of the effect of their excavations on soil nutrients. Pocket gophers also spread roots,

A valley pocket gopher (*Thomomys bottae*) yawning, showing lips that close behind the teeth to keep dirt out of its mouth when digging. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

tubers, and other plant parts as a result of their burrowing activities, and thus they contribute to the distribution of plant life in their communities. The energetic cost of the subterranean lifestyle is extraordinarily high. Thus, the advantages of living in a subterranean burrow system—including protection from predators and extreme climatic fluctuations—must be very important to pocket gopher survival.

Feeding ecology and diet

Most mammals that burrow into the earth do so simply for shelter or dens. Pocket gophers, however, actually forage through the earth in search of food, and they leave behind them a complex network of tunnels, which they also use for shelter and nesting. Pocket gophers are strict herbivores that feed on the underground parts of plants, especially the succulent parts such as bulbs and tubers. Occasionally, pocket gophers will eat the aboveground stems and leaves of forbs located near their burrow entrances. The horizontal feeding tunnels produced by pocket gophers are usually dug at the depth of greatest root density, approximately 2–8 in (6–20 cm) below the surface. In contrast, their nest and food storage chambers may be as deep as 4.9–6.5 ft (1.5–2 m).

Reproductive biology

Pocket gophers generally breed only once per year (usually in spring), although some species are capable of producing two litters per year (spring and fall) if conditions permit. During the breeding season, reproductively mature females will allow males to enter their burrow systems for brief mating encounters. The gestation period ranges from 18 days in smaller species to more than a month in the larger species. Litter size varies widely among pocket gopher species, ranging from one to 10 young per litter, with an average of three to five young. Young pocket gophers remain in their mother's burrow for one to two months, at which time they disperse in search of a place to dig their own burrow system. Some species reach reproductive maturity at only three months of age, whereas others do not breed until they are nine to 12 months of age. Adult body size is usually attained at an age of five to nine months.

Conservation status

Fifteen species of pocket gophers are listed on the World Conservation Union (IUCN) Red List. These include two species listed as Critically Endangered (*Cratogeomys neglectus* and *Orthogeomys cuniculus*), one species listed as Endangered (*Zygogeomys trichopus*), two listed as Vulnerable (*Geomys trop-*

icalis and *Pappogeomys alcorni*), and 10 additional species listed as Lower Risk/Near Threatened.

Most of the threatened species of pocket gophers occur naturally in low abundance within restricted habitats. Current threats to these pocket gophers include competition from other gopher species and, in the case of *Geomys tropicalis*, loss of habitat caused by urban expansion of humans.

Significance to humans

Pocket gophers are widely considered to be agricultural pests. In tropical areas, a single pocket gopher can destroy a family's garden in less than a month. Commercial agriculturalists regularly trap or poison pocket gophers to limit loss of crops. Early Native Americans are known to have consumed pocket gophers, and it is reported that in some areas of Latin America local people regard the meat of pocket gophers as a delicacy.

1. Querétaro pocket gopher (*Cratogeomys neglectus*); 2. Valley pocket gopher (*Thomomys bottae*); 3. Plains pocket gopher (*Geomys bursarius*); 4. Yellow-faced pocket gopher (*Cratogeomys castanops*); 5. Michoacán pocket gopher (*Zygogeomys trichopus*); 6. Buller's pocket gopher (*Pappogeomys bulleri*); 7. Large pocket gopher (*Orthogeomys grandis*). (Illustration by Marguette Dongvillo)

Species accounts

Valley pocket gopher
Thomomys bottae

TAXONOMY
Thomomys bottae (Eydoux and Gervais, 1836), coast of California, United States. One hundred ninety-one subspecies.

OTHER COMMON NAMES
English: Smooth-toothed pocket gopher, western pocket gopher; Spanish: Tuza, topo.

PHYSICAL CHARACTERISTICS
Head and body length 6–13 in (15–33 cm); weight 1.6–21 oz (45–600 g). Color ranges from pale gray to russet to black.

DISTRIBUTION
Western United States into northern Mexico. Sea level to approximately 10,000 ft (3,000 m).

HABITAT
Common in valleys, woodlands, deserts, and agricultural fields.

BEHAVIOR
Lives singly in subterranean burrow system; asocial and aggressive toward individuals of same species, except during breeding season when brief mating encounters occur.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Occasionally feeds on surface vegetation near entrance to burrow.

REPRODUCTIVE BIOLOGY
Polygamous. Breeds once, sometimes twice per year (spring and fall); generally two to four young per litter.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Common lawn, garden, and agricultural pest in some regions. ◆

Plains pocket gopher
Geomys bursarius

TAXONOMY
Geomys bursarius (Shaw, 1800), upper Mississippi Valley, United States. Twenty-one subspecies.

OTHER COMMON NAMES
English: Eastern pocket gopher.

PHYSICAL CHARACTERISTICS
Head and body length 6–13 in (15–36 cm); weight 7–21 oz (200–600 g). Color ranges from pale brown to black.

DISTRIBUTION
Extreme southern Manitoba, Canada through southern Texas.

HABITAT
Common in plains, valleys, woodlands, and agricultural fields.

BEHAVIOR
Lives singly in subterranean burrow system; asocial and aggressive toward individuals of same species, except during breeding season when brief mating encounters occur.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Occasionally feeds on surface vegetation near entrance to burrow.

REPRODUCTIVE BIOLOGY
Polygamous. Breeds once, sometimes twice per year (spring and fall); generally one to three young per litter.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Common lawn, garden, and agricultural pest in some regions. ◆

Michoacán pocket gopher
Zygogeomys trichopus

TAXONOMY
Zygogeomys trichopus Merriam, 1895, Michoacán, Mexico. Two subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 10–13 in (26–36 cm); weight 7–21 oz (200–600 g).

DISTRIBUTION
Known only from four isolated localities in central Michoacán, Mexico.

HABITAT
Small clearings in pine, spruce, and alder forests between approximately 3,000–10,000 ft (900–3,000 m).

BEHAVIOR
Lives singly in subterranean burrow system; asocial, but less aggressive than other species of pocket gopher; surface mounds are tall and conical, unlike those of all other species.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Unlike all other pocket gopher species, *Zygogeomys trichopus* is not known to feed on surface vegetation near the entrance to its burrow.

REPRODUCTIVE BIOLOGY
Unknown; probably breeds once per year; a pregnant female with a single embryo was captured in the month of December.

CONSERVATION STATUS
Listed on the IUCN Red List as Endangered; known only from small, isolated populations that may be threatened by competition from other species of pocket gophers and habitat destruction by humans.

SIGNIFICANCE TO HUMANS
None at present, although human populations are expanding into the high-elevation habitat characteristic of this species. ◆

Large pocket gopher
Orthogeomys grandis

TAXONOMY
Orthogeomys grandis (Thomas, 1893), Dueñas, Guatemala. Sixteen subspecies.

OTHER COMMON NAMES
English: Giant pocket gopher.

PHYSICAL CHARACTERISTICS
Head and body length 12–18 in (31–44 cm); weight 18–34 oz (500–950 g). Color is dark brown or black above and paler below.

DISTRIBUTION
Western regions of southern Mexico, Guatemala, El Salvador, and Honduras.

HABITAT
Variable, from arid tropical lowlands to moist tropical forests at higher elevations. Sea level to approximately 10,000 ft (3,000 m).

BEHAVIOR
Lives singly in subterranean burrow system; primarily nocturnal and less active than most other species.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Diet also includes the roots of cultivated plants, including banana trees and sugar cane.

REPRODUCTIVE BIOLOGY
Unknown; may breed throughout the year, as do other species in this genus.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
This species is considered a major agricultural pest, and in many areas of Latin America, professional *tuceros* (pocket gopher catchers) charge farmers a small price to remove pocket gophers from their land. Many Mexican villages have a *tucero*, and it is said that the job is respected and passed from father to son. In some areas of Latin America, local people regard the meat of *Orthogeomys grandis* as a delicacy. ◆

Yellow-faced pocket gopher
Cratogeomys castanops

TAXONOMY
Cratogeomys castanops (Baird, 1852), Colorado, United States. Twenty-five subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 8–16 in (20–40 cm); weight 8–53 oz (230–1,500 g). Color is yellowish brown and paler below.

DISTRIBUTION
Western United States (Colorado and Kansas) southward through northcentral Mexico.

HABITAT
Common in grassy plains, deserts, tropical lowland forests, montane forests, and agricultural fields. Sea level to approximately 12,000 ft (3,700 m).

BEHAVIOR
Lives singly in subterranean burrow system; asocial and aggressive toward individuals of same species, except during breeding season when brief mating encounters occur.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Occasionally feeds on surface vegetation near entrance to burrow. Occurs commonly in agricultural areas, especially alfalfa, banana, corn, and sugar cane fields.

REPRODUCTIVE BIOLOGY
Polygamous. May breed only once per year (spring) in the north and throughout the year in the south; generally one to three young per litter.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Common lawn, garden, and agricultural pest in some regions. ◆

Querétaro pocket gopher
Cratogeomys neglectus

TAXONOMY
Cratogeomys neglectus (Merriam, 1902), Querétaro, Mexico. No subspecies recognized.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 9–14 in (22–37 cm); weight 7–18 oz (200–500 g). Color is yellow, brown, or blackish and paler below.

DISTRIBUTION
Known only from one isolated region near the town of Pinal de Amoles, Querétaro, Mexico.

HABITAT
Locally common in mountain valleys where oak woodlands meet higher–elevation pine forests. Also occur in agricultural fields (corn, potatoes, and apples). Approximately 8,600–9,600 ft (2,600–2,900 m).

BEHAVIOR
Lives singly in subterranean burrow system; asocial and aggressive toward individuals of same species, except during breeding season when brief mating encounters occur.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Occasionally feeds on surface vegetation near entrance to burrow. Also feeds on corn and potato crops and the roots of apple trees.

REPRODUCTIVE BIOLOGY
Little is known; may breed only once per year (spring); probably only one to three young per litter. Assumed polygamous.

CONSERVATION STATUS
Listed on the IUCN Red List as Critically Endangered. The major threat to this species comes from encroachment of human agriculture into its natural range.

SIGNIFICANCE TO HUMANS
Common agricultural pest throughout its limited range. ◆

Buller's pocket gopher
Pappogeomys bulleri

TAXONOMY
Pappogeomys bulleri (Thomas, 1892), near Talpa, Jalisco, Mexico. Eight subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 7–10 in (18–27 cm); weight 3–9 oz (80–250 g). Color is orange-cinnamon to dark brown and paler below.

DISTRIBUTION
Western Mexico (Colima, Jalisco, and Nayarit).

HABITAT
Mountain slopes and plains at elevations between 3,000 and 10,000 ft (900–3,000 m).

BEHAVIOR
Lives singly in subterranean burrow system; asocial and aggressive toward individuals of same species, except during breeding season when brief mating encounters occur. Assumed polygamous.

FEEDING ECOLOGY AND DIET
Herbivorous; burrows through the soil in search of roots and tubers. Occasionally feeds on surface vegetation near entrance

to burrow. Occurs commonly in agricultural areas, especially corn and bean fields.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Common agricultural pest in some parts of its range. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Northern pocket gopher *Thomomys talpoides*	Variable in color from yellowish brown to pale gray above and paler below. Outer face of each upper incisor smooth (without grooves). Small pocket gopher: length 6–10 in (15–27 cm); weight 3–9 oz (80–250 g).	Found generally in cool, montane meadows, often near pine forests. Behavior typical of pocket gophers: fossorial and asocial.	South-central Canada through western United States.	Plant roots, bulbs, and tubers, as typical for the family.	Not threatened
Mazama pocket gopher *Thomomys mazama*	Variable in color from reddish brown to black above and paler below. Outer face of each upper incisor smooth (without grooves). Small pocket gopher: length 6–10 in (15–27 cm); weight 3–9 oz (80–250 g).	Found generally in cool, montane meadows, often near pine forests. Behavior typical of pocket gophers: fossorial and asocial.	Western Washington, western Oregon, and northern California, United States.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Southern pocket gopher *Thomomys umbrinus*	Highly variable in color from nearly white to black above and somewhat paler below. Outer face of each upper incisor smooth (without grooves). Small pocket gopher: length 6–10 in (15–27 cm); weight 3–9 oz (80–250 g).	Found a variety of habitats, including grasslands, woodlands, and pine forests from sea level to more than 12,000 ft (3,600 m). Behavior typical of pocket gophers: fossorial and asocial.	Southern Arizona, United States, through central Mexico.	Plant roots, bulbs, and tubers.	Not threatened
Mountain pocket gopher *Thomomys monticola*	Dark brown above and somewhat paler below; ears pointed, rather than rounded, as in most pocket gophers. Outer face of each upper incisor smooth (without grooves). Small pocket gopher: length 7–9 in (19–22 cm); weight 3–6 oz (80–180 g).	Found in or near pine forests in mountainous areas. Behavior typical of pocket gophers: fossorial and asocial.	Sierra Nevada of California, United States.	Plant roots, bulbs, and tubers.	Not threatened
Camas pocket gopher *Thomomys bulbivorus*	Large for genus; dark sooty brown above and somewhat paler below. Outer face of each upper incisor smooth (without grooves). Medium-sized pocket gopher: length 9–12 in (24–30 cm); weight 8–19 oz (230–550 g).	Found mainly in open valleys and grasslands. Behavior typical of pocket gophers: fossorial and asocial.	Restricted to the Willamette Valley of Oregon, United States.	Plant roots, bulbs, and tubers.	Not threatened
Desert pocket gopher *Geomys arenarius*	Very light brown to almost white above and somewhat paler below. Has two longitudinal grooves on outer face of each upper incisor. Medium-sized pocket gopher: length 9–11 in (24–28 cm); weight 8–14 oz (230–400 g).	Found in arid and sandy desert habitats. Behavior typical of pocket gophers: fossorial and asocial.	Southern New Mexico, extreme western Texas, (United States) and northern Chihuihui, Mexico.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Texas pocket gopher *Geomys personatus*	Light brown to grayish drab above and somewhat paler below. Has two longitudinal grooves on outer face of each upper incisor. Medium-sized pocket gopher: length 9–11 in (24–28 cm); weight 8–14 oz (230–400 g).	Found in areas with deep, sandy soils. Behavior typical of pocket gophers: fossorial and asocial.	Extreme southern Texas, United States, and nearby Padre and Mustang Islands.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Tropical pocket gopher *Geomys tropicalis*	Light brown above and somewhat paler below. Has two longitudinal grooves on outer face of each upper incisor. Medium-sized pocket gopher: length 9–1 in (24–28 cm); weight 8–14 oz (230–400 g).	Found in coastal areas with deep, sandy soils. Behavior typical of pocket gophers: fossorial and asocial.	Restricted to vicinity immediately north of Tampico, Tamaulipas, Mexico.	Plant roots, bulbs, and tubers.	Vulnerable
Southeastern pocket gopher *Geomys pinetis*	Light brown above and somewhat paler below. Has two longitudinal grooves on outer face of each upper incisor. Medium-sized pocket gopher: length 9–12 in (24–30 cm); weight 8–14 oz (230–400 g).	Generally found in areas with deep, sandy soils, including open grasslands and low-elevation pine forests. Behavior typical of pocket gophers: fossorial and asocial.	Southern Alabama, southern Georgia, and northern Florida, United States.	Plant roots, bulbs, and tubers.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Hispid pocket gopher *Orthogeomys hispidus*	Pelage very sparse and stiff above and almost naked below; grayish to black above and paler below. Has one longitudinal groove on outer face of each upper incisor. Large pocket gopher: length 12–18 in (31–44 cm); weight 18–33 oz (500–950 g).	Found in humid lowland habitats and low-elevation pine forests up to approximately 5,000 ft (1,500 m). Behavior typical of pocket gophers: fossorial and asocial.	Coastal regions of southeastern Mexico, Yucatán Peninsula, Belize, Guatemala, and northwestern Honduras.	Plant roots, bulbs, and tubers.	Not threatened
Big pocket gopher *Orthogeomys lanius*	Pelage soft and woolly; grayish brown above and paler below. Has one longitudinal groove on outer face of each upper incisor. Large pocket gopher: length 12–18 in (31–44 cm); weight 18–33 oz (500–950 g).	Found in meadows adjacent to pine forests. Behavior typical of pocket gophers: fossorial and asocial.	Known only from the vicinity of Xuchil, Veracruz, Mexico.	Plant roots, bulbs, and tubers.	Not threatened
Variable pocket gopher *Orthogeomys heterodus*	Pelage soft and dense; blackish above and paler below. Has one longitudinal groove on outer face of each upper incisor. Large pocket gopher: length 12–19 in (31–49 cm); weight 18–34 oz (500–950 g).	Found in open grasslands and tropical forests in highland habitats up to 8,000 ft (2,500 m). Behavior typical of pocket gophers: fossorial and asocial.	Central highlands of Costa Rica.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Chiriquá pocket gopher *Orthogeomys cavator*	Pelage soft and dense; dark brown to almost blackish above and paler below. Has one longitudinal groove on outer face of each upper incisor. Large pocket gopher: length 12–19 in (31–49 cm); weight 18–34 oz (500–950 g).	Found in tropical forests in highland habitats up to 8,000 ft (2,500 m). Behavior typical of pocket gophers: fossorial and asocial.	Mountains of southeastern Costa Rica and northwestern Panama.	Plant roots, bulbs, and tubers.	Not threatened
Darién pocket gopher *Orthogeomys dariensis*	Pelage soft and dense; dull brown to almost blackish above and paler below. Has one longitudinal groove on outer face of each upper incisor. Large pocket gopher: length 12–19 in (31–49 cm); weight 18–34 oz (500–950 g).	Found in small clearings in humid tropical forests at elevations between 1,600 and 5,000 ft (500–1,500 m). Behavior typical of pocket gophers: fossorial and asocial.	Mountains of southeastern Panama.	Plant roots, bulbs, and tubers.	Not threatened
Underwood's pocket gopher *Orthogeomys underwoodi*	Pelage generally short and sparse; blackish above with white transverse belt 0.5–1.5 in (1.3–3.8 cm) wide encircling the lumbar region; paler below. A few specimens known to lack transverse belt. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–12 in (24–30 cm); weight 8–14 oz (230–400 g).	Found in coastal tropical and semi-arid forests. Behavior typical of pocket gophers: fossorial and asocial.	Pacific coast of Costa Rica.	Plant roots, bulbs, and tubers.	Not threatened
Cherrie's pocket gopher *Orthogeomys cherriei*	Pelage generally short and sparse; dark brown to blackish above with large, triangle-shaped white spot on forehead; paler below. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–12 in (24–30 cm); weight 8–14 oz (230–400 g).	Found in low-elevation tropical and semi-arid forests. Behavior typical of pocket gophers: fossorial and asocial.	Pacific and Atlantic coastal plains and adjacent foothills of northwestern Costa Rica.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Nicaraguan pocket gopher *Orthogeomys matagalpae*	Pelage generally short and sparse; dark brown to blackish above with large, triangle-shaped white spot on forehead; paler below. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–12 in (24–30 cm); weight 8–14 oz (230–400 g).	Found in low-elevation tropical and semi-arid forests. Behavior typical of pocket gophers: fossorial and asocial.	South-central Nicaragua and east-central Honduras.	Plant roots, bulbs, and tubers.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Merriam's pocket gopher *Cratogeomys merriami*	Pelage generally short and sometimes sparse; color variable, from yellowish buff to glossy black above; paler below. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–16 in (24–40 cm); weight 10–21 oz (300–600 g).	Found in semi-arid grasslands, and nearby forests between 5,000 and 12,500 ft (1,500–3,800 m). Behavior typical of pocket gophers: fossorial and asocial.	East-central Mexico (Hidalgo, Puebla, and Veracruz).	Plant roots, bulbs, and tubers.	Not threatened
Smoky pocket gopher *Cratogeomys fumosus*	Pelage generally coarse and bristly; dark grayish brown above, paler below. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–16 in (24–40 cm); weight 10–21 oz (300–600 g).	Found in semi-arid lowland habitats. Behavior typical of pocket gophers: fossorial and asocial.	Known from one small region in Colima, Mexico.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened
Zinser's pocket gopher *Cratogeomys zinseri*	Pelage soft and lax; dark grayish brown above, paler below. Has one longitudinal groove on outer face of each upper incisor. Medium-sized pocket gopher: length 9–16 in (24–40 cm); weight 10–21 oz (300–600 g).	Found in semi-arid habitats with deep, sandy soils. Behavior typical of pocket gophers: fossorial and asocial.	Known from one small region near Lagos de Moreno, Jalisco, Mexico.	Plant roots, bulbs, and tubers.	Lower Risk/Near Threatened

Resources

Books

Hafner, M. S., J. W. Demastes, T. A. Spradling, and D. L. Reed. "Cophylogeny Between Pocket Gophers and Chewing Lice." In *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*, edited by R. D. M. Page. Chicago: The University of Chicago Press, 2002.

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Periodicals

Demastes, J. W., T. A. Spradling, M. S. Hafner, D. J. Hafner, and D. L. Reed. "Systematics and Phylogeography of Pocket Gophers in the Genera *Cratogeomys* and *Pappogeomys*." *Molecular Phylogenetics and Evolution* 22, no. 1 (2002): 144–154.

Hovey, K., and D. Rissolo. "The Process and Sociocultural Significance of Gopher Trapping in a Modern Yucatec Maya Community." *Journal of Ethnobiology* 19, no. 2 (1999): 261–276.

Reichman, O. J., and E. W. Seabloom. "The Role of Pocket Gophers as Subterranean Ecosystem Engineers." *Trends in Ecology & Evolution* 17, no. 1 (2002): 44–49.

Mark S. Hafner, PhD

Pocket mice, kangaroo rats, and kangaroo mice
(Heteromyidae)

Class Mammalia
Order Rodentia
Suborder Sciurograthi
Family Heteromyidae

Thumbnail description
Small to medium nocturnal, seed-eating rodents with external, fur-lined cheek pouches, bipedal locomotion in the kangaroo rats and mice and quadrupedal locomotion in pocket mice. Rudimentary social structure; sandbathing cleans the hair and deposits scent for communication; the medium and larger sized kangaroo rats communicate by footdrumming

Size
1.7–14.6 in (42–370 mm) total length, weight: 0.2–6.9 oz (5–195 g)

Number of genera, species: 6 genera, 60 species

Habitat
Desert, grasslands, and forest

Conservation status
Critically Endangered: 4 species; Endangered: 1 species; Vulnerable: 1 species; Lower Risk/Conservation Dependent: 1 species; Lower Risk/Near Threatened: 8 species

Distribution
Western United States, Mexico, Central America, and northern South America

Evolution and systematics

Heteromyid rodents have a long evolutionary history in North America. Hafner (1993) proposes that heteromyids diverged from their nearest relative, the subterranean pocket gopher, Geomyidae, in the Oligocene over 30 million years ago. The divergence continued as the climate of North America became increasingly cool and arid into the three distinct subfamilies and six genera extant today. Five genera diverged into multiple species in North America while one genus, *Heteromys*, entered South America. Corbet and Hill (1991) list seven species of spiny pocket mice, *Liomys*, and five species of forest spiny pocket mice, *Heteromys*, in the subfamily Heteromyinae. The subfamily Perognathinae consists of 16 species of silky pocket mice, *Perognathus*, and nine species of coarse-haired pocket mice, *Chaetodipus*). The third subfamily, Dipodomyinae, includes 21 species of kangaroo rats, *Dipodomys*, and two species of kangaroo mice, *Microdipodops*.

Physical characteristics

Heteromyids are frequently associated with the specialized morphology of kangaroo rats (weight: 1.2–6.9 oz; 33–195 g), and, to a lesser extent, the smaller kangaroo mice (0.4–0.6 oz; 10–17 g). Like kangaroos, kangaroo rats and mice move in long powerful jumps on elongated hind limbs and feet. They have especially long, beautiful tails with white tips or tufts on the end that are used for balance, and sometimes as flags. A much more generalized body type occurs in the pocket mice. *Heteromys* and *Liomys* are rat-like rodents (weights: 1.29–3.0 oz or 36.6–85.4 g and 1.2–1.8 oz or 34–50 g respectively) that have a standard quadrupedal locomotion and lack the specialized features of other species. The smaller desert pocket mice (body weights range 0.2–1.1 oz [5–31 g] in *Perognathus*, and 0.4–1.7 oz [10–47 g] in *Chaetodipus*) are quite diverse. Although they have relatively long feet, they are poor jumpers and exhibit quadrupedal locomotion. All heteromyids have external fur-lined cheek pouches that open anterior to the mouth and are nocturnal with fairly large eyes. Ears are short and rounded. Kangaroo rats and mice have inflated auditory bullae and extremely keen hearing in the low to mid-frequency ranges. The pelage varies in texture from silky and soft in kangaroo rats and mice and silky pocket mice to spiny in *Liomys* and *Chaetodipus*. Pelage color varies considerably from light to dark. Maximum longevity for these small mammals is 10 years or more.

Great Basin pocket mouse (*Perognathus parvus*) in Utah, USA. (Photo by R. J. Erwin/Photo Researchers, Inc. Reproduced by permission.)

Distribution

Schmidley et al. (1993) identify five general regions occupied by heteromyid rodents in North, Central and South America. Tropical species occur in the northern neotropical areas of Mexico, Central and northwestern South America. *Heteromys* is confined to moist areas of Mexico, and central and northern South America; *Liomys* inhabits parts of Mexico and Central America. The other four regions are arid and semiarid areas of North America in the Great Plains, the Great Basin desert, southwestern Mojave, Sonoran and Chihuahuan deserts, and California. *Perognathus* and *Chaetodipus* occur in all four arid regions. *Perognathus* ranges as far north as British Columbia and Saskatchewan throughout the central and western United States southward to Mexico. *Chaetodipus* occupies the Lower Sonoran area of the western United States north into the Great Basin. *Microdipodops* is primarily restricted to the Great Basin desert in Nevada. *Dipodomys* are widespread and inhabit arid areas from the Pacific coast north to southern Canada, east to the Great Plains and south through western Texas into Mexico. California has a diverse distribution of kangaroo rats and pocket mice in the southern Mojave Desert, coastal transition zones, and the Central Valley. Twelve of 21 species of kangaroo rat are found in California, and eight of these species occur either only or primarily there.

Habitat

Desert pocket mice and kangaroo rats inhabit a variety of arid habitats consisting of wind-blown sand, sagebrush, desert scrub, grassland, creosote bush flats, rocky hillsides, and chaparral. In contrast, kangaroo mice are mainly restricted to sandy habitats. A characteristic of heteromyid communities is their complexity in which multiple species co-exist. Brown and Harney (1993) describe a community in the Great Basin desert in Nevada composed of three species of kangaroo rat (*D. deserti*, *D. merriami*, *D. ordii*), a kangaroo mouse (*M. pallidus*), and a pocket mouse (*P. longimembris*). *Heteromys* occupies tropical wet forests, and *Liomys* is found in tropical dry forests and thorn scrub. In contrast with the high diversity of heteromyids in desert habitats, Sanchez-Cordero and Fleming (1993) note the low diversity of species in tropical habitats, probably a result of deserts being more productive in seeds, the main food source for all heteromyid rodents.

Behavior

Spacing

Heteromyid rodents have not evolved complex social systems. Most heteromyids live alone in individual burrows, except for females with young, and show the common mammalian pattern of overlapping home ranges. Male home ranges overlap those of other males and females, and females tend to occupy areas exclusive from other females. An exception is seen in the larger-sized kangaroo rats: *D. spectabilis*, *D. ingens*, and *D. deserti*. Both males and females maintain exclusive territories where they defend large seed caches, except during the breeding season when males travel to female territories for mating. Heteromyid home ranges average 6,458–26,910 ft^2 (600–2,500 m^2).

Social structure

Although heteromyids are solitary species, they are not "asocial" and exhibit a rudimentary social structure. Randall (1993, 2002) views the social system of kangaroo rats as an orderly one promoted by establishment of familiarity with

An Ord's kangaroo rat (*Dipodomys ordii*) foraging in Arizona, USA. (Photo by © Joe McDonald/Corbis. Reproduced by permission.)

The desert kangaroo rat (*Dipodomys deserti*) uses its two large hind feet for jumping. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

close neighbors, philopatric dispersal patterns so that relatives may live nearby, and well developed means of communication. Kangaroo rats recognize neighbors from strangers by footdrumming, a characteristic thumping or drumming sound made with the hind feet. They are much less aggressive toward familiar neighbors than unfamiliar ones. Neighbor recognition seems independent of the type of spacing, but species do differ in the degree of tolerance they show toward conspecifics. Little detailed information about the social behavior of other heteromyids is available. *Heteromys*, however, may be somewhat social. Eisenberg (1963) noticed that adults and mature young seem to share the same burrow, and behavioral tests in the laboratory demonstrated tolerance of conspecifics. Randall (1994) has found that the lack of sociality in heteromyids is not unusual for desert rodents.

Communication

A well developed system of communication helps to promote social order in heteromyid rodents. Sandbathing, which consists of rubbing the sides and ventrum in loose soils, is performed frequently by pocket mice and kangaroo rats. The behavior functions both to remove oils from the pelage and to deposit scent for communication. The rodents deposit scent from oils associated with the hair and from a specialized scent gland on the dorsum at sandbathing sites to communicate species, sex, individual identity, familiarity, and reproductive condition, depending on the species.

Kangaroo rats drum their large hind feet on the ground to generate both airborne and seismic signals. Randall (2001) compared footdrumming in four species of territorial kangaroo rats (*D. spectabilis*, *D. ingens*, *D. deserti*, and *D. heermanni*) and found that the complexity of the signal and its messages are species specific and vary with context. Footdrumming patterns range from individually distinct footdrumming signals to single foot thumps to communicate territorial ownership, competitive superiority, submission, and readiness to mate to conspecifics.

The dark kangaroo mouse (*Microdipodops megacephalus*) uses its long tail as a balancing aid. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Predator defense

As in many small prey, heteromyids rely on cryptic coloration and avoidance for predator defense. If a predator is encountered, the erratic path of bipedal locomotion often provides an effective escape for kangaroo rats and mice. Desert heteromyids also have sensitive low-frequency hearing, which enables them to detect approaching predators. At least three species of kangaroo rat (*D. spectabilis*, *D. ingens*, and *D. deserti*) have evolved a unique defense against snakes. Instead of avoiding a snake, they approach it to within striking distance, jump back and footdrum. Although mothers may drum to warn pups in the burrow, the drumming appears di-

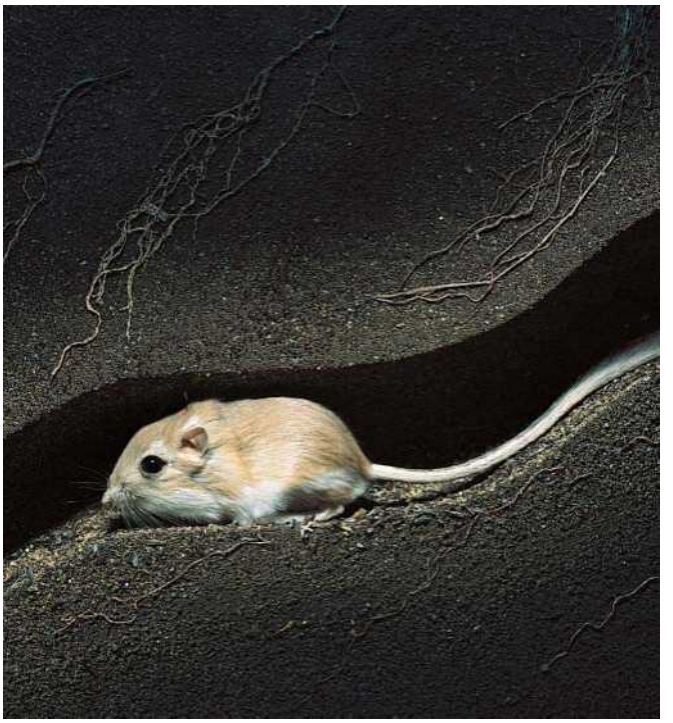
Banner-tailed kangaroo rat (*Dipodomys spectabilis*) in the scrub of New Mexico, USA. (Photo by Bob & Clara Cakhoun. Bruce Coleman, Inc. Reproduced by permission.)

Giant kangaroo rats (*Dipodomys ingens*) are granivorous. (Photo by Richard R. Hansen/Photo Researchers, Inc. Reproduced by permission.)

rected at the predator to communicate that the kangaroo rat is alert, cannot be ambushed, and to tell the snake to go away. *D. deserti* also kicks sand at the snake during defensive interactions

Feeding ecology and diet

Heteromyid rodents are primarily granivores. Seeds comprise their main food source in all habitats, supplemented by green vegetation and insects in some species. Kenagy (1973) found that the chisel-toothed kangaroo rat, *D. microps*, climbs up in saltbrush, *Atriplex*, to consume the leaves by stripping off the epidermis with specialized chisel-shaped teeth. Desert species are physiologically adapted to survive lack of water during long droughts. Each night, the rodents emerge from their burrows to dig through the soil with their forelimbs to gather seeds. They scoop up the seeds, rapidly stuff them into their fur-lined cheek pouches until they look like they have the mumps, and transport them to caches. Factors such as seed size, density and nutritional value, predation risk, and type of soil influence foraging choices. Most heteromyids scatter-hoard and bury seeds in widely spaced surface caches



Ord's kangaroo rat (*Dipodomys ordii*) in an underground burrow. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

throughout their home ranges. The Merriam's kangaroo rat can even remember the location of seed caches. Territorial kangaroo rats store seeds in a central larder in the territory and actively defend the caches from other rodents by chasing away intruders and footdrumming.

The Pacific little pocket mouse (*Perognathus longimembris*) fills its cheek pockets. (Photo by Mike Couffer. Bruce Coleman, Inc. Reproduced by permission.)

Reproductive biology

The extreme environmental conditions associated with arid habitats constrain reproduction in heteromyid rodents to times of the year when enough moisture is available in the diet to support lactation. *D. merriami* reproduces any time of the year in response to rainfall and the subsequent growth of green vegetation. *D. spectabilis* and *D. ingens* have a winter breeding season but will continue to breed into the summer under the right conditions. *D. microps* may breed only once during a few weeks in the spring when saltbrush produce new leaves. *Chaetodipus* and *Perognathus* escape winter extremes by being dormant and then usually breed in the spring before summer droughts. Those in more mesic conditions may have an extended breeding season. Tropical heteromyids reproduce during both the dry and rainy seasons and generally have longer breeding seasons than desert species.

Females are polyestrus and can produce several litters under favorable environmental conditions. Litter sizes range from one to nine and average between three and four for most species. In field studies, Randall (1991) and Randall et al. (2002) found that *D. ingens* and *D. spectabilis* females produced an average of only two pups during a breeding season.

Details of mating behavior in heteromyids are generated from field studies by Randall (1991, 1993) and Randall et al. (2002) of three species of kangaroo rats: *D. spectabilis*, *D. merriami*, and *D. ingens*. Mating is opportunistic and ranges from exclusive matings between one male and female to polygynous matings where males compete for access to an estrous female. Males always go to a female's home area or territory to mate, and one male, usually a close neighbor, attempts to chase away all other males. Larger and medium sized kangaroo rats footdrum during these competitions. Females seem to prefer to mate with familiar males, but they will mate with more than one male if possible. They also prefer the scent of familiar males and allow more amicable contact with familiar than with unfamiliar males in both natural and experimental contexts. Males, however, do not appear to discriminate and approach all females alike. Mating interactions of small to medium sized species can last for up to 30 minutes and include multiple mounts alternating with mutual circling. Larger species may mount only one to three times.

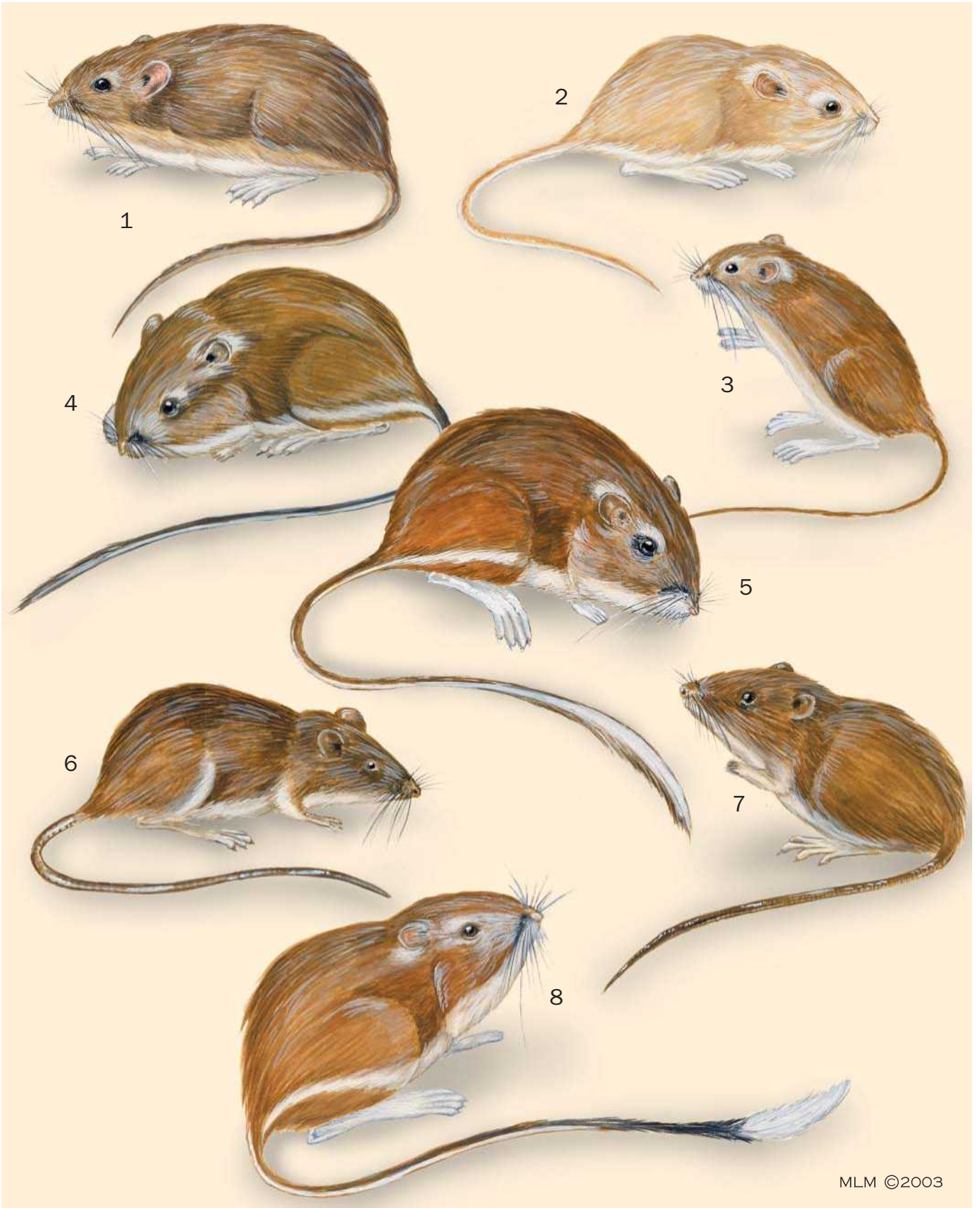
A desert kangaroo rat (*Dipodomys deserti*) sleeps in its burrow in the Mojave Desert, California, USA, (Photo by Jeff Foott. Bruce Coleman, Inc. Reproduced by permission.)

Conservation

Excessive habitat destruction and fragmentation and the loss of plant communities increasingly threaten populations of heteromyids. Currently, all heteromyid species listed as endangered by the United States Fish and Wildlife Service occur in California as a result of habitat loss from urban and industrial development, cultivation, grazing, oil and mining exploration and extraction, highway construction, and flooding. Listed species include *D. ingens*, *D. stephensi*, *D. nitratoides exilis*, *D. n. tipton*, *D. heermanni morroensis*, *D. merriami parvus*, and *P. longimembris pacificus*. Recovery plans for these species have been implemented. Fifteen species of heteromyids are on the Red List of Threatened Species of the IUCN. They include eight species of kangaroo rat, three *Heteromys*, two *Liomys*, and two *Perognathus*.

Significance to humans

Kangaroo rats are often considered keystone species because their burrows provide habitat for a variety of plants and animals, thus their presence is important to maintain biodiversity in desert environments. Many heteromyids are agents of seed dispersal. These attractive rodents can be observed in the desert at night by humans who wish to enjoy nature.



1. Hispid pocket mouse (*Chaetodipus hispidus*); 2. Pale kangaroo mouse (*Microdipodops pallidus*); 3. San Joaquin pocket mouse (*Perognathus inornatus*); 4. Heermann's kangaroo rat (*Dipodomys heermanni*); 5. Giant kangaroo rat (*Dipodomys ingens*); 6. Desmarest's spiny pocket mouse (*Heteromys desmarestianus*); 7. Salvin's spiny pocket mouse (*Liomys salvini*); 8. Banner-tailed kangaroo rat (*Dipodomys spectabilis*). (Illustration by Michelle Meneghini)

Species accounts

San Joaquin pocket mouse
Perognathus inornatus

SUBFAMILY
Perognathinae

TAXONOMY
Perognathus inornatus Merriam, 1989, Fresno County, California, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 5–6.3 in (128–160 mm); weight 0.22–0.39 oz (7–12 g); soft pelage with upperparts yellowish.

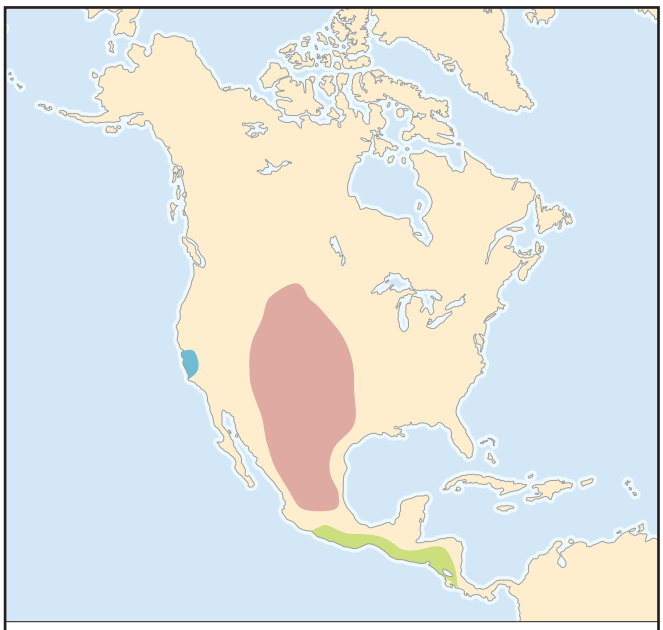
DISTRIBUTION
Found in west-central California.

HABITAT
Lives in arid annual grasslands, desert scrub, fine soils.

BEHAVIOR
Sandbathes by alternating sides and rubbing ventrum.

FEEDING ECOLOGY AND DIET
Eats seeds of grasses, shrubs, and forbs.

REPRODUCTIVE BIOLOGY
Breeds from spring to summer; has two litters of four to six young.



CONSERVATION STATUS
U.S. Fish and Wildlife Service, Department of the Interior (USDI) species of special concern. Two subspecies are Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Disperses seeds. ◆

Hispid pocket mouse
Chaetodipus hispidus

SUBFAMILY
Perognathinae

TAXONOMY
Perognathus hispidus (Baird, 1858), Tamaulipas, Mexico.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Length 7.8–8.8 in (198–223 mm); weight 0.97–1.5 oz (30–47 g); hair is coarse but not spiny, tail is not crested and only slightly longer than body. Olive-buff upper parts lined with black, lower parts are white.

DISTRIBUTION
North Dakota south through Great Plains and Texas to central Mexico, northwest to southeastern Arizona.

HABITAT
Lives in prairie and cultivated areas.

BEHAVIOR
Active all year.

FEEDING ECOLOGY AND DIET
Eats a variety of seeds, green vegetation, and insects.

REPRODUCTIVE BIOLOGY
Females have two or more litters annually from spring to late summer consisting of two to nine young.

CONSERVATION STATUS
Not listed by the IUCN, but a species of concern in Montana and Wyoming.

SIGNIFICANCE TO HUMANS
None known. ◆

Salvin's spiny pocket mouse
Liomys salvini

SUBFAMILY
Heteromyinae

TAXONOMY
Heteromys salvini (Thomas, 1983), Guatemala.

OTHER COMMON NAMES
Spanish: Ratón de monte.

PHYSICAL CHARACTERISTICS
Total length 8.3–11 in (210–280 mm); weight female 1.2–1.6 oz (35–45g), male 1.6–2.6 oz (45–75 g). Pelage is hispid consisting of stiff spines and soft hairs. Mixed dark brown hairs above, under parts buffy to white.

DISTRIBUTION
Pacific coastal lowlands of Oaxaca, Mexico to Costa Rica in Central America.

HABITAT
Lives in dry tropical forest.

BEHAVIOR
Hoards seeds in burrow; reproductive males move greater distances than females in breeding season. Less tolerant of conspecifics than *Heteromys*.

FEEDING ECOLOGY AND DIET
Prefers seeds of woody plants in dry forest and insects.

REPRODUCTIVE BIOLOGY
Limited to dry and early rainy season in Costa Rica with an average of 1.8 litters/year with 3.8 pups/litter.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Disperses seeds in its habitat. ◆

Desmarest's spiny pocket mouse
Heteromys desmarestianus

SUBFAMILY
Heteromyinae

TAXONOMY
Heteromys desmarestianus Gray, 1868, Guatemala.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 11.9 in (302 mm); weight 2.4 oz (74 g). Pelage is dark gray to black with white underside.

DISTRIBUTION
Southern Mexico to northwestern Colombia.

HABITAT
Lowland tropical forest.

BEHAVIOR
Seasonal differences in home ranges; males move greater distances than females; may be social as they tolerate conspecifics in the laboratory.

FEEDING ECOLOGY AND DIET
Feeds on seeds, green leaves, succulent plants.

REPRODUCTIVE BIOLOGY
Breeds year round with seasonal rains; three in litter.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Disperses seeds in tropical forests. ◆

Pale kangaroo mouse
Microdipodops pallidus

SUBFAMILY
Dipodomyinae

TAXONOMY
Microdipodops pallidus Merriam, 1901, Mountain Well, Nevada, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 5.9–6.8 in (150–173 mm); weight 0.33–0.54 (10.3–16.8 g). Small, bipedal rodent with dorsal surface lightly colored and white on ventrum.

DISTRIBUTION
Restricted to central Nevada and small part of eastern California.

HABITAT
Open areas of wind-blown sand.

BEHAVIOR
Nocturnal and solitary; bipedal locomotion.

FEEDING ECOLOGY AND DIET
Eats seeds and insects.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not threatened, though rare in some portions of its range. One subspecies is Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Banner-tailed kangaroo rat
Dipodomys spectabilis

SUBFAMILY
Dipodomyinae

TAXONOMY
Dipodomys spectabilis Merriam, 1890, Cochise County, Arizona, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 12.1–13.2 in (308–336 mm); weight 3.15–4.18 oz (98–130 g). Large, four-toed, with white tip on tail. Upper parts dark buff, lighter underside. Tail buff with dark upper stripe.

DISTRIBUTION
New Mexico, southeastern Arizona, eastern Texas into Mexico.

HABITAT
Found in desert scrub, arid grasslands.

BEHAVIOR
Both sexes defend territories of large dirt mounds that contain extensive burrows. Territorial ownership is communicated via individual footdrumming signatures that are modified if the animal moves into a new neighborhood.

FEEDING ECOLOGY AND DIET
Larder-hoards seeds in large dirt mounds.

REPRODUCTIVE BIOLOGY
Breeding season can extend from November to May with additional matings in late summer after abundant rainfall. Females have three or more estrous cycles in a season with male competition increasing as the breeding season progresses.

CONSERVATION STATUS
Not listed by the IUCN, but threatened by overgrazing and eradication by ranchers in some parts of range. *D. s. baileyi* listed as endangered in Arizona.

SIGNIFICANCE TO HUMANS
Mounds provide habitat in arid environments; this kangaroo rat is a keystone species. ◆

Giant kangaroo rat
Dipodomys ingens

SUBFAMILY
Dipodomyinae

TAXONOMY
*Dipodomys ingens (*Merriam, 1904), San Luis Obispo County, California, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Largest body mass in the family: total length 12.3–13.7 in (312–348 mm), weight 3–6.3 oz (93–195 g). Pelage is tan with white underside.

DISTRIBUTION
Restricted to 2% of its former range in Central California. Largest population is in the Carrizo Plain National Monument.

HABITAT
Arid grasslands.

BEHAVIOR
Defends territory, but tolerates close neighbors and can discriminate familiar neighbors from strangers. Both sexes footdrums as territorial advertisement and in response to snakes and kit fox predators; males drum during competition for estrous females. Has longest footroll of any species with up to 300 individual foot thumps in a footroll.

FEEDING ECOLOGY AND DIET
Granivores that store seeds in burrows, sometimes after allowing seed heads to cure in surface caches.

REPRODUCTIVE BIOLOGY
Reproduce from January to May. Females are polyestrus and average three estrous cycles in a breeding season. Gestation ranges from 30–35 days with a postpartum estrus an average of three days after parturition.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN. Also a state and federal endangered species in the United States.

SIGNIFICANCE TO HUMANS
Keystone species. ◆

Heermann's kangaroo rat
Dipodomys heermanni

SUBFAMILY
Dipodomyinae

TAXONOMY
Dipodomys heermanni Le Conte, 1853, Calaveras County, California, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 9.8–12.3 oz (250-313 mm), weight 2.3–2.6 oz (70-80 g). A medium-sized kangaroo rat with long silky hair and typical color pattern. Its large, dorsal sebaceous gland secrets throughout the year.

DISTRIBUTION
Central California west of the Sierra Nevada mountains.

HABITAT
Occupy discrete burrows in dry grassy plains and partly open gravel covered ground on slopes with sparse chaparral, or costal dune scrub habitat.

BEHAVIOR
Territorial around burrows but tolerate conspecifics once socialized. Footdrumming communicates social status.

FEEDING ECOLOGY AND DIET
Seeds and green vegetation are main foods.

REPRODUCTIVE BIOLOGY
Females enter estrus every 14–17 days and remain in estrus for a few hours. Breeding is concentrated from February to August with a peak in April. Gestation is 30–31 days and litter size ranges from two to four young.

CONSERVATION STATUS
One subspecies (*berkeleyensis*) is already extinct and another, *morroensis* has been on the USDI and State of California endangered species lists since in 1971 and is listed as Critically Endangered by the IUCN. The last official estimate of population size in 1995 on the remaining 37 acres (15 ha) of occupied habitat was fewer than 50 individuals.

SIGNIFICANCE TO HUMANS
Could be a keystone species in some areas. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Bailey's pocket mouse *Chaetodipus baileyi*	Large, with gray fur washed with yellow and long bicolored tail; sexually dimorphic: total length males 8–9.5 in (20.6–24 cm), weight 0.88–1.3 oz (25–38 g); females 6.7–9 in (17–22.8 cm), weight 0.8–1.3 oz (24–37 g).	Lower Sonoran desert grasslands and transition zones; sandy soil and rocky slopes.	Southern California across southern Arizona to extreme southwestern New Mexico, south along western Mexico and Baja Peninsula.	Granivore, detoxifies jojoba seeds.	Not listed by IUCN
Olive-backed pocket mouse *Perognathus fasciatus*	Small to medium sized pocket mouse with olive-colored back and yellow lateral stripe; total length 5–6 in (12.5–14.2 cm), weight 0.28–0.49 oz (8–14 g).	Resident of grasslands and desert scrub. Stores food in underground burrows.	Great Plains from southern Canada south to Colorado, United States.	Weed and grass seeds, some insects.	Not listed by IUCN, but species of concern in Nebraska, United States
Silky pocket mouse *Perognathus flavus*	Very small pocket mouse with total length 4–5 in (10–13 cm) and weighing 0.17–0.35 oz (5–10 g).	Grassy and shrubby habitats.	Great Plains south into Mexico.	Seeds.	Not listed by IUCN, but species of concern in Wyoming, United States
Spiny pocket mouse *Chaetodipus spinatus*	Hispid colorations with pronounced rump spines. Total length 3.5–5 in (8.9–12.8 cm), weight 0.45–0.63 oz (13–18 g).	Arid, rocky habitats.	Occurs in narrow strip between southern Nevada, United States, adjacent to and west of Colorado River and in southern California into tip of Baja, Mexico.	Seeds.	Not listed by IUCN
Mexican spiny pocket mouse *Liomys irroratus*	Grayish brown with white underside and stiff spiny hairs mixed with soft slender hairs on back. Males total length 8.5–10.5 in (21.6–26.2 cm), weight 1.4–2.1 oz (40–60 g); females total length 4–5 in (10.2–13.1 cm), weight 1.2–1.8 oz (35–50 g).	Dense brushy areas.	Mexican Plateau and adjacent areas extending north into southern Texas, United States.	Seeds.	Not listed by IUCN
Nelson's spiny pocket mouse *Heteromys nelsoni*	Large gray spiny pocket mouse with soft bristles instead of spines. Total length 13–14 in (32.8–35.6 cm), weight 2.1–3.9 oz (60–110 g).	Lives in moist habitats in cloud forest.	Northern Central America from southern Chiapas, Mexico, to southwest Guatemala.	Primarily granivorious.	Critically Endangered

[continued]

Common name / Scientific name/	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Dark kangaroo mouse *Microdipodops megacephalus*	Small, bipedal rodent with dark colored hair, large hind feet, and long tail. Total length 5.4–7 in (13.8–17.7 cm), weight 0.35–0.6 oz (10–17 g).	Fine gravelly soils in sagebrush desert. Constructs elaborate nests.	Upper Sonoran sagebrush desert in Oregon, Utah, California, and Nevada, United States.	Seeds and some insects.	Not listed by IUCN
Chisel-toothed kangaroo rat *Dipodomys microps*	Medium-sized, gray rodent with special flattened lower incisors. Total length is 9.5–11.6 in (24.5–29.5 cm), weight 1.4–2.5 oz (40–70 g).	Occupies desert valleys dominated by saltbush in the Great Basin. Removes outer tissues from leaves of saltbush and consumes inner layers. Sandbathes to maintain pelage and for communication.	Nevada, United States, and parts of adjacent states.	Primarily folivorous and secondarily granivorous.	Not listed by IUCN
Elephant-eared kangaroo rat *Dipodomys elephantinus*	Large-sized, large-eared kangaroo rat with long tail and tuft on end. Has five toes and is moderately dark in color. Total length is 12–13.3 in (30.5–33.6 cm) weight 2.8–3.2 oz (79–91 g).	Chaparral-covered slopes.	Very restricted in range to San Benito and Monterrey counties in California, United States.	Primarily granivorous.	Not listed by IUCN
Nelson's kangaroo rat *Dipodomys nelsoni*	Large bipedal rodent with soft, pale brownish fur. Total length 12–12.5 in (31.2–31.9 cm), weight 3–3.3 oz (84–93 g).	Occupy grassland plains. Like the banner-tailed kangaroo rats, *D. spectabilis*, they construct burrows of large, dome-shaped mounds.	Occurs in Chihuahuan Desert in Chihuahua-Zacatecas Biotic Provice of north-central Mexico.	Windblown seeds.	Not listed by IUCN
Ord's kangaroo rat *Dipodomys ordii*	Small to medium-sized kangaroo rat with relatively short tail that has a dark tail stripe broader than the white one and a ventral stripe that tapers to a point at end. Total length 8–14 in (20.8–36.5 cm), weight 1.7–3.4 oz (50–96 g).	Found in various habitats of sandy soils, semi-arid and mixed grasslands, and scrublands.	Extensive range from southern Alberta and Saskatchewan, Canada, central Oregon, and eastern California to central Kansas and Oklahoma, United States.	Granivore that eats seeds of grasses and forbes and green vegetation.	Not listed by IUCN
San Joaquin Valley kangaroo rat *Dipodomys nitratoides*	Small, four-toed species with yellowish brown back and white ventrum. Total length 4.7–7 in (12–18.2 cm), weight 1.2–1.9 oz (33–54 g).	Inhabits grassland and alkaline plains sparsely covered with grass and shrubs. Males and females establish contact before copulation.	San Joaquin Valley, California, United States.	Seeds and vegetation.	Lower Risk/Near Threatened; two subspecies are Critically Endangered
Stephen's kangaroo rat *Dipodomys stephensi*	Medium-sized five-toed kangaroo rat.	Found in sparse grasslands and coast sage-scrub habitats.	Limited to three counties in southern California, United States: Riverside, San Bernardino, and San Diego.	Granivore.	Lower Risk/ Conservation Dependent
Texas kangaroo rat *Dipodomys elator*	Medium-sized kangaroo rat with long, thick tail with white tip on end. Total length 10–13.5 in (26–34.5 cm), weight 2.3–3.2 oz (65–90 g).	Lives in scattered mesquite shrubs with open areas of short grass. They maintain open runways between burrows and mesquite shrubs and use visible dust-bathing areas.	Historically in nine counties in north-central Texas, United States, and one in adjacent Oklahoma, but now may inhabit only three Texas counties.	Grass seed and cultivated plants.	Vulnerable

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Organizations

The American Society of Mammalogists.
Web site: <http://www.mammalsociety.org/>

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United States Fish and Wildlife Service.
Web site: <http://www.fws.gov/>

Jan A. Randall, PhD

Birch mice, jumping mice, and jerboas
(Dipodidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Dipodidae

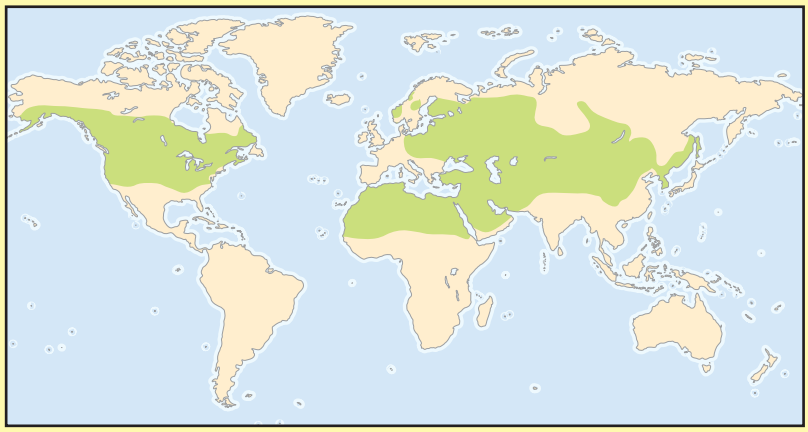
Thumbnail description
Pygmy to medium-sized quadrupedal or bipedal rodents with hind limbs slightly or much longer than forelimbs; long tails and eyes and external ears ranging in size; coarse or soft brown, brownish-yellow or jonquil fur; a dichromatic, black-and-white banner tail tip characteristic of many jerboa species specialized for the fast bipedal gallop

Size
1.8–9 in (45–230 mm); weight 0.2–15 oz (6–415 g)

Number of genera, species:
15 genera, 49–51 species

Habitat
Inhabitants of forests, meadows, steppe and desert plains and mountain regions

Conservation status
Endangered: 4 species; Vulnerable: 4 species; Lower Risk/Near Threatened: 6 species; Data Deficient: 4 species



Distribution
North America, Northern Africa, Arabian Peninsula, Europe, and Asia

Evolution and systematics

Traditional classifications based mostly on morphological similarities consider two related families: Dipodidae, including all jerboas, and Zapodidae, including jumping mice and birch mice. The family of jerboas include three subfamilies (Euchoreutinae, Cardiocraniinae, and Dipodinae), and the family of jumping and birch mice include two subfamilies (Zapodinae and Smintinae = Sicistinae). Vorontsov et al. in 1971 divided jerboas into four subfamilies (Euchoreutinae, Cardiocraniinae, Allactaginae, and Dipodinae), and Gambarianin in 1983 divided them into three families (Euchoreutidae, Cardiocraniidae, and Dipodidae with two subfamilies, Allactaginae and Dipodinae). The recent revision of plylogenetic relationships of all groups of jerboas, jumping mice, and birch mice, based on palaeontological data and complex morphological comparisons, suggests one superfamily Dipodoidea with four families: Zapodidae, Smintidae (with subfamilies Euchoreutinae and Smintinae), Dipodidae (with subfamilies Cardiocraniinae, Paradipodinae, and Dipodinae), and Allactagidae. The position of *Euchoreutes* is not clearly defined, and there are reasonable arguments to consider long-eared jerboa to represent a separate family. Considering Dipodidae as an extended interpretation, one must be aware of long-term independent evolution of jumping mice, birch mice, and at least three lineages of jerboas. Formal resemblance of long-eared jerboa (subfamily Euchoreutinae), five-toed jerboas (subfamily Allactaginae), and three-toed jerboas (subfamilies Cardiocraniinae, Paradipodinae, Didodinae) is considered now to be a result of parallel evolution of bipedality in arid open and flat landscapes. Among three-toed jerboas very deep differences, signifying early divergence, exist between pygmy jerboas (Cardiocraniinae), genus *Paradipus*, and true three-toed jerboas (Dipodinae). Fossil remains of Dipodidae have been discovered from the Eocene in North America and from the Oligocene in Eurasia. Three-toed jerboa fossils from the middle Miocene were discovered in Asia, and five-toed jerboa fossils from the middle Miocene were unearthed in North Africa as well as upper Miocene specimens from Europe and Asia.

Physical characteristics

Birch mice and jumping mice are small, mouse-like quadrupedal rodents with fairly long semi-prehensile tails. Jumping mice hind limbs are moderately elongated, whereas birch mice have no elongation. Jerboas are small to medium-sized bipedal, nocturnal rodents adapted to run fast in sparse vegetation. Both birch and jumping mice have relatively small and narrow heads, and jerboas have relatively large heads with wide muzzles and flat snouts. Jerboas also have big eyes, long vibrissa, and auricles that vary in size from relatively short among three-toed jerboas to extremely long in long-eared jer-

Lesser Egyptian jerboas (*Jaculus jaculus*) are common to northern Africa and southwest Asia. (Photo by Animals Animals ©Michael Dick. Reproduced by permission.)

boa (*Euchoreutes naso*). In pygmy jerboas (Cardiocraniinae), the auricle is tubular. Among jerboas, the neck is weakly pronounced or not pronounced at all; the neck vertebrae are fused in the Cardiocraniinae, Paradipodinae, and Dipodinae, but unfused in the other subfamilies.

All jerboas have short and compact bodies with short forelimbs and long strong hind limbs. The tail is usually long, ending as a rule, but not always, with the dichromatic black-and-white banner. The brush of long hairs may resemble a bird feather. Among pygmy jerboas (Cardiocraniinae) and in *Pygeretmus platyurus*, a specialized representative of five-toed jerboas, the tail is relatively short, bannerless, and fat. Forelimbs have five fingers. Claws are short and blunt in birch mice, jumping mice, and five-toed jerboas, or long and narrow in three-toed jerboas. Hind feet have five, four, or three toes. If toes are more than three, the first and the fifth toes are much shorter than three middle ones. In *Allactaga tetradactyla* the first toe is absent. The three central bones of the hind foot are fused to form a single cannon bone among all fast running jerboas (except in Cardiocraniinae). The pelage is coarse in the Smintinae and Zapodinae with light or dark brown or brownish yellow back hair and paler, lighter brown hair on the ventrum. Jerboas have dense, soft earthen-colored fur with lighter, sand-colored fur on the back and white on the belly. The dental formula of the Dipodidae is (I1/1 C0/0 P0–1/0 M3/3) $\times$ 2 = 16 or 18. The upper incisors are weakly grooved in the Zapodinae, but smooth in the other subfamilies. Premolar is intent for reduction. Molars are either low- (Smintinae) or high-crowned (other subfamilies) and have adult roots.

Distribution

Thirteen birch mice species are endemic to Eurasia (from Austria in Europe to Sakhalin island in the Far East). Five species inhabit mostly plains. All others are present in mountain terrains (Caucasus, Altai, Tien Shan, mountains of Central China, Pakistan, Kashmir). Jumping mice (genus *Eozapus*) occur in Central China (Quinghai, southern Gansu, Ningxia, Shaanxi, western Sichuan, northwestern Yunan provinces). Another two genera of jumping mice, *Zapus (Z. hudsonius*, *Z. princeps*, *Z. trinotatus)* inhabit North America from southern Alaska to southwestern United States, and *Napaeozapus (N. insignis)* from southeastern Manitoba to Labrador and Pennsylvania and south along Appalachian Mountains to northern Georgia. Jerboas are confined to open semi-arid and arid lands of the Palaeoarctic region. The range covers North Africa, Eastern Europe, Central, middle, and southwestern Asia, including Arabia.

Their origin is considered connected with Asia where they demonstrate the greatest species and genera diversity. By the middle Miocene, jerboas penetrated Africa but did not diverge. Ranges of nine genera are restricted to Eurasia and ranges of two genera are distributed in arid lands of both Eurasian and North African continents. Euchoreutinae and Cardiocraniinae are strictly Asian groups. Asia accounts for 30–31 species; Europe five species; Africa three species. Two centers of species diversity of jerboas in Asia, one connected with deserts of Middle Asia (Uzbekistan, Turkmenistan, and southwestern and southern portion of Kazakhstan), and the other with deserts of Mongolia and China. *Euchoreutes naso*, *Salpingotus kozlovi*, *Stylodipus andrewsi*, *Allactaga bullata*, and *A. balicunica* are endemic to Mongolian-Chinese deserts. *Salpingotus heptneri*, *Paradipus ctenodactylus*, *Eremodipus lichtensteini*, *Allactodipus bobrinskii*, and *Allactaga severtzovi* are endemic to desert middle Asia. *Pygeretmus shitkovi* and *P. platyurus* are endemic to cold deserts of Kazakhtan. Species diversity in Asia decreases from subzone of cold deserts to the south (subtropical deserts) and to the north (steppe). Jerboas did not cross the Indus River. Accordingly, there are no jerboas in the Thar Desert of India. Three species of jerboas (*Allactaga tetradactyla*, *Jaculus jaculus*, and *J. orientalis*)

Meadow jumping mouse (*Zapus hudsonius*) in a field in Lapeer County, Michigan, USA. (Photo by Animals Animals ©John Gerlach. Reproduced by permission.)

are present in North Africa. Genus *Jaculus* are also common in deserts located in the Arabian Peninsula, Middle East, Iran, Iraq, and Afganistan.

Habitat

Birch mice inhabit forests, thickets, moors, meadows, and steppe. In the mountain regions, they occur in the forest and subalpine belts. Jumping mice (genus *Zapus*) inhabit wooded areas, grassy fields, and alpine meadows. They are common in the thick vegetation bordering streams, ponds, and marshes. The woodland jumping mouse (*N. insignis*) inhabits spruce-fir and hemlock-hardwood forests where it prefers moist, cool places with dense vegetation. It is common along streams in bogs and swamps. The Chinese jumping mouse (*E. setchuanus*) is found near stream banks in cool forests at high mountain elevations of 9,840–13,120 ft (3,000–4,000 m). Jerboas occupy all type of desert habitats from moving sands to clay depressions and rocky-gravel plateau and dry mountain slopes. Up to five species can be seen in one habitat, and the local fauna can account for eight species.

Many species are habitat specific while others are less selective. Some selective species include *Paradipus ctenodactylus* that inhabits top ridges of moving sands (barkhans) in the deserts of Turkmenistan and Uzbekistan; *Allactodipus bobrinskii* that inhabits clay and rocky-clay plains covered with the thin sandy-gravel wash; and *Pygeretmus pumilio*, an inhabitant of clay depressions with hard surface covered by sparse vegetation of succulents. In general, sandy habitats are more common for tree-toed jerboas, whereas five-toed jerboas usually inhabit areas with hard clay soils. Jerboas that are adapted for locomotion on soft sandy substrate have brushes of long hard hairs on sides of their toes to stabilize the foot on the soft sand. When the three-toed jerboas run, the distal part (all toes) of their hind limbs contacts the substrate surface. In contrast, when five-toed jerboas run, they touch the hard substrate only by the tall compact callus on top of the central toe. The second and the fourth toes are shorter and mostly act as shock absorbers (bumpers).

Behavior

Locomotion

Birch mice and jumping mice are quadrupeds. During ground travel, they often climb tussock grass, shrubs, and bushes, curling the tail for additional support around branches and twigs. Jumping mice hop up to 3.3 ft (1 m) high and 6 ft (1.8 m) long. They are also a good swimmers (*Zapus*, *Napaeozapus*). All jerboas are bipedal, but differ in capacity to run fast for a long distance. The best runners among such five-toed jerboas as *Allactaga major* or *A. severtzovi*, can maintain a speed of 25 mph (40 kph). Pygmy jerboas do not increase their speed over 6 mph (9 kph). Normally, the birch mice and jumping mice use a quadrupedal walk when moving slowly. When startled, however, they often take several leaps, using their powerful hind legs for propulsion; the forelimbs are used just for support when the body contacts the substrate

Lesser Egyptian jerboas (*Jaculus jaculus*) in a dispute over food. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Two southern birch mice (*Sicista subtilis*) foraging. (Photo by Hans Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

(quadrupedal hop). The jumping mouse can make three to four jumps without touching the substrate with their forelimbs. While the pygmy jerboa moves slowly with short hops, it also can touch the substrate with forelimbs. When it increases its speed, the hind feet work simultaneously, and the forelimbs never touch the substrate. Pygmy jerboas cannot run long distances. When chased they demonstrate cryptic behavior and stretch out on the substrate in a shadow of small shrub or hollow. They never use shelter burrows to escape danger.

When running quickly, five-toed and three-toed jerboas push off the substrate with one hind foot after another. Such non-synchronous propulsion provides additional acceleration to the bipedal gallop. Large-sized and fast species escape danger by running for a distance of hundreds of feet (meters) (*Allactaga major*, *A. severtzovi*, *Paradipus ctenodactylus*, *Dipus sagitta*). The large home range of *Paradipus ctenodactylus* in the Karakum desert of Turkmenistan may reach 1.2 mi (2 km) in diameter. Smaller forms with relatively weak hind feet range in a diameter often less than of 328 ft (100 m) (*Pygeretmus pumilio*, *P. shitkovi*, *Stylodipus telum*). When moving slowly with short jumps, jerboas are unable to keep position of the body axis stable. Shifts of the body's center of gravity force it to make deep bows after each jump. Because bipedal hopping at low speeds is considered energetically expensive, the best runners among five-toed jerboas and all three-toed jerboas use another gait for slow movements—when foraging, they walk on hind feet as humans do.

Shelters and burrowing activity

Birch mice and jumping mice rarely dig. For shelters they often use space under logs, boards, or roots, or even clumps of vegetation where they build nests of dry leaves and woven grass or moss. The birch mouse (*Sicista betulina*) often uses hollows in old wood. *Sicista* also can dig shallow burrows or use burrows built by other species. The woodland jumping mouse (*Napaeozapus insignis*) also can dig simple burrows, but prefers to occupy old burrows left by other rodents. All species of jerboas dig very well and construct three types of burrows: day (summer) burrows used to sleep during the day time, shelter burrows used to escape predatory attacks in the night time, and wintering burrows used for hibernation. The first and last burrow types, including day burrows where females bear their pups, are similarly constructed and differ mostly in depth and length. Five-toed jerboas dig in a hard soil with their incisors and excavate soil with the help of forelimbs, pulling soil out of the tunnel by the snout. Jerboas start with the digging of the main inclined tunnel. From a point close to the end of the main tunnel chamber it digs a second, steep and narrow tunnel up to the surface, sometimes with one to three cavities and only one outside opening. It is indistinct and usually closed by a plug when the jerboa is in the burrow. Jerboa closes the initial tunnel by the soil dug out from the second hole.

Day burrows of three-toed jerboas are more diverse in construction, but similar in building techniques. In contrast to five-toed jerboas, forelimbs play the predominant role in digging sandy soils by the three-toed jerboas. Three-toed jerboas can build simple daily burrows with only one tunnel in a soft sand. Shelter burrows of five-toed and some three-toed jerboas look like simple short tunnels with open holes used to escape predatory attacks. Burrows contain nest chambers

Woodland jumping mice (*Napaeozapus insignis*) can move about 6 ft (1.8 m) in a single jump. (Photo by Scott Camazine/Photo Researchers, Inc. Reproduced by permission.)

loosely constructed from dry vegetation or, in the case of the desert jerboa, camel hair.

Hibernation

Birch mice, jumping mice, and most species of jerboas hibernate. Duration of hibernation is taxon dependent and also dependent on geography. Birch mice hibernate up to six, or seven months. The weight loss during the half year hibernation in *S. betulina* reaches 50%. The body temperature in a hibernating birch mouse can drop to as low as 36°F (2°C). Among the jerboa species breeding only one time in a year, the five-toed pygmy jerboa (*Cardiocranius paradoxus*) goes into winter sleep in Mongolia from the end of August up to May of the next year. Species with the spring and fall breeding cycle have shorter hibernation periods. Jerboas inhabiting subtropical deserts do not hibernate, but a state of torpor may continue for several days.

Daily activity

All groups of Dipodidae are nocturnal rodents, although the birch mice and jumping mice can be active in the day time (mostly in the morning or evening). Jerboas are strictly nocturnal and sleep in individual burrows with the entrance closed by a soil plug during the daytime. Pygmy jerboas build plugs with their tail, whereas all other jerboa species use the muzzle. Only in spring is it possible to observe jerboas feeding in dusk before sunrise or immediately after sunset.

Territoriality

Dipodidae are solitary—as a rule, each individual uses its own burrow to sleep in the daytime and to hibernate. At the same time, antagonistic behavior is taxon and dependent upon location. Very little is known about home ranges and social relationships among species of birch mice. In the woodland jumping mouse (*Napaeozapus insignis*) individuals are highly tolerant of one another. Their home ranges vary from 1 to 9 acres (0.4–3.6 ha), and overlap. For *Zapus princeps* in the Colorado mountains, Stinson in 1977 reported very small home ranges (0.4 acres [0.17 ha] for males and 0.2 acres [0.1 ha] for females). Males had overlapping home ranges and were tolerant of one another, whereas females had more exclusive territories. Neighboring individuals tend to share the shelter burrows, although their home ranges can overlap considerably. In many jerboa species, individuals avoid contact with each other within overlapping areas. Only pygmy jerboas, especially *Salpingotus crassicauda*, seem to be aggressive and territorial.

Jerboas have no well-developed, specific skin glands for scent marking. Specific marking behavior (touching substrate by ano-genital area) is identified in the long-eared jerboa (*Euchoreutes naso*). Pygmy jerboas often bathe in sand, and sites of sand bathing can play the role of chemical marks.

Feeding ecology and diet

Birch mice and jumping mice feed on fungus, nuts, berries, fruits, and arthropods. They, as well jerboas, do not store food. Jerboas represent a diverse spectra of feeding adaptations from carnivory of *Euchoreutes naso* and *Salpingotus kozlovi* to granivory-insectivory of *Salpingotus crassicauda*, granivory of *Cardiocranius paradoxus*, granivory-folivory of *Dipus sagitta* and *Stylodipus telum*, *Eremodipus lichtensteini*, *A. elater* and folivory of *Paradipus ctenodactylus* and of jerboas of genus *Pygeretmus*. Some species are omnivorous, feeding on green parts of plants, roots, bulbs, seeds, fruits, and arthropods (*Allactaga major*, *A. sibirica*, *A. severtzovi*, etc.). Based on the data on feeding of birch mice, jumping mice, and pygmy jerboas as well as on the data on teeth structure of extinct and recent Dipodidae, it is plausible that distribution of feeding resources and predation risk are predominant factors in the evolution of bipedal locomotion. In the open, desert-like habitat, the rodent that looks for sparsely distributed energy-rich food items becomes exposed to the predator much more often than in a sheltered, densely vegetated habitat. In such situations, natural selection may support an increase in acceleration of the escape flight at its initial stage, determining the vector of morphological innovations.

Western jumping mice (*Zapus princeps*) beat their tails on the ground when frightened. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Foraging strategies among jerboas are intriguing, particularly among food specialists. For instance, the long-eared jerboa (*Euchoreutes naso*) can actively locate flying insects by their extremely large, flexible auricles that are close in size to the body length. The long-eared jerboa catches moths by making vertical rushes quick as lightning. The pygmy jerboa (*Salpingotus kozlovi*) forages at sand dune slopes. Its muzzle has a snout surrounded by a field of dense, long vibrissa oriented to the side. Digging in the sand, it makes small sand-slips and detects arthropods and their larva with both the nose and vibrissa field. Its very large middle ear cavities probably facilitate hearing ground-born sounds too. The comb-toed jerboa (*Paradipus ctenodactylus*) feeds on young green twigs of succulent bushes that grow on slopes of sand dunes. It makes ver-

Sicista betulina has a black stripe down its back. (Photo by Miloš Andě. Reproduced by permission.)

tical jumps to cut off a twig and runs with it to the top of the sand dune (barkhan) to feed. Extremely acute hearing and strong hind feet protect this jerboa from predators while in open areas.

Reproductive biology

Birch mice have a single litter per year with a gestation period of four to five weeks and the duration of parental care four weeks—that is rather long for a very small rodent. Birch mice attain sexual maturity only after hibernation. In *Sicista betulina*, a single litter contains three to 11 pups. Among jumping mice, *Zapus hudsonius* is known to produce at least two litters, occasionally three, per year, but *Z. princeps* and *Z. trinotatus* have only a single annual litter. The gestation period is 17–23 days, and litter size is two to nine pups with an average of four to six young. Young females of only *Z. hudsonius* may be able to produce their own litters in the same season of their birth. In *Napaeozapus insignis*, females in southern populations give birth twice during the breeding season from early May to early September; in the north one litter per year is more common. The litter size varies from two to seven, averaging approximately 4.5 young. The gestation period is about 23 days, and the newborn pups are weaned at 34 days. Both males and females start to breed only after the first hibernation. Very little is known about reproductive biology of the Chinese jumping mouse (*Eozapus setchuanus*).

Birch mice and jumping mice are relatively long-lived creatures. The maximum reported lifetime in nature was four years for *Sicista*, *Zapus*, and *Napaeozapus*. In respect to breeding biology, jerboas can be classified into two groups. The first includes species that breed only one time during the warm season (in spring or summer). Two consecutive litters in a season is rare. This group includes *Euchoreutes naso*, *Cardiocranius paradoxus*, *Stylodipus telum*, *S. andrewsi*, *Allactaga major*, *A. sibirica*, *A. balicunica*, and *Pygeretmus platyurus*. The second group includes species that breed in the spring and fall, and can produce three litters in a year: *Dipus sagitta*, *Allactaga severtzovi*, *Allactaga elater*, *Allactodipus bobrinskii*, *Pygeretmus pumilio*, and *P. shitkovi*. Juveniles of this group of species, born in spring, can participate in the fall breeding. Juveniles of the first group of species start to breed only in the next year. The litter size of the species that breed only once per year is larger (from two to nine) than in the group that can produce multiple litters annually (from one to eight). Jerboas are polygamous. Gestation is described only for several species, and is rather long, varying from 19–20 days in *Stylodipus telum* to 25–30 days in *Dipus sagitta*, and to 28–30 days in *Allactaga severtzovi*. In many species, pups stay from five to six weeks in the nest burrow before emergence. The reasonable explanation of such a long duration of juveniles' postnatal development is that the motor skills needed for bipedal locomotion must be completely developed before the juvenile leaves the burrow. Soon after emergence pups become independent of their mother. Only in the first nights after they first go out juveniles follow the female. Some species of three-toed jerboas follow each other tail to tail and move in a linear fashion.

Conservation status

Among birch mice, the IUCN classified *Sicista armenica* as Critically Endangered. *S. caudata* is classified as Vulnerable because of progressive loss of its preferred habitat. Among jumping mice, the IUCN designates *Eozapus setchuanus* as Vulnerable because of destruction of mountain forest habitats. There are two subspecies of *Zapus hudsonius* with conservation status designated as Endangered (*Z. h. preblei*) and Vulnerable (*Z. g. campestris*). *Zapus trinotatus orarius* was designated by IUCN as Conservation Dependent, being restricted to a very small area on the northern California coast. Among jerboas, the IUCN declared special conservation status for 11 species. *Euchoreutes naso* and *Allactaga tetradactyla* were classified as Endangered; *A. firouzi* as Critically Endangered; *Cardiocranius paradoxus* and *Salpingotus crassicauda* as Vulnerable; and *S. kozlovi*, *S. heptneri*, *Jaculus orientalis*, *Allactaga euphratica*, *Pygeretmus shitkovi*, and *Allactaga bullata* as Lower Risk/Near Threatened.

The recent data from Mongolia suggest that *Cardiocranius paradoxus* and *Allactaga bullata* are common, widely distributed species in Mongolia. Another Mongolian species, *Euchoreutes naso* is characterized by a low but a stable population density in southern Gobi, where human impact is minimal (Rogovin and Shenbrot, 1995; Sokolov et al., 1996). On the other hand, *Salpingotus heptneri* must be considered critically endangered. Its range is limited to two small areas of in the northern Kyzylkum desert of Uzbekistan and Kazakhstan. The species has not been observed since the beginning of

1980. Now, due to the catastrophic desiccation of the Aral Sea and changes of the climate in the northern Kyzylkum, the future of this species is unknown and special research is needed.

Two subspecies of *Jaculus blanfordi* (*J. b. turcmenicus* and *J. b. margianus*) are also Endangered—they have small ranges restricted to northern and southern Turkmenistan and to the Kyzylkum Desert in Uzbekistan. Many areas of their typical habitat, the clay depressions and dry river streams between stabilized and semi-stabilized sand ridges, were plowed during 1970–1980. *Salpingotus pallidus* and *Allactaga vinogradovi* should be considered vulnerable because of their limited and fragmented ranges. Very little is known about *Salpingotus michaelis* and *S. thomasi* from Iran and Afganistan. New species of genus *Salpingotus* are still possible in Iran, Afganistan and northwestern China.

Significance to humans

Birch and jumping mice and jerboas have little significance to humans. In a plague, some jerboas (*Stylodipus telum* and *Allactaga elater*) can be invoked into epizootic process. Jerboas play a significant role in desert ecosystems. The density of most abundant species such as *Stylodipus telum*, *Allactaga elater*, or *Pygeretmus pumilio* can reach 40–50 individuals per 2.5 acres (1 ha).

1. Comb-toed jerboa (*Paradipus ctenodactilus*); 2. Long-eared jerboa (*Euchoreutes naso*); 3. Little five-toed jerboa (*Allactaga elater*); 4. Southern birch mouse (*Sicista subtilis*); 5. Bobrinski's jerboa (*Allactodipus bobrinskii*); 6. Five-toed pygmy jerboa (*Cardiocranius paradoxus*); 7. Hairy-footed jerboa (*Dipus sagitta*). (Illustration by Patricia Ferrer)

Species accounts

Southern birch mouse
Sicista subtilis

SUBFAMILY
Smintinae

TAXONOMY
Sicista subtilis (Pallas, 1773), Tobol River Valley, Kurgan Oblast, Russia. Four subspecies.

OTHER COMMON NAMES
English: Steppe sicista; German: (Steppen-) Streifenmaus, (Steppen-) Birkenmaus; French: Siciste des steppes; Russian: Stepnaya myshovka.

PHYSICAL CHARACTERISTICS
Head and body length 2.4–3 in (61–73 mm); tail 3–3.2 in (75–82 mm); body mass 0.2–0.4 oz (6–10 g). Upperparts striped light tan and brownish and paler underneath.

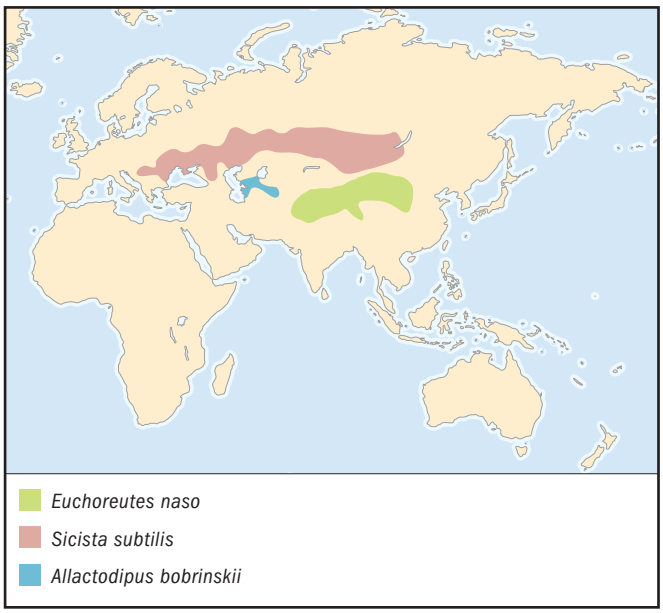
DISTRIBUTION
From eastern Austria to lake Baikal in south-central Siberia.

HABITAT
Flatland steppes of different types, fields, meadows at the southern age of forest zones.

BEHAVIOR
Solitary. In captivity, females chase away the males before the birth of pups. Active in dusk and night, and sometimes in the day time.

FEEDING ECOLOGY AND DIET
Arthropods, seeds, roots, bulbs, and plant greens.

REPRODUCTIVE BIOLOGY
Polygamous. Usually produces one litter of two to eight pups in May to beginning of June. Young from early litters can breed in the same birth year. Gestation period is not less than 25 days, lactation 33–35 days. Pups stay in the burrow 27–34 days.



CONSERVATION STATUS
Not threatened; a common species.

SIGNIFICANCE TO HUMANS
None known. ◆

Long-eared jerboa
Euchoreutes naso

SUBFAMILY
Euchoreutinae

TAXONOMY
Euchoreutes naso Sclater, 1891, Xinjiang, China.

OTHER COMMON NAMES
German: Langohrspringer, Riesenohrspringmaus; Russian: Dlinnoukhii tushkanchik.

PHYSICAL CHARACTERISTICS
Head and body length 3–4.3 in (74–110 mm); tail 6–7.3 in (152–185 mm); body mass 1–1.6 oz (23–45g). Upperparts reddish yellow to pale russset and white underneath.

DISTRIBUTION
Deserts of China (Inner Mongolia and Xinjiang) and South of Mongolia (Trans-Altai Gobi).

HABITAT
Dry, sandy gravel watercourses, stony plain watersheds, sandy-gravel plateau in deserts with very sparse vegetation.

BEHAVIOR
Solitary, but non-aggressive territoriality. Very large, highly overlapping home ranges. Often leaves scent marks with a strong smell.

FEEDING ECOLOGY AND DIET
Diet includes arthropods and even lizards. Often hunts flying insects.

REPRODUCTIVE BIOLOGY
Polygamous. In Mongolia produces one litter of two to six pups in June. Young start to breed at the next year. Gestation period is unknown. Pups stay in the burrow not less than one month.

CONSERVATION STATUS
It is considered to be a rare species due to permanently low densities, and is classified by IUCN as Endangered. Included in the Red Data Book of Mongolia.

SIGNIFICANCE TO HUMANS
None known. ◆

Five-toed pygmy jerboa
Cardiocranius paradoxus

SUBFAMILY
Cardiocraniinae

TAXONOMY
Cardiocranius paradoxus Satunin, 1903, China, Gansu.

OTHER COMMON NAMES
English: Satunin's five-toed pygmy jerboa, five-toed dwarf jerboa; German: Fünfzehige Zwergspringmaus; Russian: Patipalyi karlikovyi tushkanchik.

PHYSICAL CHARACTERISTICS
Head and body length 2–3 in (52–68 mm); tail 3–4 in (68–91 mm); body mass 0.5–0.7 oz (13–19 g). Upperparts grayish buff and white underneath.

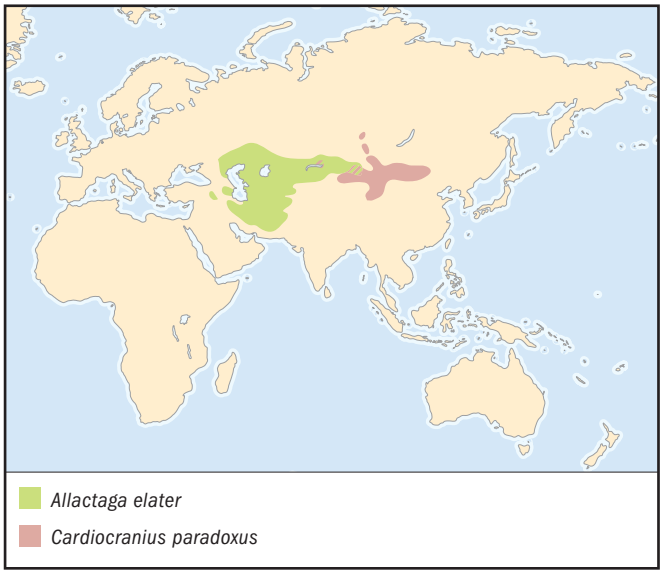
DISTRIBUTION
Deserts and semi-deserts of western and southern Mongolia, northwestern and northern China and eastern Kazakhstan. Range includes four isolated areas. Species range has at least four isolated portions.

HABITAT
Flat and slightly inclined mountain bases and foot hills with sandy to clay/gravel soils and a predominance of grass of genus *Stipa* in plant communities.

BEHAVIOR
Solitary, but with overlapping home ranges that vary from 1.5 to 7.4 acres (0.6–3 ha) in size.

FEEDING ECOLOGY AND DIET
Feeds mostly on seeds and fruits. Green vegetation present in the diet only during spring.

REPRODUCTIVE BIOLOGY
Polygamous. Breeds in summer, and has only one litter of one to five pups annually. Young breed in second year of life. Duration of gestation and lactation are unknown.



CONSERVATION STATUS
Traditionally, it is considered rare, and it is included in the Red Data Books of Russia and Kazakhstan. In Mongolia, however, it is a rather common jerboa, although is still not well studied. There is no information on effects of habitat loss as a result of overgrazing. IUCN classifies it as Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Comb-toed jerboa
Paradipus ctenodactylus

SUBFAMILY
Dipodinae (Paradipodinae)

TAXONOMY
Paradipus ctenodactylus (Vinogradov, 1929) Turkmenistan.

OTHER COMMON NAMES
German: Kammzehen-Springmaus; Russian: Grebnepalyi tushkanchik.

PHYSICAL CHARACTERISTICS
Head and body length 5.5–6.5 in (140–165 mm); tail 7–9 in (180–225 mm); body mass 4–6.5 oz (112–185 g). Upperparts hazel to pinkish cinnamon and white undernath.

DISTRIBUTION
Deserts of Turkmenistan, Uzbekistan, and northern Iran.

HABITAT
Inhabitant of moving sands (barkhans) with very sparse vegetation.

BEHAVIOR
Solitary with vast home ranges of up to 1.2 mi (2 km) oriented along sand ridges.

FEEDING ECOLOGY AND DIET
Feeds on plant greens of a few species of perennial sand desert plants. Seeds appear in a diet only at the end of summer and in fall. Forages at slopes of dunes, but transports food to the top ridges to ingest.

REPRODUCTIVE BIOLOGY
Polygamous. In Karakum desert breeds one time in spring, in western Kyzylkum two times, once in the spring and summer. Only two- to three-year old females participate in the second wave of breeding. Litter size is small and stable with two to three pups. Duration of gestation and lactation periods are unknown.

CONSERVATION STATUS
Common. Density is always low, but stable from one to five individuals per 2.5 acres (1 ha). Arrangements for stabilization of moving sands negatively effect this jerboa.

SIGNIFICANCE TO HUMANS
None known. ◆

Hairy-footed jerboa
Dipus sagitta

SUBFAMILY
Dipodinae

TAXONOMY
Dipus sagitta (Pallas, 1773), Pavlodarskaya Oblast, Kazakhstan. Ten subspecies.

OTHER COMMON NAMES
English: Rough-legged jerboa, feather-footed jerboa, northern three-toed jerboa; German: Rauhfub-Springmaus, Raufübige Wüstenspringmaus, Pfeilspringmaus; Russian: Mokhnonogii tushkanchik.

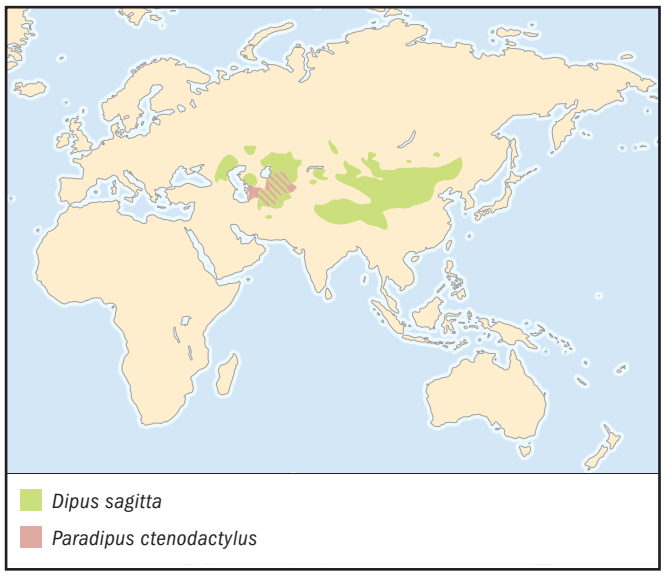
PHYSICAL CHARACTERISTICS
Head and body length 4.5–6 in (115–145 mm); tail 7–7.1 in (175–180 mm); body mass 2.4–4 oz (69–104 g). Upperparts orangish and black during winter and pale sandy buff during summer. White underneath.

DISTRIBUTION
Sand deserts of northern Iran, Middle Asia (Turkmenistan, Uzbekistan, southwestern Kazakhstan), Kazakhstan, Central Asia (Mongolia, China), southeast of European Russia, and south of Altai Republic (RF). There are 10 large isolated range fragments and several small ranges.

HABITAT
Inhabitant of sandy habitats found in steppe, semi-desert and desert zones. In Central Asia (Mongolia, China), the hairy-footed jerboa also lives in areas with hard, rocky/gravel surfaces. Vegetation is always sparse. At the most northern part of the range inhabits pine forests.

BEHAVIOR
Solitary with overlapping home ranges. In Mongolia, non-aggressive contacts dominate in nature. In captivity, hairy-footed jerboas easily form pairs and the male and female sleep in one nest.

FEEDING ECOLOGY AND DIET
Feeds mainly on seeds and desert plant greens. Arthropods sporadically supplement diet.



REPRODUCTIVE BIOLOGY
Polygamous. Adult female bears two litters in spring and fall. Juveniles of first litters become mature at the age of 2.5 to three months, and participate in the fall breeding. Pregnancy continues not less than 35 days, lactation 40–45 days. Litter size varies from one to eight pups, commonly three to five offspring. In spring, lactation overlaps with gestation.

CONSERVATION STATUS
Common, not threatened. One subspecies *D. sagitta nogai* is considered vulnerable because of steppe expansion in Southeastern European Russia beginning in 1990 and resulting in overgrowth of open sand dunes.

SIGNIFICANCE TO HUMANS
None known. ◆

Little five-toed jerboa
Allactaga elater

SUBFAMILY
Allactaginae

TAXONOMY
Allactaga elater (Lichtenstein, 1828), Kyrgiz steppe, Kazakhstan. Seven subspecies.

OTHER COMMON NAMES
English: Small five-toed jerboa; French: Petite jerboa; German: Zwerg-Pferdespringer, Kleiner Erdhase, Kleine Springmaus; Russian: Malyi tushkanchik.

PHYSICAL CHARACTERISTICS
Head and body length 3.5–5 in (90–120 mm); tail 5.5–7.5 in (140–190 mm); body mass 1–3 oz (32–77 g). Upperparts sandy colored and paler underneath.

DISTRIBUTION
Deserts and semi-deserts of southeastern Europe, Kazakhstan, Middle Asia, Iran, northeastern Turkey, Afghanistan, western Pakistan, northwestern China, and southwest Mongolia. Species range appears uniform with two relatively small isolated pockets.

HABITAT
Inhabitant of diverse spectra of desert and semidesert habitats with patchy vegetation of small perennial shrubs, herbs, and succulents. Soils vary from hard clay to sometimes stony and also sandy.

BEHAVIOR
Solitary with overlapping home ranges. Avoidance of contact.

FEEDING ECOLOGY AND DIET
Feeds mainly on seeds and desert plant greens. Arthropods and plant roots are rarely ingested.

REPRODUCTIVE BIOLOGY
Polygamous. Adult female can bare two litters in spring and fall. Juveniles born in spring participate in the fall breeding. Duration of pregnancy is unclear. Juveniles emerged from the maternal burrow 35–40 days of life. In spring, lactation overlaps with gestation. Litter size varies from one to nine pups, commonly three to six offspring.

CONSERVATION STATUS
Common, not threatened. Ranges of two subspecies, *A. elater caucasicus* (Nehring, 1900) and *A. elater aralychensis* (Satunin, 1901) are small.

SIGNIFICANCE TO HUMANS
Can be implicated in epizootic spread of plague. In some regions, the little five-toed jerboa is considered an agricultural pest. ◆

Bobrinski's jerboa
Allactodipus bobrinskii

SUBFAMILY
Allactaginae

TAXONOMY
Allactodipus bobrinskii Kolesnikov, 1937, Uzbekistan.

OTHER COMMON NAMES
German: Bobrinski's Pferde-Springer; Russian: Tushkanchik Bobrinskogo.

PHYSICAL CHARACTERISTICS
Head and body length 4–5 in (110–135 mm); tail 7–8 in (170–200 mm); body mass 2–3 oz (52–77 g). Upperparts reddish brown and black to sandy and grayish buff; whitish underneath.

DISTRIBUTION
Endemic to central Turan lowland. Range consists of six isolated portions, three in Turkmenistan and three in Uzbekistan.

HABITAT
Inhabitant of clay and clay-stony plains with a thin sand-gravel sheet. Vegetation is sparse and represented by small succulent shrubs from the Chenopodiaceae family.

BEHAVIOR
Solitary with overlapping home ranges of 2.5–6 acres (1–2.5 ha). Two to three daily burrows are used in rotation. Contact between neighbors is avoided.

FEEDING ECOLOGY AND DIET
Feeds mainly on vegetative parts of plants. Seeds and insects are ingested to a lesser degree.

REPRODUCTIVE BIOLOGY
Little information is available. Assumed polygamous. Adult females can produce two litters in spring and fall. There is no exact data on the duration of gestation and lactation. Juveniles emerge from the maternal burrow at the age of 40–45 days. In spring, lactation overlaps with gestation. Litter size vary from two to seven pups, commonly four to six offspring.

CONSERVATION STATUS
A fairly common species with a restricted and fragmented range, and a relatively low population density that varies from 0.5 to 3 individuals per 2.5 acres (1 ha) in optimal habitats.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Four-toed jerboa *Allactaga tetradactyla* German: Pferdespringer	Upperparts mixed russet and black to sand and grayish buff. Underparts are white, white stripe on hip. Eyes are large, ears are long and slender. Head and body length 3.5–10.4 in (9–26.3 cm), tail length 5.6–12 in (14.2–30.8 cm), weight 1.8 oz (52 g).	Coastal salt marshes and clay deserts. Burrows are simple, about 23.6–59.1 in (60–150 cm) deep. Nocturnal.	Coastal gravel plains of Egypt and eastern Libya, from near Alexandria to the Gulf of Sirte.	Primarily vegetarian.	Threatened
Lesser fat-tailed jerboa *Pygeretmus platyurus*	Sandy brown above and white below. Tail has no terminal tuft. Head and body length 2.9–3.7 in (7.5–9.5 cm), tail length 3–3.5 in (7.8–9 cm).	Clay and saline deserts and semideserts. Nocturnal, terrestrial, poor jumpers and diggers. One reproductive season from May to June. Five to six young per litter.	Western, central, and eastern Kazakhstan.	Green vegetation, bulbs, spiders, and insects.	Not threatened
Greater fat-tailed jerboa *Pygeretmus shitkovi*	Sandy brown above and white below. Tail has no terminal tuft. Head and body length 3.8–4.8 in (9.7–12.2 cm), tail length 3.7–5 in (9.4–12.8 cm).	Clay and saline deserts and semideserts. Nocturnal, terrestrial, poor jumpers and diggers. One reproductive season from May to June. Five to six young per litter.	Eastern Kazakhstan, in region of Lake Balkhash.	Green vegetation, bulbs, spiders, and insects.	Lower Risk/Near Threatened
Thick-tailed pygmy jerboa *Salpingotus crassicauda*	Upperparts sandy or buffy, underparts are pale yellowish. No terminal tuft on tail. Head and body length 1.6–2.2 in (4.1–5.7 cm), tail length 3.6–4.9 in (9.3–12.6 cm).	Sand dunes overgrown with tamarisk, saxaul, and saltwort. Burrows are up to 10 ft (3 m) in length.	Steppes and deserts of northwest China.	Animal (insects and arachnids) and vegetable food.	Vulnerable
Lichtenstein's jerboa *Eremodipus lichtensteini*	Upperparts dark sandy or buff, underparts are whitish. White stripe on hip. Eyes and ears are relatively large. Head and body length 3.7–6.3 in (9.5–16 cm), tail length 5–9.8 in (12.8–25 cm).	Variety of habitats, including both rolling and relatively flat sandy deserts, saline deserts, rocky valleys, and meadows. Has only one litter per year. Two to eight offspring per litter.	Kazakhstan, Turkmenistan, and Uzbekistan, from Caspian Sea to Aral Sea, and south of Lake Balkhash.	Roots, sprouts, seeds, grains, and cultivated vegetables.	Not threatened
Lesser Egyptian jerboa *Jaculus jaculus*	Upperparts pale to dark sandy or buff, underparts are white. Head and body length 3.7–6.3 in (9.5–16 cm), tail length 5–9.8 in (12.8–5 cm), weight 1.9 oz (55 g).	Variety of habitats, including both rolling and relatively flat sandy deserts, saline deserts, rocky valleys, and meadows. Has only one litter per year. Two to eight offspring per litter.	Desert and semidesert areas from Morocco and Mauritania to southwestern Iran and Somalia.	Roots, sprouts, seeds, grains, and cultivated vegetables.	Not threatened
Greater Egyptian jerboa *Jaculus orientalis*	Upperparts pale to dark sandy or buff, underparts are white. Head and body length 3.7–6.3 in (9.5–16 cm), tail length 5–9.8 in (12.8–25 cm).	Variety of habitats, including both rolling and relatively flat sandy deserts, saline deserts, rocky valleys, and meadows. Has only one litter per year. Two to eight offspring per litter.	Morocco to southern Israel.	Roots, sprouts, seeds, grains, and cultivated vegetables.	Lower Risk/Near Threatened
Andrews's three-toed jerboa *Stylodipus andrewsi*	Upperparts sandy or buff sprinkled with black tips and black hairs. Buffy appearance along sides of body. Underparts, backs of feet, and hip stripe are white. Ears are small. Head and body length 3.9–5.1 in (10–13 cm), tail length 5.1–6.4 in (13.2–16.3 cm).	Deserts and steppes, as well as cultivated fields and pine forests. Digs seasonal burrows, the permanent ones being complex. Generally nocturnal, hibernating from September to March.	Mongolia.	Lichens, rhizomes, bulbs, seeds, and wheat.	Not threatened
Chinese jumping mouse *Eozapus setchuanus*	Upperparts tawny orange, underparts are white. Tail is dark above and white below. Hind feet, legs, and tail are very long. Dark streak down middle of breast and belly, white tip on tail. Head and body length 3.1–3.9 in (8–10 cm), tail length 3.9–5.9 in (10–15 cm).	Beside streams in cool forests. Behavioral and reproductive patterns unknown.	Qinghai, Gansu, Ningxia, Shaanxi, Sichuan, and northwestern Yunnan, China.	Unknown, but most likely vegetarian or some insects.	Vulnerable

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Woodland jumping mouse *Napaeozapus insignis* German: Waldhüpfmaus	Pelage is coarse with tricolor pattern. Back brown to black, sides are orange with yellow or red tint, underparts are white. Tail is grayish brown above and white below. Head and body length 3.1–3.9 in (8–10 cm), tail length 4.5–6.3 in (11.5–16 cm), weight 0.6–0.9 oz (17–26 g).	Spruce-fir and hemlock-hardwood forests in cool, moist places with dense vegetation. Also found in bogs and swamps or along streams but also may occur far from free surface water. Mainly nocturnal.	Southeastern Manitoba to Labrador, Canada, and Pennsylvania, United States, and south along the Appalachian Mountains to northern Georgia.	Fruits, nuts, and other kinds of vegetation.	Not threatened

Resources

Books

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Organizations

The American Society of Mammalogists.
Web site: <http://www.mammalsociety.org/>

IUCN—The World Conservation Union. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41 (22) 999 0000. Fax: +41 (22) 999 0002. E-mail: mail@hq.iucn.org
Web site: <http://www.iucn.org>

United States Fish and Wildlife Service.
Web site: <http://www.fws.gov/>

Konstantin A. Rogovin, PhD

△

Rats, mice, and relatives I

Voles and lemmings (Arvicolinae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Muridae
Subfamily Arvicolinae

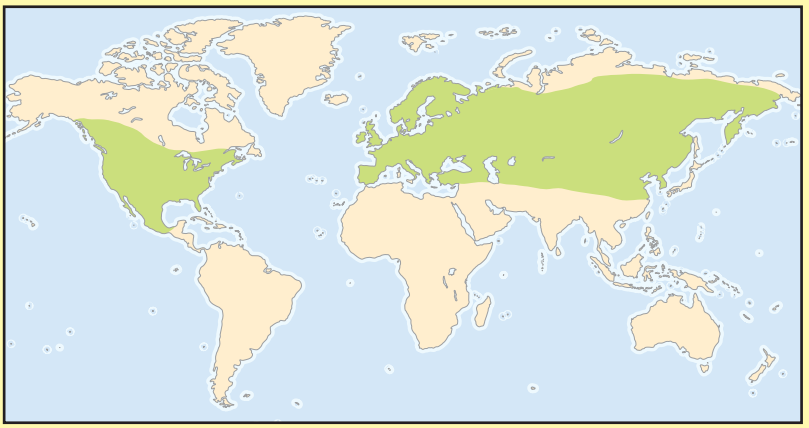
Thumbnail description
Generally small rodents with cylindrical, thickset bodies, and short legs and tails; eyes and ears are normally small and often inconspicuous and the head is broad and rounded

Size
3.5–24.5 in (8.5–62 cm); 0.5 oz to 4 lb (15–1,820 g)

Number of genera, species
26 genera; at least 143 species

Habitat
Forest, woodlands, scrub, grassland, mountains, rivers, and lakes

Conservation status
Critically Endangered: 3 species; Endangered: 2 species; Vulnerable: 4 species; Lower Risk/Conservation Dependent: 1 species; Lower Risk/Near Threatened: 25 species; Data deficient: 7 species; a further 42 subspecies are listed by the IUCN



Distribution
Europe, north, south, and west Asia, and North America

Evolution and systematics

The Muridae is a huge family of more than 1,326 species, the taxonomy of which has long been the subject of considerable and repeated revision. It has previously been considered to comprise a number of separate families, one of which, the Cricetidae, previously included the voles and lemmings. They have also been considered to be a family in their own right, the Arvicolidae, but are currently recognized as one of 17 subfamilies of the Muridae. The junior synonym Microtinae is sometimes used for this subfamily.

The evolutionary origin of voles and lemmings has been the subject of much deliberation. A number of fossil forms are known to have occurred in Asia and North America, but the subfamily has undergone a rapid morphological evolution in the recent past, and the genus *Microtus* is believed to still be rapidly adapting to fragmentations and new niches. There is very little general consensus over the taxonomy of *Microtus*, but at least 61 species are currently recognized and the taxonomic status of a number of isolated populations still remains unclear. Many island populations exist that are morphologically distinct from individuals of the same species residing in mainland populations. The Arvicolinae is the third largest subfamily of the family Muridae, containing at least 143 species grouped into 26 genera.

Physical characteristics

Most voles are remarkably consistent in general size, shape, structure, and body form. They are usually small (0.7–2.6 oz [20–75 g]), stocky rodents with compact bodies and short legs and tails, which are generally less than 50% of the head and body length. Most species are some shade of brown with paler ventral surfaces, although there are some exceptions. The high mountain voles (*Alticola*) are attractive gray, buff, or cream voles with long silky fur. Water voles (*Arvicola*) and round-tailed muskrats (*Neofiber alleni*) are similar in general structure to most voles, although considerably larger than all the other species, weighing as much as 15.8 oz (450 g).

The three species of tree vole (*Arborimus*) are all adapted to an arboreal lifestyle and consequently have much longer tails than the other species of vole, being up to 70–80% of the head and body length. The mole voles (*Prometheomys* and *Ellobius*) are the most aberrant of all the voles and, unlike other species, are highly adapted for a fossorial lifestyle. They have cylindrical bodies with very short tails and forward-facing incisor teeth, superficially resembling mole rats in their external morphology.

Lemmings are generally similar to the voles but, in most species, are even more thickset, with stouter, robust bodies and shorter tails. The true lemmings (*Lemmus*) are highly pat-

A northern collared lemming (*Dicrostonyx groenlandicus*) in winter pelage showing elongated claws for digging in the snow. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

terned with mixtures of buff, gray, white, and brown, while the collared lemmings (*Dicrostonyx*) have a pure white winter pelage and also develop an enlarged third and fourth claw on the forefeet during the winter, which is unique among rodents.

The muskrat (*Ondatra zibethicus*) is much larger than any other members of the subfamily. They can weigh as much as 4 lb (1,820 g). Although they are superficially similar to the voles, they are adapted for an aquatic lifestyle, with a proportionally much longer tail that is flattened laterally to act as a rudder. They possess partially webbed feet, which also have fringes of hairs to assist with swimming.

Distribution

Voles and lemmings have a very widespread Holarctic distribution, being found right across temperate North America, Europe, and Asia. Lemmings occur at extreme northern latitudes right up into the Arctic Circle, and a number of vole species are endemic montane specialists. The muskrat is native to North America, although it has been widely introduced in Europe and also into parts of South America.

Habitat

Voles and lemmings occupy a huge range of habitats. Typically, they are associated with open grassland areas and are extremely numerous in the American prairies and Eurasian steppes. Some species such as the red-backed voles (*Clethrionomys*) or tree voles occur extensively in scrub and woodland, including northern boreal forests. A number of species are endemic to mountain regions and high mountain voles occur up to 19,690 ft (6,000 m) above sea level in the Himalayas.

Water voles and the muskrat are associated with freshwater aquatic habitats, both rivers and still-water lakes. Water voles will even occur in brackish estuarine lagoons and coastal marshes. Lemmings are associated with extreme northern latitudes, occurring in taiga and tundra regions.

Behavior

Voles are both diurnal and nocturnal, and a number of foliage-feeding species such as many of the meadow voles (*Microtus*) are known to be active on successive cycles of feeding and resting of around four hours duration, both day and night. Species that feed on a higher proportion of seed and insects, such as the red-backed voles (*Clethrionomys*), tend to have more nocturnal activity patterns. Many of the montane species are mainly diurnal. Lemmings are often active both day and night, with much of the activity in the winter occurring underneath the safety of a thick cover of snow.

A meadow vole (*Microtus pennsylvanicus*) eating strawberries. (Photo by Dwight R. Kuhn. Bruce Coleman, Inc. Reproduced by permission.)

A northern bog lemming (*Synaptomys borealis*) in tall grass. (Photo by Gary Meszaros/Photo Researchers, Inc. Reproduced by premission.)

A variety of social systems are known in voles and lemmings. One common system that occurs in many species is comprised of mutually exclusive female territories and larger overlapping male territories that vary in location and size in response to receptive females. However, in the field vole (*Microtus agrestis*) it is the males whose territories are strongly defended and exclusive, while the females have widely overlapping home ranges. Some species of meadow vole are believed to be highly monogamous, and the social systems and the degree of territoriality or tolerance almost certainly vary with density in many of the cyclic species.

Muskrats are territorial, but will live as extended families for periods, sharing the same lodge. When young muskrats do finally disperse, they often move very short distances and establish their own lodges within feet (meters) of the parental territory. The long-clawed mole vole (*Prometheomys schaposchnikowi*) is reported to live in small groups comprising several reproductive individuals, all sharing the same burrow system along with youngsters. Lemmings often defend just a very small core area that they are using at any one time, which is much smaller than their actual home range, most of which is not territorial.

Some vole species occur at very high densities and, in extreme circumstances, can be as numerous as 1,000–3,000 per 2.5 acres (1 ha). Some meadow vole and red-backed vole species have cyclic populations with peaks every three to five years and, at these peaks, can almost reach plague proportions. Lemmings are also renown for such population peaks, at which time populations of *Lemmus* can become very transient and large-scale migrations occur. Conversely, at population troughs, densities are so low that the species can be very difficult to locate or are apparently absent from large regions. These large-scale migrations are the origin of the myth of hordes of lemmings committing suicide by throwing themselves from cliffs.

Many populations undergo localized extinctions and recolonizations, so dispersal is an important feature of vole and lemming social systems. Most species disperse as juveniles during the summer or autumn months as they get driven away by the female. Some species such as water voles have much more unusual systems of dispersal, which take place in the spring and involve reproductive over-wintered adults, including pregnant females. This can result in rapid recolonization by even a small number of animals.

Feeding ecology and diet

Most species of voles and lemmings are highly herbivorous. Many are foliage eaters and consequently consume

A northern collared lemming (*Dicrostonyx groenlandicus*) in defensive position, claws ready to scratch. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A Norway lemming (*Lemmus lemmus*) foraging in the grass. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A field vole (*Microtus agrestis*) eats grass in its burrow. (Photo by Ernest A. Janes. Bruce Coleman, Inc. Reproduced by permission.)

larges quantities of leaves in order to meet their energetic demands. Meadow voles that feed on the cellulose-rich foliage of grasses can eat as much as their own body weight each day. Their activity cycles often reflect a constant cycle of eating to fill the stomach, followed by several hours of rest and digestion before commencing the cycle of feeding again. Some species are much more cosmopolitan in their diet and red-backed voles feed on a variety of leaves, seeds, and insects.

High mountain voles (*Dinaromys*) and snow voles (*Chionomys*) make large food stores of dried foliage and stems. This is cut and left to dry before being transported to burrows and rock crevices to provide food during the winter months when fresh foliage is scarce. Lemmings feed largely upon mosses and lichens, especially the wood lemming (*Myopus schisticolor*), which is almost totally reliant upon just one or two species of moss. Much of this feeding during the winter occurs underneath the cover of snow.

The tree voles are highly arboreal and known to eat large quantities of pine needles, with which they also construct their arboreal nests. The fossorial mole voles consume a variety bulbs and tubers and, in some parts of their range, they can be so numerous as to be a pest of root crops. Among the most carnivorous of all the species is the muskrat that feeds on substantial amounts of aquatic crustaceans, bivalve mollusks, and small vertebrates.

Reproductive biology

Voles and lemmings are renown for their huge reproductive rates and populations can reproduce exceedingly quickly; consequently, many species occur at very high densities and are also very important for sustaining many predator populations. The density of many predators has been shown to reflect direct changes in the vole and lemming populations of an area. Meadow voles can exceptionally produce as many as 17 young in a single litter, although average litter size is normally much less. Often northern populations have a larger litter size than southern populations of the same species.

The young of all species are born blind and naked, although development is usually very rapid and weaning can occur as quickly as two weeks after birth. The young are often reproductive themselves before they are one month old.

The bank vole (*Clethrionomys glareolus*) harvests seeds, berries, and nuts and stores them in underground caches. (Photo by Ernest A. Janes. Bruce Coleman, Inc. Reproduced by permission.)

A brown lemming (*Lemmus sibiricus*) in sedge. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Arctic lemming (*Dicrostonyx torquatus*) young. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Most species experience a receptive period within hours of giving birth (postpartum estrus), at which time they are mated and conceive, so females are routinely suckling young and pregnant with their next litter simultaneously.

The tree voles have a much slower reproductive process than that seen in other voles and lemmings. The gestation period is normally around 28 days, although it can be extended up to nearly 50 days if the female is suckling a previous litter. Litters of only one to three young are born and the young are routinely not weaned until around 30–35 days old.

One of the most amazing aspects of reproduction within the group is the genetic determination of sex seen in some lemming and vole species. The wood lemming produces three different genotypes of female, each of which produces different sex ratios of offspring. Some females produce the normal 1 male: 1 female ratio, while the other two genotypes produce either a 1 male: 3 female ratio or all-female litters, respectively.

Conservation status

While some species of voles and lemmings are undoubtedly among the most numerous of small mammals, there are others that are highly threatened. In 2002, the IUCN considered nine species to be threatened, including three, that are Critically Endangered (*Microtus evoronensis*, *M. mujanensis*, and *Dicrostonyx vinogradovi*). A further 26 species are considered Near Threatened or Conservation Dependent, so despite the high reproductive rate and extreme abundance of some species, a quarter of all the vole and lemming species are considered to be threatened or Near Threatened. Many local populations of other species are also declining, and a further 42 subspecies are listed by the IUCN.

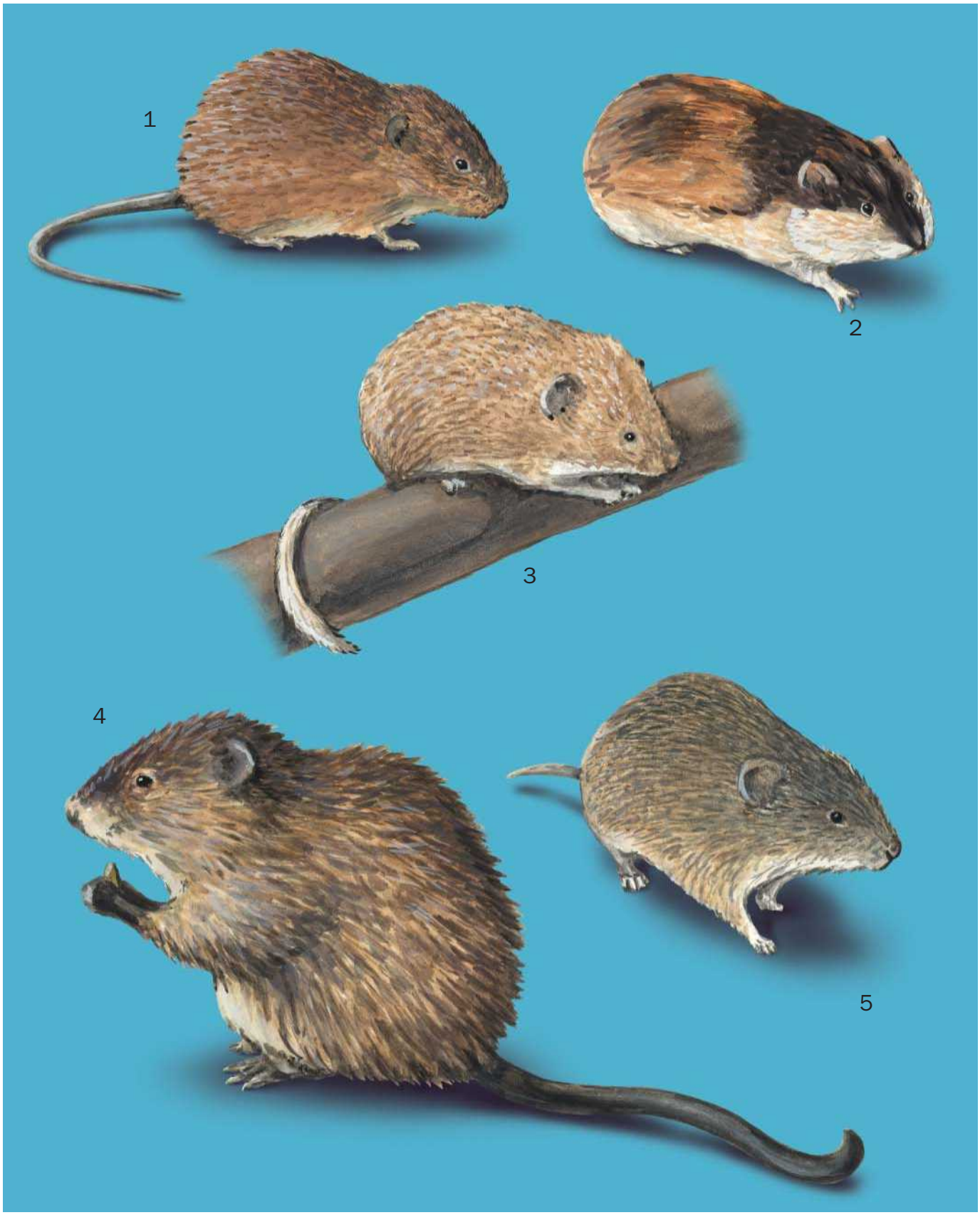
Habitat loss is the key factor contributing to the decline of most voles and lemmings. The loss of natural steppe and prairie habitats to agriculture has affected many species, and some of the more specialized genera such as tree voles or water voles have also lost significant habitat to logging or wetland drainage and development. The water voles have also been significantly affected by the introduction of American mink (*Mustela vison*) to Europe. Some species such as the northern water vole (*Arvicola terrestris*) and root vole (*Microtus oeconomus*) have been the subject of successful conservation breeding and reintroduction programs carried out by zoos in Europe.

Significance to humans

Voles and lemmings are highly significant within their environments. Some species can be significant pests of agricul-

ture, especially in the cyclic species when densities become very high during population peaks. They are pests of arable crops and also forestry and orchards by removing bark from the bases of trees or destroying the roots. The fossorial species also cause extensive damage to root crops. They can significantly affect stocking densities of grazing animals by directly competing for forage and damaging pastures. Some species are also important wild reservoirs of livestock or zoonotic diseases, uch as plague and tularaemia.

The muskrat is a very important fur-bearing species, widely hunted for its pelt, but also kept and farmed, which has resulted in the escape or release and establishment of the species in Europe, Asia, and South America. Several other species such as the mole voles, water voles, and collared lemmings are also locally hunted for their fur. Lemmings are important species of myth and legend among a number of indigenous peoples from northern latitudes.



1. Northern water vole (*Arvicola terrestris*); 2. Norway lemming (*Lemmus lemmus*); 3. Red tree vole (*Arborimus longicaudus*); 4. Muskrat (*Ondatra zibethicus*); 5. Prairie vole (*Microtus ochrogaster*). (Illustration by Brian Cressman)

1. Silvery mountain vole (*Alticola argentatus*); 2. Steppe lemming (*Lagurus lagurus*); 3. Wood lemming (*Myopus schisticolor*); 4. Bank vole (*Clethrionomys glareolus*); 5. Long-clawed mole vole (*Prometheomys schaposchnikowi*). (Illustration by Brian Cressman)

Species accounts

Muskrat
Ondatra zibethicus

TAXONOMY
Ondatra zibethicus (Linnaeus, 1766), eastern Canada. Sixteen subspecies have been recognized, although not all may be valid.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 15.5–24.5 in (40–62 cm); weight 1.1–4 lb (550–1,820 g). Upperparts are dark brown, underparts are light grayish brown.

DISTRIBUTION
United States and Canada; introduced to parts of Europe, Asia, and South America.

HABITAT
Always found around water, lakes, rivers marshes, and brackish lagoons.

BEHAVIOR
Muskrats either dig burrows in the bank or build large floating lodges of vegetation. They are known to sometimes live as extended family groups.

FEEDING ECOLOGY AND DIET
Aquatic vegetation, invertebrates, and small vertebrates.

REPRODUCTIVE BIOLOGY
Litters of 4–8 young are born after a gestation period of 25–30 days. As many as five or six litters a year may be produced.

CONSERVATION STATUS
Not threatened; generally widespread and numerous. The status of the Rio Grande muskrat (*O. zibethicus ripensis*) is unclear and this subspecies may be threatened.

SIGNIFICANCE TO HUMANS
A very important fur-bearing species that is widely hunted and farmed. It has become a major pest in some regions where it has escaped or been released. ◆

Northern water vole
Arvicola terrestris

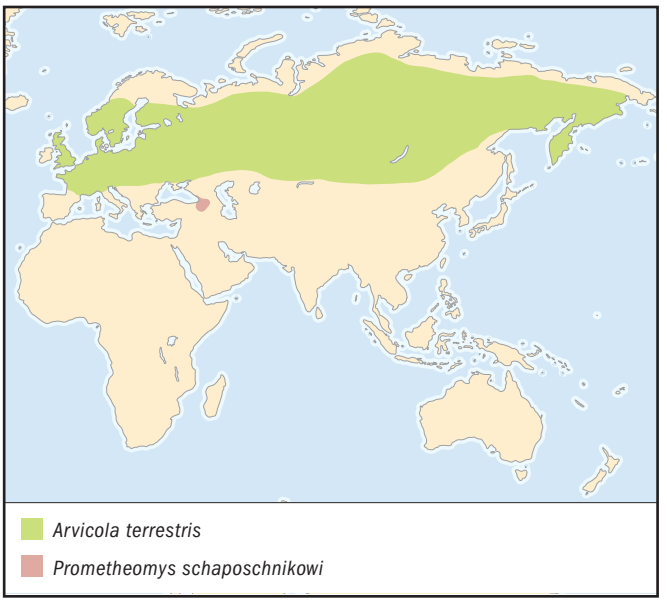
TAXONOMY
Arvicola terrestris (Linnaeus, 1758), Uppsala, Sweden. As many as 40 subspecies have been recognized, although many are probably not valid.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 7–15 in (18–38 cm); weight 2.5–15.8 oz (70–450 g). Upperparts are light to dark brown, underparts are buffy to slate gray.

DISTRIBUTION
Northwestern and central Europe, and Asia.

HABITAT
Aquatic forms adjacent to rivers, lakes, marshes, and lagoons; the fossorial form occurs in dry pastures and occasionally woodland.



BEHAVIOR
Two clear and very different ecological forms exist: a large aquatic form and a much smaller fossorial form. Almost all aspects of ecology differ between these two. The fossorial forms live at high density and are cyclic, while the aquatic populations occur at much lower densities and do not exhibit cycles.

FEEDING ECOLOGY AND DIET
Foliage, roots, and tubers.

REPRODUCTIVE BIOLOGY
Litters of 4–8 young are produced after a gestation period of around 21 days. Weaning is very early at 14–18 days.

CONSERVATION STATUS
The aquatic forms are declining and locally highly threatened, while the fossorial forms are often numerous pests. Captive breeding and reintroduction has occurred in threatened populations.

SIGNIFICANCE TO HUMANS
Hunted for fur across some parts of its range, can also be a pest to root crops and fruit trees. ◆

Prairie vole
Microtus ochrogaster

TAXONOMY
Microtus ochrogaster (Wagner, 1842), Indiana, United States. Seven subspecies have been recognized.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 5–7 in (13–18 cm); weight 1–2 oz (35–50 g). Upperparts dark brown to black, underparts light tan.

DISTRIBUTION
United States across the central prairies and an isolated population in the coastal southeast.

HABITAT
Dry open grassland.

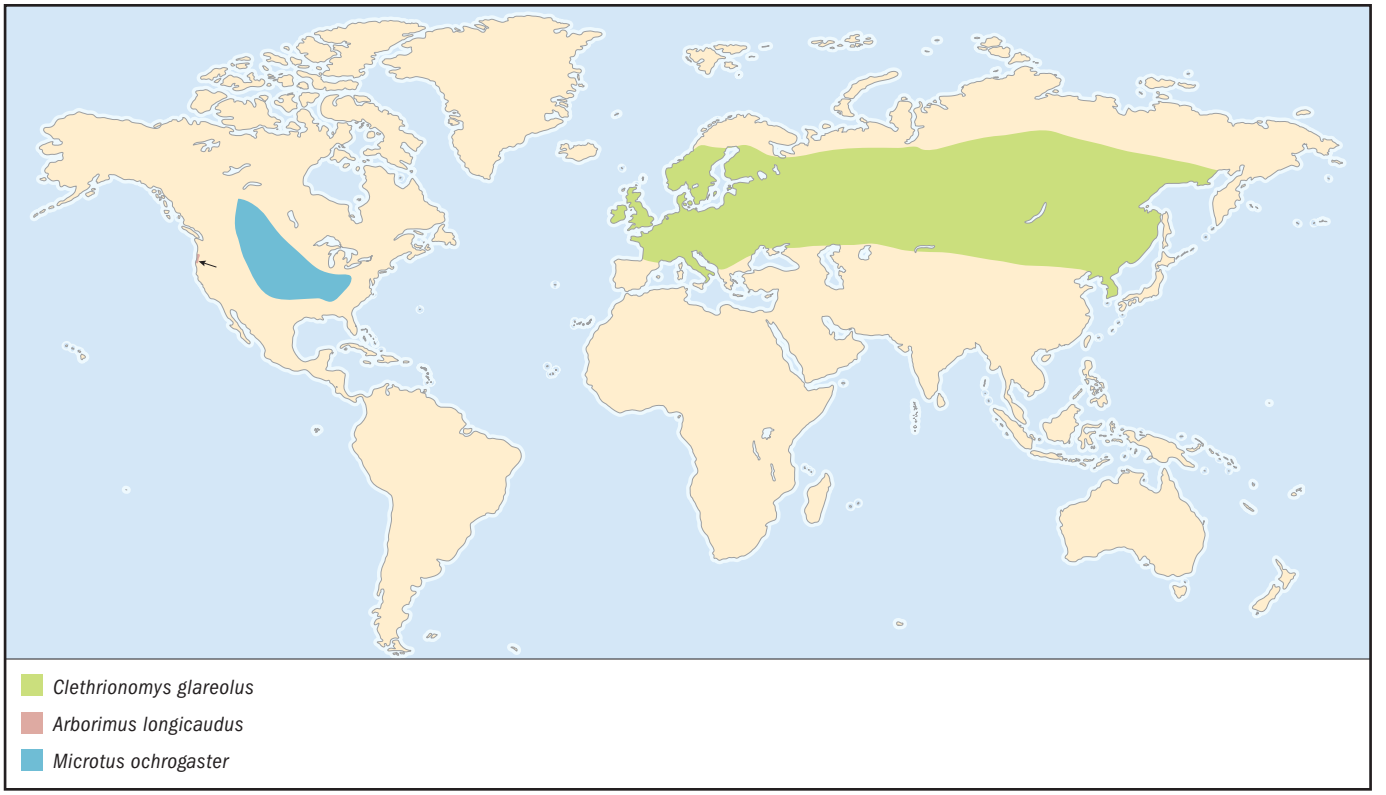
BEHAVIOR
A very important prey species across the prairies. They occupy tunnel systems at or around ground level and are active day and night. Populations are cyclic every three or four years.

FEEDING ECOLOGY AND DIET
Foliage and roots.

REPRODUCTIVE BIOLOGY
Monogamous. Litters of 2–4 young are born after a gestation period of around 21 days.

CONSERVATION STATUS
Not generally considered threatened; in fact, it may be a very numerous species in many areas. The isolated population in Louisiana may be Extinct.

SIGNIFICANCE TO HUMANS
An important species for sustaining the prairie ecosystem. ◆



Red tree vole
Arborimus longicaudus

TAXONOMY
Arborimus longicaudus (True, 1890), Oregon, United States. Two subspecies are recognized, one of which, *A. longicaudus silvicola*, is sometimes considered a separate, distinct species.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 6.5–8 in (16–20.5 cm); weight 1–2 oz (30–50 g). Upperparts reddish brown or cinnamon, underparts whitish to gray.

DISTRIBUTION
United States along the Pacific coast of Oregon.

HABITAT
Old coniferous forests.

BEHAVIOR
Mainly nocturnal and arboreal. Living high up in trees and constructing large stick and needle nests in the branches.

FEEDING ECOLOGY AND DIET
Fir needles, predominantly Douglas fir (*Pseudotsuga menziesii*).

REPRODUCTIVE BIOLOGY
Litters of 1–3 young are born after a gestation of around 28 days, although implantation is delayed if the female is already lactating with a previous litter.

CONSERVATION STATUS
Not threatened yet, although populations are declining due to logging of their habitat.

SIGNIFICANCE TO HUMANS
None known. ◆

Norway lemming
Lemmus lemmus

TAXONOMY
Lemmus lemmus (Linnaeus, 1758), Lappmark, Sweden. No subspecies are recognized.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 3–7 in (8–17.5 cm); weight 0.5–4.5 oz (20–130 g). Fur color is brown to black.

DISTRIBUTION
Scandinavia.

HABITAT
Open tundra and subarctic bogs.

BEHAVIOR
Mainly nocturnal and populations are highly cyclic undergoing mass migrations in peak years; active year-round, often underneath the cover of snow. Ecologically, a very important prey species in the tundra.

FEEDING ECOLOGY AND DIET
Mosses, lichens, bark, and some grasses.

REPRODUCTIVE BIOLOGY
They have very fast reproductive rate and can produce litters of up to 13 young after only a 16-day gestation. Up to six litters can be produced during the summer.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A familiar animal of Scandinavian myths and legends. ◆

Wood lemming
Myopus schisticolor

TAXONOMY
Myopus schisticolor (Lilljeborg, 1844), Gulbrandsdal, Norway. Five subspecies are recognized.

OTHER COMMON NAMES
None known.

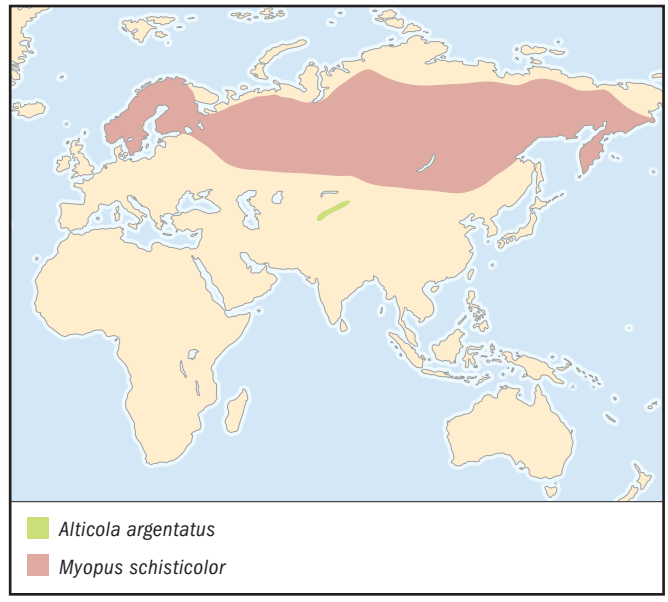
PHYSICAL CHARACTERISTICS
Head and body length 3.5–5.5 in (9–13.5 cm); weight 0.5–1.5 oz (20–45 g). Upperparts are dark grayish black with a reddish brown area along the center back. Underparts are paler.

DISTRIBUTION
From Scandinavia across to the Pacific coast of Russia.

HABITAT
Old coniferous forests.

BEHAVIOR
Mainly nocturnal, living in runs among deep forest litter and moss. Populations are known to be cyclic.

FEEDING ECOLOGY AND DIET
Mosses, lichens, and some grasses during the summer.



REPRODUCTIVE BIOLOGY
Sex ratio is chromosomally manipulated; only around 25% of the population is male. Females occur of three different genotypes, one of which only gives birth to female offspring. Litters of up to six young are produced every 25 days.

CONSERVATION STATUS
In 2002, considered by the IUCN to be Lower risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Long-clawed mole vole
Prometheomys schaposchnikowi

TAXONOMY
Prometheomys schaposchnikowi Satunin, 1901, Caucasus Mountains, Georgia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 6.5–8.5 in (17–22 cm); weigth 2–3 oz (50–80 g). Upperparts grayish brown, underparts pale gray. Cinnamon tint throughout.

DISTRIBUTION
Caucasus Mountains, in Georgia and Turkey.

HABITAT
Alpine and subalpine meadows.

BEHAVIOR
A burrowing, subterranean rodent that throws up heaps of soil, rather like a mole rat. They live in small groups that share a common burrow system.

FEEDING ECOLOGY AND DIET
Stems, shoots, and roots.

REPRODUCTIVE BIOLOGY
Two litters of approximately three young are born each year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Silvery mountain vole
Alticola argentatus

TAXONOMY
Alticola argentatus Severtzov, 1879, Kazakhstan. Nine subspecies are recognized; the taxonomic status of several is unclear.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 4.5–7.5 in (12–19 cm); weight 0.7–1.9 oz (20–55 g). Upperparts gray or brown, underparts whitish.

DISTRIBUTION
Central Asia in the Tien Shan mountains.

HABITAT
Alpine scree slopes and other rocky areas.

BEHAVIOR
Both nocturnal and diurnal. It builds large nests among rocks and is also active underneath snow cover during the winter.

FEEDING ECOLOGY AND DIET
Foliage, stems, seeds, and roots. They construct food stores of cut plants that they dry in the sun before caching for the winter months.

REPRODUCTIVE BIOLOGY
Produces 2–3 litters of around five young a year. Reproductive output varies with altitude and higher productivity tends to occur in lower altitude populations.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Bank vole
Clethrionomys glareolus

TAXONOMY
Clethrionomys glareolus (Schreber, 1780), Denmark. At least 30 subspecies have been described, but the taxonomic status of many of these is uncertain.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 5–8 in (12.5–20 cm); weight 0.5–2 oz (15–50 g). Upperparts dark gray with reddish tint, underparts dark gray to white.

DISTRIBUTION
Western Europe, across Russia to north Asia.

HABITAT
Forest, scrub, parkland, gardens, and hedgerows.

BEHAVIOR
Both nocturnal and diurnal, living in burrows and climbing in low vegetation. Populations in the north of its range are cyclic, while southern ones are more stable.

FEEDING ECOLOGY AND DIET
Seeds, fruit, buds, bark, and insects.

REPRODUCTIVE BIOLOGY
Produces litters of 3–5 young following a gestation of 16–22 days. It will breed all year if conditions are favorable and tree seed is available.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Steppe lemming
Lagurus lagurus

TAXONOMY
Lagurus lagurus (Pallas, 1773), Kazakhstan.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 3.5–5.5 in (9–14 cm); weight 0.5–1 oz (10–25 g). Upperparts light gray to cinnamon gray, underparts whitish. Black stripe along spine.

DISTRIBUTION
Central Asian steppes from the Ukraine to China.

HABITAT
Open grassland steppe, semi-deserts, and cultivated fields.

BEHAVIOR
Mainly nocturnal, but occasionally diurnal also. It lives in burrow systems that can join up to cover large areas. Populations fluctuate and they can be exceedingly numerous in some years.

FEEDING ECOLOGY AND DIET
Seeds, foliage, shoots, and roots.

REPRODUCTIVE BIOLOGY
They can produce up to five litters of young each year, with as many as 12 young in a litter. Pregnancy lasts around 20 days and the young are reproductive by 30–45 days old.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A serious pest of crops and grazing pastures when populations are high. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
White-footed vole *Arborimus albipes*	Pelage is long, fine, dark brown. Underparts are white, gray, or pinkish buff. Tail is long, ears are small, feet are long. Head and body length 3.7–4.3 in (9.5–11 cm), tail length 2.3–3.4 in (6–8.7 cm), weight 0.8–0.9 oz (25–26 g).	Close to small streams and are often found near fallen trees from sea level to over 3,280 ft (1,000 m). Most abundant in deciduous forest. Reproduce throughout the year, mean litter size is three. Arboreal, nocturnal.	Pacific coastal zone south of Columbia River, from western Oregon to extreme northwestern California, United States.	Roots, wide variety of leaves from those of grasses to deciduous trees, mosses, and pollen.	Data Deficient
Southern red-backed vole *Clethrionomys gapperi*	Dense, long, soft fur that is dark gray above and chestnut brown stripe running along back from head to tail. Face and sides are yellowish brown, underparts are dark slate gray to almost white. Head and body length 2.7–4.4 in (7–11.2 cm), tail length 0.9–3.4 in (2.5–6 cm).	Cool, mossy, and rocky boreal forests in both dry and moist areas, as well as tundra and bogs. Active during day and night. Construct spherical nests.	Most of Canada from northern British Columbia to Labrador, excluding Newfoundland; south in the Appalachians to northern Georgia, in the Great Plains to northern Iowa, and in the Rockies to central New Mexico and east-central Arizona, United States.	Leaf petioles, young shoots, fruits, berries, bark, roots, lichens, fungi, and insects.	Not threatened
Northern collared lemming *Dicrostonyx groenlandicus*	Short, stocky, heavy year-round coat that varies seasonally in color. Light to dark gray with buffy to reddish brown tone. Dark lines run down back and on sides of head. Winter coat is white. Head and body length 3.9–6.1 in (10–15.7 cm), tail length 0.4–0.8 in (1–2 cm), weight 1–4 oz (30–112 g).	Tundra. Is generally terrestrial, but has been seen in the water. Burrows lead to nests that are protected by males.	Northern Greenland and Queen Elizabeth Islands, south to Baffin and Southampton islands and northeastern District of Keewatin, Canada.	Willow buds, fruits, flowers, grasses, and twigs.	Not threatened
Sagebrush vole *Lemmiscus curtatus*	Pale gray and buff dorsally, ventral side is silver, white, and buff. Fur is dense, long, and soft. Body is stocky with short tail, stout claws, and small ears. Head and body length 3.5–5.1 in (9–13 cm), tail length 0.6–1.2 in (1.6–3 cm).	Areas largely dominated by bunch grasses and sagebrush, including semi-arid prairies, brushy canyons, and rolling hills with loose soil. Active throughout day and year. Occur in pairs or are solitary.	Southern Alberta and southeastern Saskatchewan, Canada, south to northwestern Colorado and east-central California, including the Columbia Basin of interior Oregon and Washington, United States.	Flower and fleshy parts of vegetation.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Rock vole *Microtus chrotorrhinus*	Ventral color is grayish brown on the back, face is orange, rich yellow around the nose. Winter coat is longer and glossier. Moderately large with sparsely haired tail. Underparts are slightly paler, ears are large. Head and body length 5.5–7.3 in (14–18.5 cm), weight 1–1.7 oz (30–48 g).	Among mossy rocks and boulders in forests with moderately open canopies and a rich herbaceous under story. Primarily diurnal, good nest builder. Low survival rate of young.	Southern Labrador southwest through southern Quebec and Ontario, Canada, to northeastern Minnesota, United States; south in Appalachian Mountains to eastern Tennessee and western North Carolina, United States.	Mainly bunchberry.	Not threatened
Meadow vole *Microtus pennsylvanicus*	Dorsal surface is dark blackish brown to dark reddish brown with coarse black hairs. Ventral surface is gray or white. Head and body length 5–7.7 in (12.8–19.5 cm), tail is about 40% of body length.	Meadows, lowland fields, grassy marshes, and along rivers and lakes. Active during all times of day. Females are territorial. Promiscuous.	From central Alaska to the Atlantic Coast. South of the Canadian border, western limit is the Rocky Mountains. Found as far south as New Mexico and Georgia, United States.	Fresh grass, sedges, and herbs, as well as a variety of seeds and grains.	Not threatened
Woodland vole *Microtus pinetorum*	Dorsal varies from light to dark brown, ventral side is whitish or silvery. Head and body length 3.2–4.7 in (8.3–12 cm), tail length 0.6–1.6 in (1.5–4 cm).	Deciduous forests in eastern North America. Form monogamous pairs. One to 13 offspring per litter.	Eastern U.S. shoreline from southern Maine to northern Florida, west to central Wisconsin and eastern Texas.	Tubers, roots, seeds, leaves, and nuts, as well as berries and insects.	Not threatened
Round-tailed muskrat *Neofiber alleni*	Outer fur is composed of coarse guard hairs and is dark brown and glossy in color. Undercoat is dense, becoming gray at base. Tail is round. Head and body length 15–21 in (38.1–54.6 cm).	Wet moist areas on mainland and islands. Construct dome-shaped lodges. Nocturnal.	Most of peninsular Florida to extreme southeastern Georgia, United States.	Aquatic grasses as well as roots, stems, and seeds.	Lower Risk/Near Threatened
Western heather vole *Phenacomys intermedius*	Fur is long, soft, and varies geographically. Dorsal fur is generally brown to grayish, ventral side is gray. Feet are white to gray, ears are orange. Head and body length 5–5.5 in (13–14 cm), weight 1–1.7 oz (30–50 g).	In stands of spruce, lodgepole pine, aspen, and grassy meadows in montane forest, subalpine, and alpine tundra. Active year round, does not hibernate. Solitary, except during breeding season.	Southwestern British Columbia and adjacent Alberta, Canada, south to northern New Mexico, central Utah, and northern California, United States; disjunct populations in east-central California and western Nevada.	Leaves and fruits of willows, myrtle blueberry, snowberry, bog birch, kinnikinnik (bearberry) in the summer months. The rest of the year, they feed on bark and buds of willow, birch, and blueberry trees.	Not threatened
Northern bog lemming *Synaptomys borealis*	Stocky build with short legs and long tail. Ears are small, nose is blunt. Pelage is coarse and ruffled, and varies from grayish brown to chestnut brown, underside is pale gray. Tail is brown above and white below. Head and body length 4.8–5.5 in (12.2–14 cm), tail length 0.7–1 in (2–2.7 cm), weight 0.9–1.2 oz (27–35 g).	In burrows among sedges and grasses where water level is high. Breeding season is from May to August, litters contain two to eight individuals.	Alaska to northern Washington, United States, eastwards across much of interior Canada to Labrador; disjunct range segment from Gaspe Peninsula, Quebec, to central New Hampshire, United States.	Sedges and grasses.	Not threatened

Resources

Books

Carleton, M. D., and G. G. Musser. "Muroid Rodents." In *Orders and Families of Recent Mammals of the World*, edited by S. Anderson and J. K. Jones Jr. New York: John Wiley and Sons, 1984.

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Mike J. R. Jordan, PhD

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Rats, mice, and relatives II

Hamsters (Cricetinae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Muridae
Subfamily Cricetinae

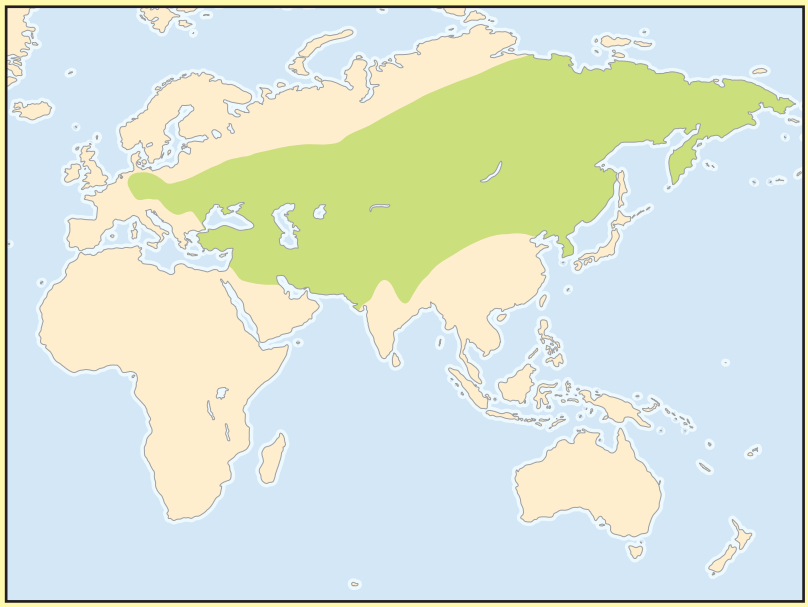
Thumbnail description
Hamsters are mouse-like Old World rodents with chunky bodies; short, furry tails; and large cheek pouches, used to transport food; they have dexterous forepaws with four digits plus a "thumb knob"; hind feet have five digits; individual hamsters live alone in underground burrows, are active at night, and hibernate in winter

Size
2–13.4 in (5–34 cm); 0.9–31.7 oz (25–900 g)

Number of genera, species
7 genera; 18 species

Habitat
Deserts, dry plains, steppes, and cultivated fields

Conservation status
Endangered: 2 species; Vulnerable: 1 species; Lower Risk/Near Threatened: 4 species



Distribution
Throughout the Palearctic zone of Europe and Asia

Evolution and systematics

Members of the group Cricetinae appear in the European fossil record in the Middle Miocene (11.2 to 16.4 million years ago [mya]) and in the Asian fossil record in the late Miocene (6 to 11 mya). As of 2003, 15 extinct fossil genera have been documented.

Hamsters are related to voles, lemmings, and New World mice. In the mid-twentieth century, taxonomists split the group from the Muridae as a separate family, Cricetidae; however this split has been reversed.

The number of genera in Cricetinae is still debated. Some taxonomists place *Calomyscus* and/or *Mystromys* in this group; others place these two genera in their own subfamilies.

Some sources specify 18 species in 7 genera, while others describe 24 species in 5 genera. According to the Wilson and Reeder classification for 18 species in 7 genera, the rat-like hamsters, genus *Cricetulus*, include six Eurasian species; the golden hamsters, genus *Mesocricetus*, include four European and Middle Eastern species; the dwarf hamsters, genus *Phodopus*, include three Asian species; the Mongolian hamsters, genus *Allocricetulus*, include two Asian species; with the *Cansumys* genus having only one species, the Gansu hamster. Black-bellied hamsters are also the sole species in genus *Cricetus*, as well as the greater long-tailed hamster in genus *Tscherskia*.

Physical characteristics

Dwarf hamsters, genus *Phodopus*, are the smallest members of the group, averaging 2–4 in (5.3–10.2 cm) in length; the largest hamster is the black-bellied hamster, *Cricetus cricetus*, which at 7.9–13.4 in (20–34 cm) is about the size of a large rat or guinea pig.

Described as "all head and rump," hamsters have stout bodies and short legs and tails. The feet are wide, sometimes furry; the body fur is soft and thick and varies in color (depending on species) from gray to reddish brown; underparts can be white, gray, or black. Most hamsters have large cheek pouches.

Unusual for small mammals, the hamster stomach has two compartments; the forestomach, or cardiac stomach, has tough keratin as a structural component and is non-glandular, similar in structure and function to the rumen of cattle and other grazing animals. The second compartment—the pyloric, or glandular, region—is separated from the forestomach by muscular folds.

Hamsters have excellent hearing and an acute sense of smell; some species have scent glands on their flanks and use scent to mark their territories.

Distribution

The group is widely distributed in Eurasia, although a few species—the golden hamster is one example—have quite re-

Cricetus cricetus female taking newborn pups in her mouth. (Illustration by Wendy Baker)

A Dzhungarian (Rissoam dwarf) hamster (*Phodopus sungorus*). (Photo by © Leach/OSF/Animals Animals. Reproduced by permission.)

stricted ranges. In the northern part of Eurasia, hamsters are found from central Europe through Siberia to northern China and Korea. In the south, various species occur from Syria to Pakistan.

Habitat

Most hamsters live in dry, open habitats such as desert borders, short-grass steppes, and rocky foothills, although the black-bellied hamster sometimes digs burrows along riverbanks. With the spread of agriculture, many species have moved into cultivated lands.

Behavior

Hamsters are active rodents with bodies well suited for running and digging. Most excavate their own burrows (some occupy burrows abandoned by—or still occupied by—other rodents). All are nocturnal and range far from their burrows at night to collect food that they carry home in large, internal cheek pouches. Inside the burrow, where special chambers are reserved for food storage, they stroke cheeks with paws to force the seeds out. In winter, hamsters hibernate if temperatures are sufficiently cold.

Some hamsters are gregarious, even highly social, while others tend to live alone or in pairs. *Phodopus* may be pair-bonded; paternal care is unusual in hamsters and only *Phodopus* can be kept as mated pairs. Where burrows are closely spaced, this is only because appropriate habitat, soil loose and deep enough for digging, is in limited supply. Hamsters are fierce for their size and very aggressive to members of their own species. Pet golden hamsters must be maintained solitary. In addition to taking prey such as smaller rodents or baby birds the larger hamster species will attack humans and dogs when threatened.

Some species hibernate continuously, while others enter shallow daily torpor during the winter. In winter, rat-like hamsters do not hibernate continuously but awaken from time to time to eat stored food. Hibernation for uninterrupted periods of up to 28 days has been experimentally induced in the golden hamster through exposure to cold. The mouse-like hamster is active only at night during the summer, but it is also active by day in the autumn and winter.

Hamsters have a poor sense of sight despite their large protruding and round eyes. This is compensated by their well-developed sense of hearing that allows them to hear a wide range of sounds, including sounds in the ultrasonic frequen-

Hibernating hamsters in their nest chamber. (Illustration by Wendy Baker)

A black-bellied hamster (*Cricetus cricetus*) foraging in grass. (Photo by Hans Reinhard/Okapia/Photo Researchers, Inc. Reproduced by permission.)

A male golden hamster (*Mesocricetus auratus*). (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

cies, which helps them communicate with each other without being heard by other animals. Hamsters also have an acute sense of smell and can distinguish one another by their distinct scents. Olfactory communication has been shown to play an intricate role in the daily activities of the golden hamster. Olfaction allows these nocturnal, burrowing, solitary, and territorial animals to communicate important individual information to one another and to receive information from their environment.

Feeding ecology and diet

Living in dry, comparatively unproductive habitats, hamsters often travel long distances in search of food. Besides carrying seeds and grain in their roomy cheek pouches, they carry large items such as root vegetables in their teeth. By storing food, hamsters make sure they will have enough to eat when food is in short supply—especially in winter.

Hamsters eat frequently throughout the day; their mixed diet is mostly seeds and grains but also includes green plant parts along with insects such as moths, beetle larvae, earth-

A 20-day-old hamster. (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

A Dzhungarian hamster (*Phodopus sungorus*) gathers nesting material. (Photo by Kenneth W. Fink/Photo Researchers, Inc. Reproduced by permission.)

The Dzhungarian hamster (*Phodopus sungorus*) will fill its cheeks with food to carry to its burrow. (Photo by © Jorg & Petra Wegner/Animals Animals. Reproduced by permission.)

worms, and grasshoppers. Some hamsters kill smaller rodents, lizards, frogs, or baby birds, and they will eat carrion as well.

Reproductive biology

Hamster are sexually mature at a very young age, soon after they are weaned. Typically, males and females come together only to mate. The gestation period is quite short, ranging from 17 to 22 days. Litter size ranges from one to 16 pups with the average litter size around 11; females have eight to 17 nipples depending on species. In the wild hamsters may have two to four litters per year but species kept in captivity reproduce more frequently.

Hamsters are born hairless, with their eyes and ears closed and legs still somewhat undeveloped. The young do have teeth at birth, however, and eat solid food at seven to 10 days. They are weaned at 21 days.

Though most male hamsters play no role in raising the young, male Dzhungarian hamsters (*Phodopus sungorus*) are at-

tentive fathers that assist at births, lick newborns clean, help keep them warm, and care for them when the female leaves the nest to feed. Like their mouse relatives, most hamsters live one to three years.

Conservation status

Threats to hamsters include loss of habitat, widespread use of rodenticides on farms, and, formerly, trapping for fur and as a pest-control measure. According to the IUCN Red List of 2002, two species are classified as Endangered: the golden hamster, *Mesocricetus auratus* of Syria, and the Hotson's mouse-like hamster, *Calomyscus hotsoni* of Pakistan. Four species are classified as Lower Risk/Near Threatened: the gray hamster, *Cricetulus migratorius*; the Afghan mouse-like hamster, *Calomyscus mystax*; Tsolov's mouse-like hamster, *C. tsolovi*; and the Urartsk mouse-like hamster, *C. urartensis*; one species is classified as Vulnerable, the Romanian hamster, *Mesocricetus newtoni*.

Significance to humans

Humans have long regarded hamsters as agricultural pests. Large species, particularly *Cricetus cricetus*, have been trapped for their fur; as recently as 2001, hamster fur made headlines as a controversial high-fashion item. Historically, farmers from China to Germany dug up hamster burrows to get at the stored grain—sometimes to feed farm animals, and sometimes—when times were hard—to feed themselves.

Since the twentieth century hamsters have been most important to humans as a biomedical research animal. Chinese hamsters were the first species to be used in laboratory research, in 1919. As of 2002, eight different species have been used in research on infectious diseases, cytogenetics, toxicology, and oncology, as well as obesity and diabetes, photoperiod changes, social behavior, and hibernation physiology. The species most widely used in research is the golden hamster.

Hamsters are also very popular pets; they are also bred for specialized colors and patterns, entered in shows, and exhibited at zoos.

1. Black-bellied hamster (*Cricetus cricetus*); 2. Golden hamster (*Mesocricetus auratus*). (Illustration by Wendy Baker)

Species accounts

Black-bellied hamster
Cricetus cricetus

SUBFAMILY
Cricetinae

TAXONOMY
Cricetus cricetus (Linnaeus, 1758), Germany.

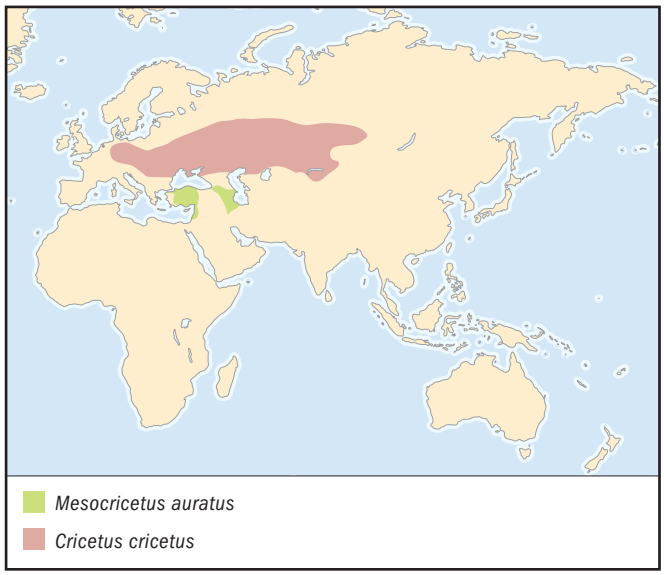
OTHER COMMON NAMES
English: Common hamster, European hamster, field hamster.

PHYSICAL CHARACTERISTICS
The largest hamster, 8–12 in (20–34 cm) long; males larger than females (10.5–12.5 in [27–32 cm] versus 8.7–9.8 in [22–25 cm]). Tail short and hairless, 1.6–2.4 in (40–60 mm). Weight 4.5–36.3 oz (112–908 g), averaging 18 oz (450 g) for males and 14 oz (350 g) for females. Thick fur is reddish brown above with white patches on the flanks, nose, cheeks, and throat, and black underparts—unusual in mammals. Color variations, from albino to melanistic, are common.

DISTRIBUTION
Black-bellied hamsters live in lowlands of central and Eastern Europe, from Belgium to the Altai region of Siberia.

HABITAT
Throughout much of their range, the hamsters' natural steppe habitat has been converted to agricultural land; they have adapted to living in and along farm fields, especially where both grain and root crops are grown. Occasionally, they dig burrows along riverbanks. These hamsters generally prefer low elevation habitat but can found up to an altitude of 2,000 ft (610 m).

BEHAVIOR
When suitable burrowing sites are in short supply, black-bellied hamsters may burrow quite close together; however these clusters are not true colonies; like most hamsters, members of this species are solitary in their habits. They are also active nocturnally and hibernate in winter. Winter burrows can be very deep, extending more than 6 ft (2 m) below the soil surface. *Cricetus* burrows are particularly complex, with several entrance tunnels, numerous chambers for nesting and food storage, and a dead-end tunnel used as a toilet area. The size of the burrow is correlated with the hamster's age; old females with young have the most complex burrows.



Black-bellied hamsters live in regions that can be quite cold in winter; they hibernate but wake up every 5–7 days to feed on their stored supplies. The length of hibernation is influenced by weather and other factors but typically occurs from the end of September through April.

When the hamster population in a given area reach a very high density, some members of the population become restless and leave, spreading out into new locations. Capable of swimming, the hamsters sometimes cross large rivers during these wanderings.

FEEDING ECOLOGY AND DIET
As with most hamsters the diet includes grains, beans, roots, and the green parts of plants; black-bellied hamsters also eat insect larvae—especially beetle larvae—frogs, earthworms, and field mice. They often store very large quantities of cereal grains, seeds, peas and potatoes in their winter burrows; there are reports of burrows containing as much as 198 lb (90 kg) of food.

REPRODUCTIVE BIOLOGY
Most breeding activity takes place between June and August, although breeding can begin earlier or continue later, depending on location and climate. Probably serially monogomous. A courting male will enter the female's territory and mark the area with secretions from glands in his flanks. A lengthy courtship ritual ensues, in which the male runs after the female, making a loud sniffing noise that serves as his mating call. After mating occurs, the female becomes aggressive and drives the male away. (In captivity, however, male black-bellied hamsters sometimes help to raise the young.)

The female cushions the floor of the nest chamber with grass stalks. The gestation period is 18–20 days. A typical litter is 4–12 pups; the female has eight nipples and usually raise no more than eight young. Newborns weigh about 0.2 oz (7 g). They start to eat solid food at one week, when their eyes are still closed; at age two weeks they open their eyes and have acquired a full coat of fur. At three weeks they are weaned; they will reach adult size at eight weeks. A female typically has two litters per year in the wild. These are comparatively long-lived hamsters, sometimes reaching the age of eight years old.

CONSERVATION STATUS
Sometimes considered a serious pest on farms, black-bellied hamsters in the twentieth century were often systematically poisoned with rodenticides. This practice, combined with habitat loss, due both to changes in farming practices and

spreading industrial construction, has led serious population declines in some locations. As of 2000, this hamster was protected under the European Community Habitats Directive as a threatened species in Germany, Belgium, the Netherlands, France, and Austria. They are also protected in Bulgaria, Croatia, and Slovenia, where they are uncommon, not because of human actions, but because they are at the edge of their range.

SIGNIFICANCE TO HUMANS

As land was increasingly cleared for farming in the Middle Ages, this probably created conditions favorable for hamsters and led to a rise in populations. Historically this species has been widely hunted for food and trapped for its colorful fur, which was used to make clothing or as a warm lining; as of 2001 hamsters were still being trapped in eastern European nations where they are common, such as Hungary, and the fur was still being used in some high-fashion garments.

Black-bellied hamsters have historically been a particular pest in corn fields; corn is often the last crop to be harvested, so hamsters from neighboring fields congregate in corn fields after their other food sources are gone. It's worth noting that this species can also be helpful to farmers because it hunts field mice and insect pests.

Finally, the black-bellied hamster is sometimes used as a lab animal, particularly in oncology research. ◆

Golden hamster

Mesocricetus auratus

SUBFAMILY

Cricetinae

TAXONOMY

Mesocricetus auratus (Waterhouse, 1839), Aleppo, Syria.

OTHER COMMON NAMES

English: Syrian hamster; Syrian golden hamster.

PHYSICAL CHARACTERISTICS

Medium sized, about 6–7 in (15–18 cm) long, stubby white or pink tail is 1.2 cm (0.5 in); weight 3–4 oz (90–120 g), with females larger than males. Fur is light reddish brown to golden with white or cream-colored underparts; domesticated animals have been bred for a wide variety of colors, patterns, and fur textures. Cheek pouches are very large, extending back behind the shoulders. Females have 12–17 nipples. Life span is 2–3 years.

DISTRIBUTION

Although some accounts assert that this species is extinct in the wild, it may in fact be locally common; specimens were collected in the Mount Aleppo region, in northwestern Syria in 1999; other specimens were sighted near Jarablus in Syria in 1986 and near Gaziantep in Turkey, mostly recently in 1999.

HABITAT

Historically, this hamster's native habitat has been described as dry, rocky steppe or brushy slopes. The wild population discovered in 1999 was living in agricultural fields planted with annual crops including barley, chickpeas, lentil, melons, tomatoes, and others; hamsters were most often found on plots of legumes. Burrows were also found on the embankments around irrigation wells; all of the burrows were in sandy clay soil overlaying limestone bedrock.

BEHAVIOR

Though mostly nocturnal, golden hamsters are sometimes active in daytime. Burrow depths measured on the 1999 expedition ranged from 14 to 41.3 in (36 to 106 cm), averaging about 25.4 in (65 cm). Burrow entrances averaged 1.6–2.0 in (4–5 cm) in diameter and led to vertical entrance tunnels. Occupied burrows had their entrances plugged with lumps of earth slightly below the soil surface. Nest chambers ranged from 2.9–7.8 in (10–20 cm) wide; the spherical nests were made of dry plant materials. In contrast to black-bellied hamster burrows, which are complex and often have more than 10 branches, a golden hamster's burrow is relatively simple, with few side tunnels. This species reserves a blind-end tunnel for urination but defecates throughout the burrow. They are thought to hibernate in winter from November to February, although the hibernation state is not total. In the lab, hibernation can be induced at temperatures below 46°F (8°C). Predators are uncommon in the are where these hamsters occur (because of the dense human population) but in 1999 hamster remains were found in a barn owl pellet.

FEEDING ECOLOGY AND DIET

Although lab diets have been carefully worked out, very little is known about how these hamsters live in the wild.

REPRODUCTIVE BIOLOGY

In the wild the breeding season is thought to begin in February (lab animals breed year round). Males and females meet only to breed and the males do not assist in rearing the young. The female's estrous cycle is four days long and estrus lasts 27.4 hours. After conception the gestation period is usually 16 (but sometimes up to 19) days. The litter size can range from one to 16 pups; litters of six to nine are typical. The pups are blind and hairless at birth and typically weigh 0.07–0.1 oz (2–3 g); they grow quickly, are weaned by 20 days, and are sexually mature and ready to breed at 7–8 weeks old. If she feels threatened, the mother may transport her young in her cheek pouches (this occurs only during their first three days of life).

CONSERVATION STATUS

This species is listed as Endangered.

SIGNIFICANCE TO HUMANS

Among endangered species, golden hamsters are unusual in that humans may have helped to prevent the species from becoming extinct by taking animals from the wild to use in biomedical research. The story begins in 1930, when four juvenile animals were taken from a burrow in a Syrian wheat field in 1930 and brought to the Microbiological Institute of Jerusalem, with the goal of using them instead of Chinese hamsters, which had failed to breed in captivity in a study of the disease *Leishmaniasis*. The golden hamsters reproduced very well in captivity; their descendents, along with the descendents of another 12 animals collected in 1971, have been distributed to research institutions all over the world. Although as of 2003, eight hamster species are used in research, golden hamsters are by far the most the most common experimental subject; in addition, they are the most popular of all the hamster species kept as pets. Escaped pets have established wild populations in some locations in the British Isles.

Despite their endangered status, in Syria the remnant wild populations are still considered as pests and trapped or poi-

soned using rodenticides provided by the government. Farming practices are another problem. In May and June fields are harvested, then burned or ploughed under; meanwhile sheep are turned out to graze in any remaining fields. At this time it may be hard of hamsters to find cover, nutrition, or the extra food they need to store for the winter. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Mongolian hamster *Allocricetulus curtatus* German: Mongolische Zwerghamster; Spanish: Hámster enano de Mongolia	Back is yellowish gray, belly is off-white. Lacks typical pectoral spot, young are completely gray, later turning grayish yellow. Head and body length 4.3–5.9 in (11–15 cm).	Dry steppes, forests, fields, and gardens.	Steppes of Mongolia north of the Altai and eastwards to Inner Mongolia.	Cereals and various seeds of wild plants.	Not threatened
Eversmann's hamster *Allocricetulus eversmanni* German: Eversmann-Zwerghamster; Spanish: Hámster enano de Eversmann	Upperparts dark brown or reddish sand, underparts are gray or white. There is a brownish gray or reddish brown spot on the chest. Small eyes, ears, and limbs. Head and body length 5.9–7.4 in (15–19 cm).	Desert or steppe habitats, as well as cultivated areas in the vicinity of the Caspian Sea and south of the region.	Northern Kazakhstan steppes from Volga River to the upper Irtysh at Zaysan.	Cereals and fruits, as well as insects, spiders, and snails.	Not threatened
Greater long-tailed hamster *Tscherskia triton* German: Zwerghamster; Spanish: Hámster-rata enano	Back is dark brown, belly is off-white to gray. Dark ears, sometimes with white edges. Extended snout. Head and body length 7–9.8 in (18–25 cm), tail length 2.7–3.9 in (7–10 cm).	Humid zones, fens, valleys, as well as forests full of hazel trees at low elevations. Breeding season from May to October. Four to five litters per year, averaging seven young per litter.	Northeastern China from Shaanxi to southeastern Manchuria (Heilongjiang) and south to Anhui, Korea, and north to upper Ussuri in Russia.	Cereals, such as wheat, oats, barley, and maize, as well as cherries, nuts, and acorns.	Not threatened
Gray dwarf hamster *Cricetulus migratorius* German: Graue Zwerghamster; Spanish: Hámster armeno	Fur is long, mouse gray in color. May be reddish or buffy. Underparts are light gray or white. Robust body, blunt muzzle, short legs and tail, large internal cheek pouches. Head and body length 3.1–9.8 in (8–25 cm), tail length 0.9–4 in (2.5–10.6 cm).	Open dry country, such as steppes and the borders of deserts. In Afghanistan, occurs at 1,310–11,810 ft (400–3,600 m) on rocky slopes and plateaus almost devoid of vegetation. Nocturnal in winter, diurnal in summer. Live in burrows. Extremely aggressive.	Southern European Russia and southeastern Europe (Greece, Romania, Bulgaria) through Kazakhstan to southern Mongolia and northern China (Xinjiang, Ningxia; Qin), north nearly to Moscow, south to Israel, Jordan, Lebanon, Iraq, Iran, Pakistan, Afghanistan, and Turkey.	Young shoots and seeds.	Lower Risk/Near Threatened
Striped dwarf hamster *Cricetulus barabensis* German: Daurischer Zwerghamster; Spanish: Hámster listrado chinês	Fur is long, mouse gray in color. May be reddish or buff. Underparts are light gray or white. Dark brown dorsal stripe. Robust body, blunt muzzle, short legs and tail, large internal cheek pouches. Head and body length 3–10 in (8–25 cm), tail length 0.9–4.1 in (2.5–10.6 cm)	Open dry country, such as steppes and the borders of deserts. Nocturnal in winter, diurnal in summer. Live in burrows. Extremely aggressive.	Steppes of southern Siberia from River Irtysh to Ussuri region, and south to Mongolia, northern China (Xinjiang through Nei Mongol), and Korea.	Young shoots and seeds.	Not threatened
Brandt's hamster *Mesocricetus brandti* English: Turkish hamster	Upperparts are light reddish brown, underparts are white or creamy. Skin is loose, enormous cheek pouches. Head and body length 6.6–7 in (17–18 cm), tail length 0.4 in (1.2 cm).	Dry, rocky steppes or brushy slopes. Nocturnal. Maximum of two litters per year.	Anatolian Turkey, south into Israel, Lebanon, Syria, northern Iraq, northwestern Iran, northern Transcaucasia, and Kurdistan.	Green vegetation, meat, seeds, and fruit.	Not threatened
Dzhungarian hamster *Phodopus sungorus* German: Zwerghamstern; Spanish: Hámster ruso	Thick body, short tail, cheek pouches. Grayish or pinkish buff. Dorsal stripe runs along length of body. Underparts and muzzle, upper lips, limbs, and tail are white. Tail and feet are covered with hair. Head and body length 2–4 in (5.3–10.2 cm), tail length 0.2–0.4 in (0.7–1.1 cm).	Semi-arid areas, usually grassy plains, sand dunes, or wormwood steppes. Solitary, except for breeding. Nests are built in burrows.	Eastern Kazakhstan and southwestern Siberia.	Seeds and any available plant matter.	Not threatened

Resources

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Cynthia Ann Berger, MS

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Rats, mice, and relatives III

Old World rats and mice (Murinae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Muridae
Subfamily Murinae

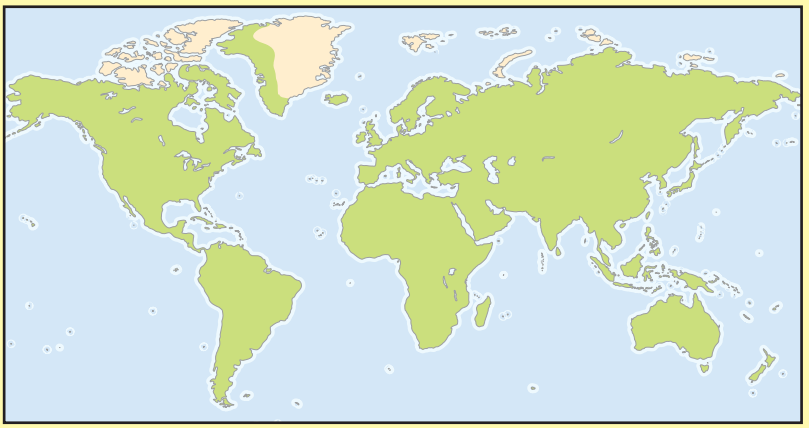
Thumbnail description
Old World rats and mice can grow up to the size of rabbits and have long tails, either furry or scaly, sometimes longer than the body itself; aquatic species may use their tails as rudders and others use their tails and unique opposable digits on their front feet to climb; characteristics vary widely, but all Murinae have a row of tubercles on the inside of their upper molars

Size
1.9–14.7 in (5–36 cm); 0.2–52.9 oz (5–1,500 g)

Number of genera, species
122 genera; 529 species, with more identified annually

Habitat
Forests, fields, bushes, flatlands, steppes, etc.; some are aquatic, some live in burrows, tunnels, beneath logs or other forms of shelter, or in nests; also can live in trees, in sewers and cellars, and in various parts of houses

Conservation status
Critically Endangered: 18 species; Endangered: 33 species; Vulnerable: 56 species



Distribution
Worldwide

Evolution and systematics

The Muridae family contains 25% of all living mammals, and it appeared in the fossil record during the Upper Miocene (10–15 million years ago [mya]). Recent molecular evidence has supported the belief that the family radiated quickly and suddenly, which, as a result, has caused a lack of consensus in the scientific community about the evolution of the family and its subfamilies. One relationship to be addressed in murine systematics is the difference between rats and mice. In general, animals that have a body length of less than 5.1–5.9 in (13–15 cm) are called mice, and rats are those that are larger. Still, rats and mice diverged about 12 mya, and scientists believe that murines evolved from rodents in Eurasia.

A Natal multimammate mouse (*Mastomys natalensis*) perched on a rock. (Photo by Rudi van Aarde. Reproduced by permission.)

Physical characteristics

The smallest murines, like the African native mice, only reach 1.9 in (5 cm), while the largest can grow significantly bigger. The greater bandicoot rats (*Bandicota*), for example, can have a body length of 14.7 in (36 cm) and can weigh up to 3.3 lb (1.5 kg). In some cases, their tails are semi-prehensile and assist in climbing, and can either be scaly or slightly

The Australian jumping mouse (*Notomys alexis*) is the most common of all hopping mice. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A long-tailed field mouse (*Apodemus sylvaticus*) eating a seed. (Photo by Stephen Dalton/Photo Researchers, Inc. Reproduced by permission.)

furred. They can have opposable thumb knobs, and their bodies are adapted for climbing (strong feet and semi-prehensile tails), jumping (long hind feet), or swimming (using their tails as rudders). They have, in general, 16 teeth (I1/0 C0/0 P0-3/1 M0/0-3), and their rooted molars are either laminate or cuspidate. Females have 4–24 nipples.

Distribution

The murine rodents are endemic to the Old World, including Eurasia, Africa, and Australiasia, but human intervention has spread many species throughout the Americas and across the world. Some murine rodents have even established populations in Antarctica.

Habitat

The animals can live in a variety of habitats, from arid deserts to the jungles of the Indo-Pacific. Many of the rodents have become commensal with humans and are known to be pests. Murines live in nests or burrows, either in trees, on the ground, or in and around houses. Certain murine rodents, like the brown rat, are known to live in burrows, which has led animal biologists to study them in mazes—which simulate their natural habitat—in order to understand how

The zebra mouse (*Lemniscomys barbarus*) gets its name from the stripes on its back. (Photo by S. R. Maglione/Photo Researchers, Inc. Reproduced by permission.)

A house mouse (*Mus musculus*) carrying its newborn offspring. (Photo by Kim Taylor. Bruce Coleman, Inc. Reproduced by permission.)

When threatened, the Egyptian spiny mouse (*Acomys cahirinus*) expands its bristles to appear larger. (Photo by E. R. Degginger/Photo Researchers, Inc. Reproduced by permission.)

they find their way and how they learn. Once put in a maze with food at the end, brown rats will search through the maze and make a series of errors, but eventually will run at high speed, without deviations, directly to the end. They also can find their way in lit and dark mazes, are not confused by inclined floors, and it is speculated that they use their whiskers to feel the walls, and even listen to the echoes of their noises off the walls of the maze to orient themselves. They perform better in mazes than humans, which has lead scientists to believe that the rats have memories and minds conditioned, from living in underground tunnels, to a sort of navigation.

Behavior

Old World rats and mice can be social creatures. They are known to travel in groups (hence the term "rat packs") and sleep together peacefully, but can be aggressive towards members of other rat colonies and are known to form colonial territories. Scientists have identified up to 20 pheromones that rats use to attract mates, as well as other scents that the animals use to mark territory or objects.

Rats are also vocal creatures and emit various sounds. Encounters between brown rats, for example, may begin with percussive chattering, while bush rats scream and whistle at each other.

Feeding ecology and diet

These animals can be nocturnal or diurnal and exhibit a wide range of foraging behavior and food preferences. Some species feed only on nuts and berries, while other species have been known to gnaw on just about anything. They often forage or

A golden spiny mouse (*Acomys russatus*) forages among leaf litter. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

The plains mouse (*Pseudomys australis*) is endemic to Australia. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

hunt in packs, and certain species are known to be able to catch birds. Aquatic species hunt fish.

Reproductive biology

These animals are some of the most successful rodents in the world, in part because they reproduce frequently. Murid rodent pups, the murines included, are usually born naked and blind. For the most part, their eyes open and they grow hair within a week or two, and they are weaned shortly thereafter. A common behavior among these rodents is that the mothers carry their young on their nipples, which allows them to flee from danger without making multiple trips to carry the pups to safety. When conditions are optimal, they generally are able to mate year-round.

A four-striped grass mouse (*Rhabdomys pumilio*) drinking from a small pool of water. (Photo by Rudi van Aarde. Reproduced by permission.)

Conservation status

The murine rats are one of the most hardy mammalian species. They reproduce often and in great numbers and are highly adaptable to many environments. However, there are a

A house mouse (*Mus musculus*) nursing young. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

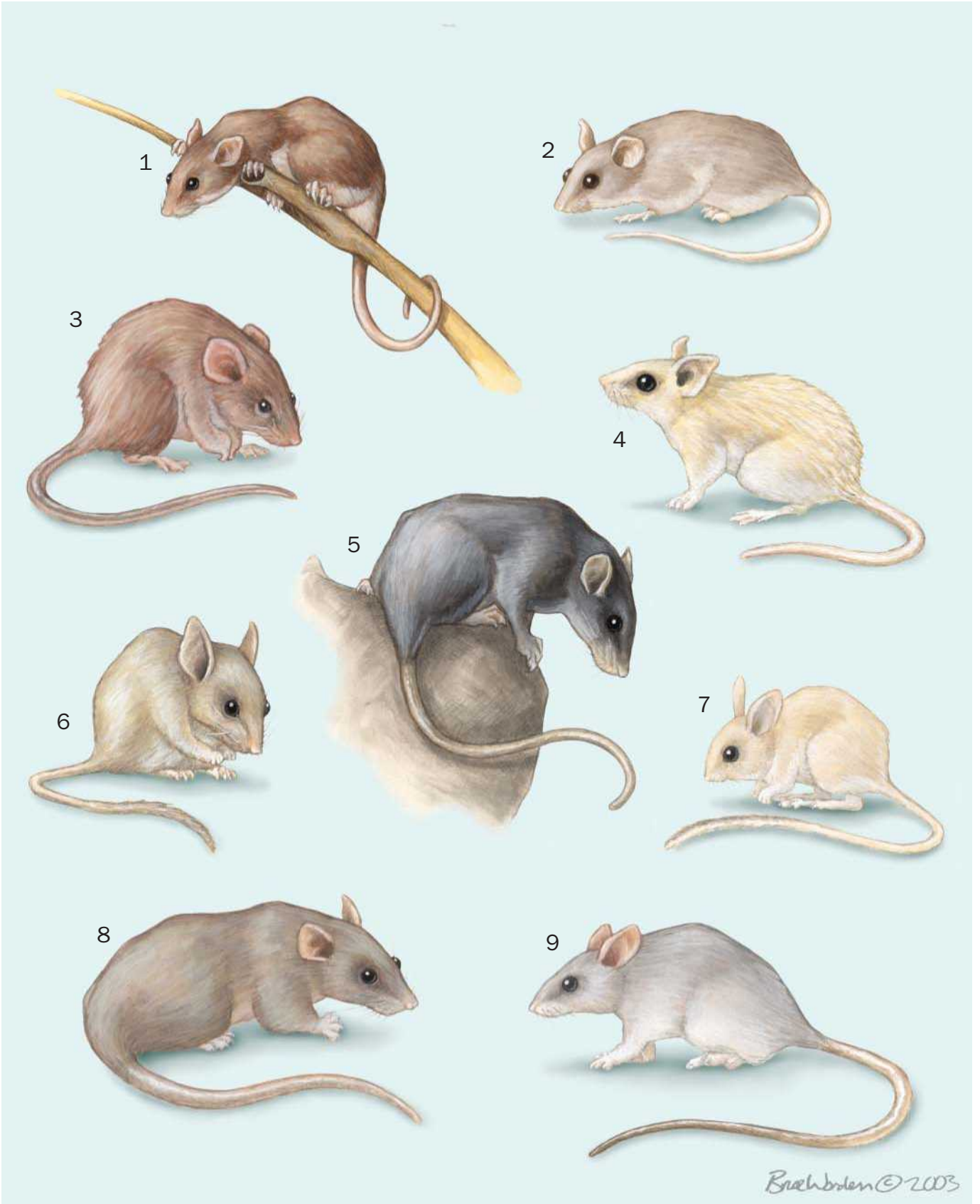
A western chestnut mouse (*Pseudomys nanus*) foraging on the ground in northern Australia. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A brown rat (*Rattus norvegicus*) contemplates a swim to shore. (Photo by Kim Taylor. Bruce Coleman, Inc. Reproduced by permission.)

few species that are in need of conservation action if they are to survive. Generalist species such as the black rat and brown rat are not imperiled, but certain rats, especially those endemic to island ecosystems, have faced habitat destruction by man and animals. A total of 18 species are on the verge of extinction and are classified as Critically Endangered by the IUCN.

Significance to humans

Old World rats have a long history with humans. Some are seen as cuddly pets, like the spiny rats (genus *Echimys*), while others are considered pests that eat stored food and are indirectly responsible for killing millions of people by spreading the black plague, typhus, and other maladies. However, these pestilent creatures have become invaluable to humans: the common lab rats and mice are descendents of the murines. These animals have been, and will continue to be, essential research animals, and many of the major discoveries in medical psychological and research are a direct result of the murines and their healthy ability to reproduce.



1. Harvest mouse (*Micromys minutus*); 2. House mouse (*Mus musculus*); 3. Creek rat (*Pelomys fallax*); 4. Egyptian spiny mouse (*Acomys cahirinus*); 5. Black rat (*Rattus rattus*); 6. Greater stick-nest rat (*Leporillus conditor*); 7. Australian jumping mouse (*Notomys alexis*); 8. Brown rat (*Rattus norvegicus*); 9. Tree rat (*Thallomys paedulcus*). (Illustration by Bruce Worden)

Species accounts

House mouse
Mus musculus

TAXONOMY
Mus musculus Linnaeus, 1758, Uppsala, Sweden.

OTHER COMMON NAMES
English: Mouse; French: Souris domestique; German: Hausmaus; Spanish: Ratón común.

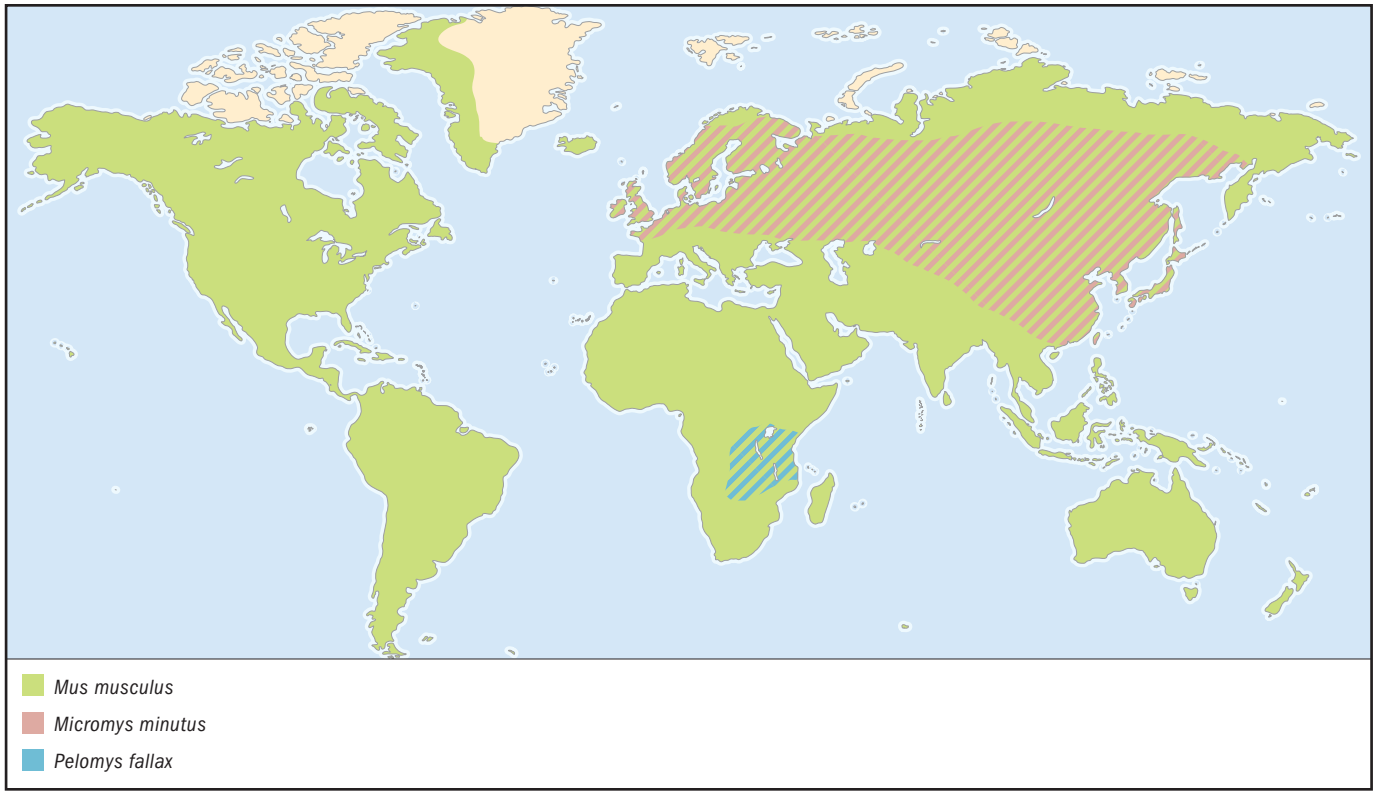
PHYSICAL CHARACTERISTICS
Body length 5.1–9 in (13–20 cm); tail 2.3–3.9 in (6–10 cm); weight 0.6–0.8 oz (18–23 g). A typical, stereotypical mouse, with grayish brown hair on its top, relatively big ears, and a dusky, scaly, nearly hairless tail; the fur on its bottom is only slightly lighter than the fur on its top, and it has ungrooved incisors.

DISTRIBUTION
Mice spread to Europe from Asia and appeared in the sixteenth century in the New World on the ships of explorers. In the seventeenth century, they appeared in northern North America and have proliferated since due to high reproductive capacity. House mouse subspecies can be found across the world.

HABITAT
Underground burrows, which some subspecies equip with storage rooms. Each mouse will make its own nest, but will share burrows with other individuals in the colony. Many house mice are co-habitants with humans, living beneath large appliances or inside of walls in human homes. Some house mice live temporarily in grain fields, which they migrate into, breed, feed, and leave when the field is plowed; in 1926–1927, house mice nearly took over the fields of California's Central Valley, living in them in a density of 202,000 mice per 2.5 acres (1 ha). Sometimes, they eat animal and plant pests in the fields, but they inevitably wind up in barns and silos where they tend to contaminate food. In general, the house mouse does not stray far from cover, with the best habitat offering copious amounts of food, water, and places to hide. Their home ranges vary, from 120 ft (36.5 m) for some indoor mice to more than 2 mi (3.2 km) for certain ones outside.

BEHAVIOR
A social species, it lives in groups with others of its kind, and aggressive males have hierarchical ranks and tend to dominate colonies. Each group lives in a territory bound by scent markers, and animals within the colony have their own nests. They will groom each other and display aggressive and submissive postures common in the species.

FEEDING ECOLOGY AND DIET
Eat up to 10% of their body weight daily, and feed up to 20 times each day. They consume grains, fruits, vegetables, meat, insects, and have been known to eat glue, paste, and even soap. If they eat moist food or a seed diet of 12% protein, they can live without water. The house mouse has been known to feed on caterpillars, flightless moths, and earthworms.



REPRODUCTIVE BIOLOGY
Polygynous. They reproduce copiously, and a biological contraceptive keeps their populations in check: females' ovaries become inoperative and the animals become infertile. They breed throughout the year, with females giving birth to litters of 3–12 offspring about 5–10 times annually. Gestation is about three weeks. When the young arrive, they are hairless and their eyes are closed. Young are weaned by 21 days, they begin to reproduce in their second month of life, and they can live, depending on predation, to be six years old. Most wild mice live about a year, while those in captivity generally live about two years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Over the centuries, they have spread disease and have been used by scientists to help cure disease. The albino lab mouse, the icon of scientific lab research, was bred from the house mouse and has been used in everything from cancer studies to stem cell research. At one point, cooked mouse was a folk remedy for flu-like symptoms, and house mice were considered a helper for conditions like baldness and constipation. They also carry a variety of germs and viruses that are dangerous to humans, including tularemia, bubonic plague, spotted fever, typhus, and Salmonella. ◆

Black rat
Rattus rattus

TAXONOMY
Rattus rattus (Linnaeus, 1758), Uppsala, Sweden.

OTHER COMMON NAMES
English: House rat, ship rat; French: Rat noir, rat commun; German: Hausratte; Spanish: Rata de los techos, rata común.

PHYSICAL CHARACTERISTICS
Body length 6.3–8.6 in (16–22 cm); tail 6.7–9.8 in (17–25 cm); weight (70–300 g). Its tail is always longer than its relatively slender body, and it has very large ears. Several subspecies exist, with various colorings: one has black fur on the top and gray fur on the bottom of the animal; one is agouti above and white below; and one is agouti above and slate below. The animal occasionally has a white spot on its chest.

DISTRIBUTION
Has spread throughout the world, though it is likely native to peninsular India.

HABITAT
Found around the world because they tended to become stowaways on ships, it is believed that more than 90% of rats on ships were black rats. They have been found in fruit plantations, palm trees, or bushes, either in conical nests or burrows. Black rats in the modern era tend to inhabit the upper stories of wooden buildings, leading some to speculate that the observed decline in parts of Europe may have to do with the gradual disappearance of wooden buildings. But they are a hardy species, and now take refuge in sewers or cellars or even in trees in parts of Europe.

BEHAVIOR
These mostly nocturnal rats have used their climbing skills to their advantage, by traveling along power lines and cables to spread from house to house. They are highly social creatures, which travel in packs, sleep in piles, and when they meet, they crawl beneath one another. They also can be territorial and display various postures similar to other animals in the genus, including the threat posture, a hunched, hair-bristled pose that aggressive individuals assume to display animosity.

FEEDING ECOLOGY AND DIET
Primarily vegetarians, feeding on fruit and seeds, but will eat insects and other invertebrates if necessary.

REPRODUCTIVE BIOLOGY
Polygamous. Breed year-round in conducive habitats, producing up to five litters per year. The females, which have 12 nipples, give birth to litters consisting of between 6–12 young, with the average litter size being eight. Young open their eyes at 15 days of age.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Have been closely tied with humans for thousands of years, and are vermin-infested creatures responsible for spreading various diseases to humans, including the bubonic plague that swept Europe in the fourteenth century and various other eras. The rats harbor fleas, which, after biting the rat, can transfer the bacteria responsible for the plague to humans. Black rats, especially those in tropical climates, still spread the bubonic plague. The animals are known to strip the bark off of trees and they tend to infiltrate food caches and eat anything people have tried to store, including grains, seeds, cereals, and fruits. The main predator of the black rat is the house cat. ◆

Tree rat
Thallomys paedulcus

TAXONOMY
Mus paedulcus (Sundevall, 1846), interior of Kaffirland, South Africa.

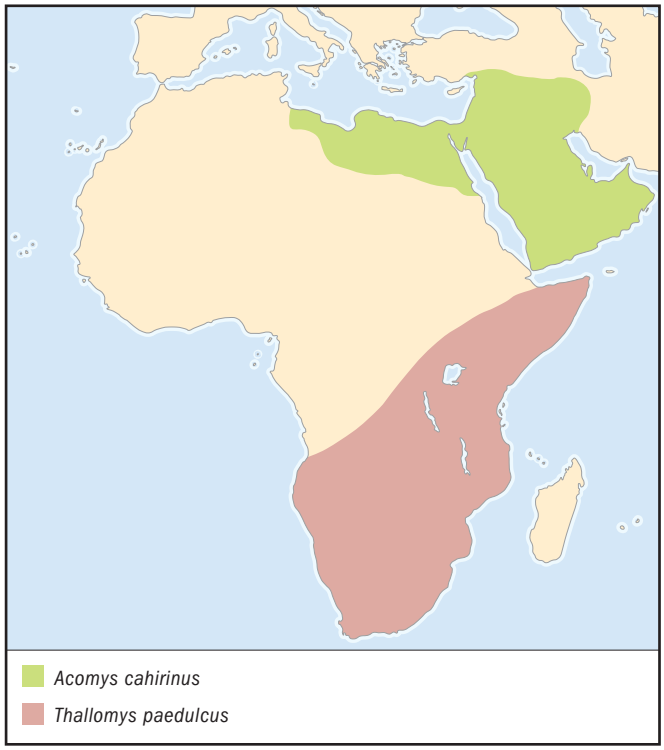
OTHER COMMON NAMES
English: Acacia rat.

PHYSICAL CHARACTERISTICS
Body length 4.7–6.4 in (12–16.3 cm); tail 5.1–8.2 in (13–21 cm); weight 2.2–3.5 oz (63–100 g). Has long fur that ranges from soft to coarse. Its coloring ranges from yellowish gray to gray to fawn on its upper parts, it has a brown tail, grayish or white feet and hands, red-tinted, nearly hairless ears, and a white belly. As a rule, tree rats have tails roughly 140% the length of their bodies. They have hind feet with strong claws and a well-developed fifth digit, which enables it to climb trees well.

DISTRIBUTION
Found in Africa, between western Somalia, southern Ethiopia, Angola, and South Africa.

HABITAT
Also known as the acacia rat, it makes its home in the acacia tree. It sometimes builds messy nests from twigs and grass in forks or in branches, and the nests are very obvious during winter, when the trees lose their leaves. On occasion, however, it will live in holes, beneath loose bark, and inside of hollow trunks. It uses the plant's thorns as protection from predators and can sometimes be found up to 13 ft (4 m) aboveground.

BEHAVIOR
Shy animals, and will rarely leave their shelters. They are known to weather major storms in their nests, even during floods. Sometimes, however, they will be forced to make their way back up the tree to home. Navigation is aided by scent markings, which they lay on branches. They are expert climbers and live in communities, usually in some sort of family arrangement, with a pair of adults and their offspring and other descendents.



FEEDING ECOLOGY AND DIET
Forage in their acacia trees, and are nocturnal. They eat acacia seeds and leaflets, but if necessary will eat insects and meat. They are able to survive without water.

REPRODUCTIVE BIOLOGY
Does not breed during the African winter, from April–July, which coincides with the lack of water during that time. When the rainy season hits, the females will produce litters of 2–5 young, however, and can breed about every 3.5 months. Observed climbing trees with their young attached to their nipples.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
An unsuitable lab rat because it does not breed well, and it is capable of spreading plague and other diseases. It is often infested with the stick tight flea (*Echidnophaga gallinacea*) as well as *Xemonpsylla brasiliensis*. It also harbors ticks and mites. ◆

Brown rat
Rattus norvegicus

TAXONOMY
Rattus norvegicus (Berkenhout, 1769), Great Britain.

OTHER COMMON NAMES
French: Rat d'égout, surmulot; German: Wanderratte; Spanish: Rata noruega.

PHYSICAL CHARACTERISTICS
Body length 8.6–10.2 in (22–26 cm); tail 7–8.6 in (18–22cm); weigh 7–14 oz (200–400 g); can reach 1.1 lb (0.5 kg) on rare occasions. Different than the black rat, in that the brown rat grows larger, has a thicker build, shorter ears and tail, and coarser fur. It is reddish brown to grayish brown on the back and often has darker sides. Fur on its belly is a light slate.

DISTRIBUTION
Believed to have originated in the northern regions of Asia, perhaps in China or Mongolia, and spread westward. It reached Western Europe in 1716 via a ship docking in Copenhagen; hit France in 1735, and then the shores of America in 1755, it spread to England by 1750. Ships and ocean vessels have spread the rodents to nearly all of the world's seaports.

HABITAT
Lives just about anywhere, but it does not fare well in hotter climates. It is well adapted for the colder climes, and the species has actually inhabited a whaling station in Antarctica. It lives in close proximity to humans, often found anywhere from burrows and cavities to sewers and cellars. In homes, brown rats, which are poor climbers, are at ground level. Although the species is not aquatic, it can swim well and has been spotted in rivers or ocean waters.

BEHAVIOR
Social animals that live and hunt in groups with close familial relationships, although they do allow non-related animals in on

occasion. They can form groups as large as 200 animals usually with a dominant male overseeing the social order. Dominance hierarchies are determined by size and weight rather than age.

FEEDING ECOLOGY AND DIET
Eats a variety of things, although it prefers meat. It can swim, dive, and catch fish. In the 1940s, a pack of 15,000 brown rats decimated the bird population of a sanctuary on the island of Nooderoog, eating eggs and catching seagulls, ducks, passerines, and other species. They have also been known to eat mice, chickens, ducks, and geese, and will gnaw on lambs and piglets. Rat packs have ganged up to kill cats and dogs that have been deployed to keep their populations in check. They have been known to feed on elephants, invalids, and newborn babies. They have also been described as cannibalistic. It will take its catch back to its den for feasting, and can live without water as long as it consumes sufficiently moist food.

REPRODUCTIVE BIOLOGY
They will breed throughout the year, although they peak in the spring and fall. When females go into heat, which lasts for six hours, a collection of males will mate with her. Each female will produce between 2–12 litters each year, with each litter consisting of 6–12—and as many as 22—young. The pups are born blind and pink, they open their eyes after about two weeks, and they leave the nest after three weeks. In a pack, the females give birth to their pups in the same room and assist each other in raising their young. The young are able to breed after 90 days. In optimal conditions, the animals are capable of producing up to 800 offspring per year, but this number is considerably lower in the wild.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Best known as carriers of the bubonic plague, and for centuries have eaten and contaminated human food. A descendent, the white albino lab rat, has proven invaluable to scientific research and discoveries in human health research. ◆

Harvest mouse
Micromys minutus

TAXONOMY
Micromys minutus (Pallas, 1771), Ulyanovsk, Russia.

OTHER COMMON NAMES
English: Old World harvest mouse; French: Souris des moissons; German: Eurasiatische zwergmaus; Spanish: Ratón espiguero.

PHYSICAL CHARACTERISTICS
One of the smallest rodents: length 2.1–2.9 in (5.5–7.5 cm); tail 1.9–2.7 in (5–7 cm); weight 0.17–0.24 oz (5–7 g). Brownish color with lighter tint on top, its fur grows longer in the winter, and it has small ears, broad feet, and no hair on the top of the end of its tail, which is semi-prehensile. Its feet are adapted to a climbing lifestyle.

DISTRIBUTION
Generally found where there is high grass, specifically in northern Eurasia. It is also distributed throughout Siberia, Korea, China, Great Britain, Japan, and Taiwan.

HABITAT
Lives in high grass, in areas such as pastures, grain fields, and rice fields. It can also be found in bamboo thickets. The animal builds nests, suspended between grass stems, about 3.2 ft (1 m) aboveground. The nests, which can take two days to build, are made from woven leaves, with the inner layer being finely shredded to provide a soft spot for young. The animals also nest in holes or, in some circumstances, on the ground during winter. They may also move into human structures like barns to avoid the cold.

BEHAVIOR
Nocturnal. The animals live in crowded conditions, but are not as social as black or brown rats. Captive males have been known to fight each other, and males and females only come together to build nests and to mate. Females chatter to attract mates and squeal during aggressive outbursts.

FEEDING ECOLOGY AND DIET
Forages in the grass fields primarily before dawn and just after dusk. It feeds on seeds and vegetables, but does on occasion take insects and eggs of small birds. Their unique climbing adaptations, like their semi-prehensile tail and their feet, allow them to climb through grass fields and counterbalance themselves as they move about.

REPRODUCTIVE BIOLOGY
Polygamous. Females reproduce during the warmer months, from May–September, and they are capable of giving birth several times in succession. Gestation time is about 2.5 weeks. Each litter ranges from one to 13 pups, with an average of five. They are blind and naked at birth, but within 10 days can see and have fur. They are weaned at two weeks and start to reproduce at one month of age. They are capable of living to nearly five years in captivity, but rarely live longer than six months in the wild.

CONSERVATION STATUS
Not threatened, but certain populations near farm machinery are in decline due to habitat loss.

SIGNIFICANCE TO HUMANS
No major significance. ◆

Creek rat
Pelomys fallax

TAXONOMY
Pelomys fallax (Peters, 1852), Zambezi River, Mozambique.

OTHER COMMON NAMES
English: Swamp rat, groove-toothed swamp rat.

PHYSICAL CHARACTERISTICS
Body length 3.9–8.2 in (10–21 cm); tail 3.9–7 in (10–18 cm); weight 3.9–7 oz (100–170 g). The animal has rusty brown fur on top and a dirty white on bottom; the fur is rough, but not spiny. There is also a variable dorsal line that runs to the tail that is especially prominent in young animals. The tail is haired, with white below and black on top, and its length varies with populations. It has grooved upper incisors, which is unusual in the murines.

DISTRIBUTION
Distributed throughout southern Africa, in northern Mozambique, northwestern Zimbabwe, northern Botswana, Zambia, the Congo, Malawi, Tanzania, southwestern Uganda, and southern Kenya.

HABITAT
Inhabit streams, rivers, riverbanks, and swamps, or anywhere there is substantial amounts of water and vegetation. They can

also live in grasslands, provided these areas border swamps or rivers.

BEHAVIOR
Generally diurnal and aquatic, it is an excellent swimmer and is said to be difficult to trap. It is often found sunbathing on matted reeds and grasses.

FEEDING ECOLOGY AND DIET
Vegetarian, and it eats reeds, grasses, seeds, and other plants and plant material.

REPRODUCTIVE BIOLOGY
Little is known, other than no predictable breeding season exists. The animals tend to reproduce in the warmer months, from August–April, and litter sizes ranger from 2–4 young. It is not determined if they live above or below ground: some believe they make shallow burrows, since their bodies have turned up in tilled fields, while others have surveyed habitat areas and have found no holes that could be burrows.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Not considered a pest and is eaten by tribes in Angola. ◆

Egyptian spiny mouse
Acomys cahirinus

TAXONOMY
Mus cahirinus (Desmarest, 1819), Cairo, Egypt.

OTHER COMMON NAMES
English: Spiny mouse; French: Rats épineux; German: Stachelmäuse; Spanish: Ratón espinoso.

PHYSICAL CHARACTERISTICS
Body length 2.7–6.7 in (7–17 cm); tail 1.9–4.7 in (5–12 cm); weight 1–2.4 oz (30–70 g). The defining feature is the gray-brown to sandy spiny hairs covering its back. The large-eared animal has a gray to white belly and a scaly, hairless tail.

DISTRIBUTION
Distributed through Africa and the Middle East. The Egyptian spiny mouse is widely distributed, but it was first discovered in Egypt.

HABITAT
Live in arid and semi-arid environments like deserts and savannahs. They live in and around rocks and can be found in burrows, which they presumably do not dig themselves, and have been found in trees even though they are terrestrial. They tend to avoid altitudes above 4,920 ft (1,500 m), and in some places, particularly in Egypt, the animals live with and off of humans.

BEHAVIOR
Different spiny mice species (there are eight) feed at different times and thus avoid competing with each other over the amount of insects they eat. Still, they are also known to be relatively social, and live in small groups with a dominant male who, when challenged, will fight. The animals are excellent jumpers and fairly active. Humans do keep them as pets.

FEEDING ECOLOGY AND DIET
Takes arthropods; certain species forage at different times in order to reduce interspecies competition. However, the animals also feed on snails as well as plant materials, including grains and grasses. Some species have begun to live in close proximity to humans, and are known to feed on grains and other foods that have been stored away.

REPRODUCTIVE BIOLOGY
Build a rudimentary nest in which to give birth. The gestation period is 5–6 weeks, or about two weeks longer than the mouse norm, and small litters of 1–5 young are born. They are capable of breeding again almost immediately after birth, and they have been known to string together over 12 litters in succession. What sets the spiny mouse apart from other mice is that the young are well developed at birth. They are born with hair that, although thin, is enough to allow the pups to thermoregulate, which means the mother does not need to give them much body warmth. Further, their eyes are either open at birth or within a day or two of birth. By day three, the young are exploring. Due to the social nature of the creatures, females help each other during the birthing process. In function, all the females in a group help raise the young.

CONSERVATION STATUS
Not threatened, although *Acomys cilicicus* is listed as Critically Endangered, while *Acomys minous* is Vulnerable.

SIGNIFICANCE TO HUMANS
Although the animals are known to spread typhus, they have recently received significant attention as a worthwhile pet. Apparently, people enjoy keeping the animals because their urine is relatively devoid of odor, and they are docile. The spiny mouse pet trade appeared in the mid 1980s. ◆

Greater stick-nest rat
Leporillus conditor

TAXONOMY
Leporillus conditor (Stuart, 1848), New South Wales, Australia.

OTHER COMMON NAMES
English: Stick nest rat, Australian stick nest rat, house-building rat, Franklin Island stick-nest rat, Franklin Island house-building rat; French: Léporilles; German: Zweignestratten.

PHYSICAL CHARACTERISTICS
Body length 6.7–10.2 in (17–26 cm); tail 5.7–7 in (14.5–18 cm); weight (180–450 g). It has large eyes and large ears, which are round and dark. Its tail has hair, with longer bristles at the end. Covered in soft fur that is light gray or white below and yellowish brown or gray on top.

DISTRIBUTION
Originally distributed throughout southern Australia, from the Shark Bay vicinity to western New South Wales. It was also found in Franklin Island and northwestern Victoria. Currently, due to declining numbers, it is found naturally occurring only on the East and West Franklin Islands. Captive-bred individuals have been successfully reintroduced on other islands, as well as only a few fenced-in areas in the original distribution range.

HABITAT
Inhabit arid regions with little or no fresh water. They use regional twigs and shrubs to build enormous nests that can reach over a 3.2 ft (1 m) high.

BEHAVIOR
The nocturnal rodents are sometimes known to build giant, towering nests called “wurlies” from sticks, twigs, and plant

stalks. They usually use a preexisting shrub, and sometimes, large rocks, to scaffold the nest; they proceed to weave sticks around the framing shrub. They occasionally incorporate stones into the nest, which serve to anchor it against winds, and they line the center with grasses. Up to 20 rats can live in the largest nests, which are filled with tunnels leading from the nest center to its outside. Younger generations inherit the nests and the task of tending to them. In fact, the nests have been shared with bandicoots, snakes, penguins, and shearwaters. Further, they are known to be docile and do not bite humans when handled. However, the social animals live in groups and display aggression towards unknown greater stick-nest rats.

FEEDING ECOLOGY AND DIET
Completely vegetarian, feeding on leaves and fruits and succulents for hydration.

REPRODUCTIVE BIOLOGY
When conditions are optimal, the animals can breed anytime of the year. Gestation lasts for about six weeks, litters consist of only several young weaned after a few months, and they reproduce only two or three times annually, making their reproductive rates far less than more successful murine rodents like black rats.

CONSERVATION STATUS
Recently upgraded from Endangered to Vulnerable due to recovery efforts; its relative, the lesser stick-nest rat, is assumed to be Extinct.

SIGNIFICANCE TO HUMANS
None, but theirs numbers have disappeared in part because of humans. Introduced animals like sheep have overgrazed and subsequently destroyed much of their preferred shrubland habitat. Scientists have been trying to repopulate various offshore Australian islands with the rats after having eradicated feral cats and other pests that could prey on the animals. Over the past few years, a successful breeding program in captivity has produced a large number of rats used to repopulate Australia, and the total greater stick-nest rat population has increased fivefold to over 5,000 individuals. ◆

Australian jumping mouse
Notomys alexis

TAXONOMY
Notomys alexis (Thomas, 1922), Northern Territory, Australia.

OTHER COMMON NAMES
English: Australian hopping mouse, jerboa mouse; French: Souris sauteuses d'Australie; German: Australische Hüpfmäuse; Spanish: Ratón saltador.

PHYSICAL CHARACTERISTICS
Body length 3.9–5.9 in (10–15 cm); tail 3.5–8.2 in (9–21 cm); weight 0.7–1.7 oz (20–50 g). Their upper coloring is light sandy brown to gray. Their bellies are white to light gray. They have long tails and large ears, but their distinguishing feature is the narrow, large hind feet that enable them to effortlessly jump higher than 3.2 ft (1 m), and relatively small forefeet. Their tails are long and finely coated and, like the rest of the genus, have sebaceous glands, which are utilized for territorial marking.

DISTRIBUTION
Endemic to and spread throughout central Australia's deserts arid landscapes.

HABITAT
Live in dunes and grasslands and dig burrows that can vary in complexity.

BEHAVIOR
Nocturnal social creatures, they involve themselves in grooming, huddling, walking over each other, crawling under each other, and sleeping together. When they fight, they not only rush at each other and punch each other with their fore legs, but they also leap at each other. The hopping mice generally walk on all fours, but in cases of haste and aggression will leap with their hind legs. They also live in groups with a high maximum density.

FEEDING ECOLOGY AND DIET
Eat berries and other vegetation, but they can live without water provided they receive sufficient hydration from their regular diet. They have extremely concentrated urine and avoid dehydration by staying underground during periods of intense heat.

REPRODUCTIVE BIOLOGY
A month-long gestation period leads to a litter of about three pups. They are born naked and blind, but open their eyes by week three and are weaned after five weeks and are ready to reproduce at three months. Females carry their young by their nipples. Their reproductive rates vary widely, depending on ecological conditions.

CONSERVATION STATUS
The dusky hopping mouse, *N. fuscus*, is listed as Vulnerable.

SIGNIFICANCE TO HUMANS
There is no major significance to humans, but they have become popular pets. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Golden spiny mouse *Acomys russatus* German: Goldene Stachelmaus	Light golden brown, underparts are white. Pelage is bristly, the ends of the spines are black or gray. White patch below each eye and ear. Head and body length 2.7–5.9 in (7–15 cm), tail length 1.5–5.1 in (4–13 cm), weight 0.5–2.8 oz (15–80 g).	Arid regions consisting of deserts and savannas dominated by rocky crevices. Breeds throughout the year.	Eastern Egypt, Sinai, Jordan, Israel, and Saudi Arabia.	Animal matter but also includes snails, insects, seeds, and other plant material.	Not threatened
Cyprus spiny mouse *Acomys nesiotes* German: Zypern-Stachelmaus	Predominantly golden brown. Long, drawn-out pointed face that tapers out into a pointed nose. High-standing funnel ears. Head and body length 3.5–5.1 in (9–13 cm), tail length 3.5–4.7 in (9–12 cm).	Deserts, savanna, and dry steppes with stony areas. Build nests; good runners and climbers.	Cyprus.	Mainly snails and insects.	Data Deficient
Striped field mouse *Apodemus agrarius* German: Brandmaus	Yellow-brown with black, mid-dorsal stripe. Head and body length 3.7–4.5 in (9.4–11.6 cm), tail length 0.7–8 in (1.9–2.1 cm).	Grassy fields, cultivated areas, paddies, woodlands, and forests. Breeding season throughout the year. Females can produce up to six litters per year, each of up to six young.	Central Europe to Lake Baikal, south to Thrace, Caucasus, and Tien Shan Mountains; Amur River through Korea to eastern Xizang and eastern Yunnan, western Sichuan, Fujiau, and Taiwan, China; and Quelpart Island, Korea.	Roots, grains, seeds, berries, nuts, and insects.	Not threatened
Long-tailed field mouse *Apodemus sylvaticus* German: Waldmaus; Spanish: Ratolí de rostoll	Grayish buff, grayish brown, brown with yellow or red, mixed with pale sand color. Underparts are white or light gray. Feet are white, tail not prehensile. Head and body length 2.3–5.9 in (6–15 cm), tail length 2.7–5.7 in (7–14.5 cm).	Grassy fields, cultivated areas, woodlands and forests. Produces up to four litters a year, each with four to seven young. Nocturnal.	Europe north to Scandinavia and east to northwestern Ukraine and northern Belarus, and on many islands, as well as mountains of northern Africa from Atlas Mountains in Morocco east across Algiers to Tunisia.	Roots, grains, seeds, berries, nuts, grasses, grain kernels, fruits, and insects.	Not threatened
African grass rat *Arvicanthis niloticus*	Stout body, short legs. Coloration ranges from buff to olive brown to dark gray-brown. May have dorsal stripe. Under parts are lighter. Weight 1.7–4.2 oz (50–120 g).	Savanna grasslands. Five to six young per litter. Gregarious, live in burrow systems.	Most of Africa.	Grains, seeds, grass shoots, as well as insects and fruits.	Not threatened
Golden-bellied water rat *Hydromys chrysogaster* German: Australische Schwimmratte	Webbed, broad front and hind feet. Blunt muzzle with whiskers, flat head with small ears and eyes. Thick, white-tipped tail.	Found near permanent fresh water. Dependent on water for food. Breeds in spring and summer, lives alone or in pairs in burrow system. Diurnal, sedentary, and generally solitary.	Australia, Tasmania, and New Guinea.	Crustaceans, mollusks, fish, ducks, poultry, frogs, turtles, bats, house mice, and aquatic insects.	Not threatened
Short-tailed bandicoot rat *Nesokia indica*	Dull brown or grayish brown on back, underparts are light gray. Pelage ranges from dense and coarse to long and smooth. Head and body length 5.5–8.4 in (14–21.5 cm), tail length 3.4–5 in (8.8–12.9 cm).	Moist areas or along streams and canals, as well as deserts, steppes, cultivated areas, and forests. Nocturnal and fossorial. Make extensive burrows with several chambers. A single rat occupies each burrow.	Egypt to Sinkiang and northern India.	Leaves and roots of lawn grass.	Not threatened
Dusky hopping mouse *Notomys fuscus* French: Souris sauteuse; Spanish: Ratones saltadores de Australia	Long tail, large ears, and dark eyes. Upperparts range from pale sandy brown to yellowish brown to ashy brown or grayish. Underparts are white. Head and body length 3.5–7 in (9.1–17.7 cm), tail length 4.9–8.8 in (12.5–22.5 cm).	Sand dunes, grasslands, tree and shrub heaths, and lightly wooded areas. Build nests; glands used for marking territories and individuals.	Australia.	Seeds, berries, leaves, green plants, and occasionally insects.	Vulnerable

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Long-tailed mouse *Pseudomys higginsi*	Grayish brown above, underparts are white. Bicolor tail, tipped with white. Nostril is pink and naked. Head and body length 5 in (13 cm), weight 2.1–2.5 oz (60–70 g).	Areas with high annual rainfall, such as rainforests, wet sclerophyll forests, wet scrub, and eucalyptus scrub. Breeding season from November to April. One to two litters in a season, each with a litter size of three to four offspring. Nocturnal, motile, and sedentary.	Australia and Tasmania.	Monocotyledons, subterranean fungi, fruits of shrubs, and invertebrates.	Not threatened
False water rat *Xeromys myoides* French: Faux rat d'eau; Spanish: Rata bastarda de agua	Long, flat head with small eyes and short, rounded ears. Coloration is dark gray, white underside. Coat is water resistant. Tail is scaled. Head and body length 4.5–10.6 in (11.5–27 cm), tail length 3.3–3.9 in (8.5–10 cm), weight 1.4–2.1 oz (40–60 g).	Coastal swamps with mangrove forest. Nocturnal. Litter size is small, two offspring. Little is known of reproductive patterns.	Northern Territory and Melville Island off the coast of Northern Territory, Australia.	Small crustaceans such as crabs, marine polyclads, marine pulmonates, shellfish, and worms.	Vulnerable

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American Zoo and Aquarium Association Behavioral Advisory Group's ethograms.org.
Web site: <http://www.ethograms.org>

The Department for Environment and Heritage of Southern Australia. GPO Box 1047, Adelaide, South Australia 5001 Australia. Phone: (8) 8204-9000. Web site: <http://www.environment.sa.gov.au/>

The Department of Conservation and Land Management for Western Australia. Hackett Drive, Crawley, Western Australia 6009 Australia. Phone: (8) 9442-0300. Fax: (8) 9386-1578. Web site: <http://www.calm.wa.gov.au/>

IUCN—The World Conservation Union. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41 (22) 999 0000. Fax: +41 (22) 999 0002. E-mail: mail@hq.iucn.org Web site: <http://www.iucn.org>

The National Wildlife Federation. 1045 Sansome St., Suite 304, San Francisco, CA 94111 USA. Phone: (415) 732-7000. Fax: (415) 732-7007. Web site: <http://www.nwf.org/> and <http://www.enature.com>

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Nathan S. Welton

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Rats, mice, and relatives IV

South American rats and mice (Sigmodontinae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Muridae
Subfamily Sigmodontinae

Thumbnail description
Small- to medium-sized mice and rats; in general brownish or blackish upper pelage and grayish or whitish underparts; tail usually thinly haired; molars with two rows of cusps

Size
Head and body length: 2.4–11.4 in (61–290 mm); tail length 1–6.3 in (30–160 mm); weight: 0.4–18 oz (12–510 g).

Number of genera, species
71 genera; 373 species

Habitat
All habitats (e.g., dry deserts, wet tropical forests, wetlands, savannas, steppes, temperate woodlands, high altitude grasslands, salt flats, scrublands) found in their distribution range up to 17,000 ft (5,200 m) above sea level

Conservation status
Extinct: 6 species; Critically Endangered: 8 species; Endangered: 24 species; Vulnerable: 23 species; Lower Risk/Near Threatened: 36 species; Data Deficient: 3 species

Distribution
Endemic to the New World; living forms range from Tierra del Fuego, the southernmost part of South America, up to southern United States; also distributed on some islands adjacent to the continent as well as in the oceanic Galápagos archipelago

Evolution and systematics

Over the last several decades, the contents and limits of the subfamily Sigmodontinae have been a center of much debate. However, as of 2001, an agreement has been reached in defining Sigmodontinae to only encompass the predominantly South American complex-penised mice and rats, leaving out of the subfamily those predominantly North American simple-penised mice and rats (e.g., the wood rats *Neotoma*, the grasshopper mice *Onychomys*, and deer mice *Peromyscus*). Now defined, the subfamily Sigmodontinae includes 71 living genera and 373 species. Remarkably, these numbers keep growing as new genera and species are being discovered and identified from both field and museum based work. New sigmodontines are being discovered even in areas that are presumably well known from a mammalogical point of view. For example, *Oxymycterus josei* was described in 2002 for the first time from areas near the southern coast of Uruguay. These areas have been frequently visited by mammalogists since the early nineteenth century. Sigmodontines include several familiar rats and mice, such as the cotton rats (*Sigmodon*), and the rice rats (*Oryzomys*), but the subfamily also encompasses an enormously diverse collection of other rodents practically unknown to most people.

Traditionally, sigmodontine genera have been arranged into different groups, some have been formalized as tribes in zoological classifications. Depending on the relative weight that is given to different trenchant characters, the number and content of sigmodontine groups vary from author to author. In the early 1990s an almost universal adoption of a phylogenetic approach to delimit these groups caused major reconsiderations on the identity of the groups as well as on their limits and contents. These studies have promoted: the recognition of a previously unnoted group (the abrothricines, mostly confined to the central and south Andes); the subsuming of some main groups within others (e.g., scapteromyines into akodontines); the corroboration of the distinction of some groups (e.g., reithrodontines, wiedomyines); and called into question the nature of at least one group (the thomasomyines) and the composition of most groups. As of 2003, nine main sigmodontine groups are recognized (Smith and Patton, 1999).

Plains harvest mice (*Reithrodontomys montanus*). (Photo by Stephen Dalton/Photo Researchers, Inc. Reproduced by permission.)

Diversity is not evenly distributed among them. The akodontines, oryzomyines, and phyllotines account for more than half of extant genera. The abrotrichines, the ichthyomyines, the reithrodontines, the sigmodontines, the thomasomyines, and the wiedomyines are groups of one to five extant genera each. In addition, there are several extant genera whose phylogenetic relationships are not clear; these genera cannot be assigned with certainty to any monophyletic group less inclusive than the subfamily. In formal classifications these genera (e.g., *Abrawayaomys*, *Delomys*, *Irenomys*, *Juliomys*, *Phaenomys*, *Punomys*, *Rhagomys*, *Wilfredomys*) are generally considered as *incertae sedis* (of uncertain taxonomic position). Phylogenetic relationships among sigmodontine main groups or tribes are mostly unclear. The only point that appears well corroborated is that the Sigmodontini, composed only of one extant genera (*Sigmodon*), is the sister group of all remaining sigmodontines.

Although extensive, past sigmodontine diversity is not as great as the present (Pardiñas et al. in press). The oldest South American known sigmodontine comes from the latest Miocene sediments of the Argentinean province of La Pampa. Sigmodontines are rare in early Pliocene beds and become more abundant in late Pleistocene sediments. While, more than a half of extant genera are also recorded as fossils (many from Holocene beds), only seven known genera have become extinct during geologic times. In addition, three genera presumably became extinct in historic times. The sigmodontine nature of some North American fossils, such as *Prosigmodon*, *Bensonomys*, and *Symmetrodontomys*, is questionable and deserves further scrutiny.

The understanding of sigmodontine evolutionary history has proved to be a complex task. All students agree on the fact that in spite of most sigmodontines being endemic to South America, the immediate ancestor of the group did not originate in South America. In other words, at some point in history sigmodontines or their immediate ancestor invaded South America. The basis for this agreement lies on the fact that no potential ancestor has yet been discovered in South America. The fossil record indicates that this invasion was as late as Late Miocene. As of 2003, two main aspects of sigmodontine historical biogeography remain unresolved. These are: 1) whether the geographic origin of the stock that gave rise to the sigmodontines was in the Old World or in Central-North America; and 2) the geographic placement of the basal sigmodontine radiation; in other words, how many sigmodontine lines invaded South America? Evidence at hand tends to indicate that the sigmodontine ancestor inhabited Central-North America. However, the numbers of sigmodontine lines that invaded South America remains to be solved. Therefore, it is not clear if North American sigmodontine are direct descendents of the first sigmodontines or if they represent secondary invasions to North America of lines first differentiated in South America.

Physical characteristics

Although most sigmodontines are typical mice and rats, the group exhibits several deviations from this morphotype.

A cactus mouse (*Peromyscus eremicus*) in the California desert, USA. (Photo by Anthony Mercieca/Photo Researchers, Inc. Reproduced by permission.)

A deer mouse (*Peromyscus maniculatus*) standing on lichen. (Photo by Maslowski/Photo Researchers, Inc. Reproduced by permission.)

Examples of these departures are the shrew mouse *Blarinomys*, the mole mouse *Geoxus*, the chinchilla mouse *Chinchillula*, and the rabbit rat *Reithrodon*. Sigmodontines are small. They range from about 0.4 to about 14.1 oz (12 to about 400 g). The largest living form, *Kunsia tomentosus*, does not surpass 11.8 in (300 mm) of head and body length. External ears vary from almost absent or much reduced (e.g., the aquatic rat *Anotomys* and the long-clawed mole mouse *Geoxus*) to moderately large (e.g., the long-eared mice of the genus *Phyllotis*) or large (e.g., the rabbit rats of the genus *Reithrodon*). Climbing, arboreal and scansorial species tend to have tails longer than head and body length; tail approximately equal to combined head and body is characteristic of the more generalized terrestrial sigmodontines; while the tail of fossorial species is usually less than half of head and body length. The tail is usually thinly haired, but in some sigmodontines ends in a penciled tip (e.g., *Andalgalomys*). Most sigmodontines have a brownish or blackish upper pelage and grayish or whitish underparts. However, *Chinchillula* is noticeable in this regard; its upper parts are buffy or grayish with black lines, the underparts are white, and the white hips and white rump banded with black. Sigmodontine fur may be velvety, soft, woolly, long, thick, harsh, composed of underfur and guard hairs. *Abrawayaomys*, *Neacomys*, and *Scolomys* have some hairs modified into spines. Sigmodontine feet also show variation. In general, feet are relatively small, but those of fossorial forms like the giant rat *Kunsia* are robust and extremely long clawed; those of swimmers like the marsh rat *Lundomys* are large and webbed, and those of climbers (e.g., *Rhipidomys*) are broad and strongly grasping. Finally, the hindfoot of the arboreal mouse *Rhagomys* is remarkable among sigmodontine because the fifth toe is long, and the big toe presents a nail instead of a claw.

As in all rodents, one upper and one lower incisor (sometimes grooved) are found on each side of the jaw, and canines and premolars are never present. After an empty space, called diastema, following the incisor, three cheek teeth, or molars, occur on each side. The total number of teeth is 16. The exception to this pattern is the ichthyomyine *Neusticomys oyapocki* that has two molars per upper and lower jaw. There is a large variation in molar size, morphology, and number of roots. For example, Reig in 1977 nominated more than 30 cusps, cuspules, styles, lophs, folds, and islands, in an idealized sigmodontine molar. Molar crown height seems to be related to diet. In general, sigmodontines that feed on animals, seeds, fruits, or fungus have low-crowned molars (brachydont) that retain complex occlusal surface. High-crowned molars (hypsodont), which extend far above the gumline, are usually present in those sigmodontines, as *Andinomys* and *Reithrodon*, which feed on abrasive vegetation (e.g., grass). Usually, the hypsodont condition is associated with a simplification of the occlusal surface, connection of lophs on each tooth side to form lamina, planation of the crown, and an increase in the number of tooth roots.

With a few well recognized exceptions, sigmodontines have complex penises. A complex penis has two lateral horns on the cartilagenous distal baculum, making it appear as trident shaped.

Distribution

Sigmodontines are a New World group; currently they range from Tierra del Fuego, the southernmost part of South America, north to the southern United States. They are also distributed on some islands adjacent to the continent, as well as in some oceanic islands as the Galápagos archipelago. However, most of extant sigmodontine diversity is confined to the South American continent. In fact, 61 living genera are endemic to South America and the neighboring islands such as Trinidad. Three genera: *Oligoryzomys*, *Oryzomys*, and *Sig-*

The saltmarsh harvest mouse (*Reithrodontomys raviventris*) is active primarily at night, but may be seen during the day. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Brush mice (*Peromyscus boylii*) are omnivorous. (Photo by Anthony Mercieca/Photo Researchers. Reproduced by permission.)

modon inhabit areas of the three Americas. Seven genera are distributed in Central and South America, although three of these, *Ichthyomys*, *Oecomys*, and *Rhipidomys*, have only Panama as their extra South American part of the range. The water mouse *Rheomys* is the only mainland genus not present in South America. In addition, the living genus *Nesoryzomys* is endemic to the Galápagos Islands. Finally, three genera that presumably became extinct in historic time: *Megalomys*, *Megaoryzomys*, and *Noronhomys* were endemic, respectively, to the Lesser Antillas, and the oceanic Galápagos and Fernando de Noronha Islands. However, this last statement may change since an undescribed fossil from mainland Argentina may be assignable to *Noronhomys* (Pardiñas, pers. com.).

The past distribution of the subfamily as a whole roughly matches current distribution. Lack of fossil records from some areas (e.g., most of the Amazon basin or the highland Puna) is probably due to the lack of adequate sediment beds and/or insufficient exploratory work. However, it is worth noting that the distributions of several genera, such as *Bibimys*, *Kunsia*, and *Pseudoryzomys*, have markedly shifted in a few thousand or even hundred years (Pardiñas, 1999).

It has to be emphasized that much still remains to be learned about sigmodontine distribution, as is shown by the results of field work conducted in the late twentieth and early twenty-first centuries, which prompted extensions of the sigmodontine known distribution. For example, the genus *Rhagomys*, previously known from the Atlantic coastal Brazilian state of Rio de Janeiro, has been reported from the eastern slopes of the Peruvian Andes (Luna and Patterson, 2003). A less spectacular example, although still remarkable was reported by Emmons in 1999, who collected in eastern Bolivia specimens of *Juscelinomys*, a genus previously considered to be restricted to the Brazilian Federal District.

Habitat

Sigmodontines occupy almost all ecosystems found through their distributional range, including dry deserts, wet tropical forests, wetlands, savannas, steppes, temperate woodlands, high altitude grasslands, salt flats, and scrublands. Some species, such as *Nectomys squamipes*, are semiaquatic inhabitants of forests, and others, like *Scapteromys tumidus*, are semiaquatic inhabitants of grasslands. *Notiomys edwardsii* and *Kunsia tomentosus* are largely fossorial species that live in arid steppes and savanna forest, respectively. *Thomasomys aureus* and *Irenomys tarsalis* are arboreal species that live in cloud forest and temperate forest, respectively.

Some sigmodontines inhabit more than one habitat type. For example, the rabbit rat *Reithrodon auritus* is found, among others, in steppes, bunchgrass prairies, dense grasslands, beech forests, and sparse shrub lands. Similarly, Azara's field mouse *Akodon azarae* lives in several types of open environments, including dry and humid Chaco, pampas grasslands, and agrosystems. Meanwhile, other sigmodontines appear restricted to specific habitat types. For instance, the poorly known *Punomys lemminus* occurs only in the treeless Puna of Peru between 14,600 and 17,000 ft (4,450–5,200 m) of elevation.

While some sigmodontines appear to be highly sensitive to habitat destruction (e.g., *Anotomys leander* and *Pearsonomys annectens*), others appear to adapt well to human disturbed habitats. The latter is the case of the field mouse *Akodon azarae*, which successfully invaded agroecosystems. Similarly, the forest mouse *Akodon montensis* is collected in abundance in secondary grown forests of Argentina, Brazil, and Paraguay. In addition, some sigmodontines are commensal with humans. For example, *Akodon reigi* has been collected inside rural houses in Uruguay.

Microhabitat selection has been studied in relatively few sigmodontines. It was documented for three sympatric sigmodontines from the Patagonian steppes. *Abrothrix longipilis*

A deer mouse (*Peromyscus maniculatus*) mother and five-day-old litter. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A northern grasshopper mouse (*Onychomys leucogaster*) eating a little pocket mouse (*Perognathus longimembris*) that it killed. It is the only carnivorous North American rodent. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

prefers the steppe's bushy patches, *Eligmodontia morgani* prefers the bunchgrass patches, and *Abrothrix olivaceus* evenly distributes in both microenvironments. Similarly, in the humid forest where it lives, the water rat *Nectomys squamipes*, prefers places close (< 10 m) to water courses with tree ferns and exposed tree roots.

Bilenca and Kravetz (1999) studied in agroecosystems of central Argentina the seasonal changes in microhabitat use by the field mouse *Akodon azarae* and the vesper mouse *Calomys laucha*. They showed that the structure of this sigmodontine community is highly influenced by seasonal changes in habitat structure and rodent abundance. In summer, both species were equally distributed between the mature crop fields and their surrounding weedy borders. In the crop fields both species preferred covered microhabitats and at the borders they did not select microhabitats. In contrast, in winter there was sharp habitat segregation. The vesper mouse was numerically dominant in post-harvest crop fields and the field mouse was more abundant in borders. In addition, there were clear differences in microhabitat selection at the borders, *A. azarae* occupying the more covered microhabitats and *C. laucha* the less covered ones.

Field ecology studies are scarce in sigmodontine literature; therefore, basic information is lacking for most species. A field study of the water rat *Nectomys squamipes* shows that its home range covers 0.5–3.9 acres (0.2–1.6 ha). Similarly, Gentille and collaborators (1997) showed that the size of the home range of the forest mouse *Akodon cursor* is seasonally constant, and that on average covers 0.91 and 0.47 acres (0.37 and 0.19 ha). for males and females respectively. Females of *A. cursor* are territorial while males are not. With males having a larger territory, they have contact with several females, while females would defend food and nesting resources. Interestingly, the size of the home range of *A. cursor* is neither affected by individual body size nor by population densities. Therefore, the overlap of different individuals would increase at higher population densities. Similarly, males of *Abrothrix olivaceus*, *Akodon azarae*, and *Necromys lasiurus* have larger home ranges than females. On the other hand, males and females of *Eligmodontia morgani* have home ranges of similar size.

Behavior

Field and laboratory observations of sigmodontine behavior are scarce, and limited to a small number of species. Therefore, no generalizations can be made.

Not much is known about sigmodontine social behavior; most reports are of anecdotic fashion. *Wiedomys pyrrhorhinos* may be gregarious, since eight adults and 13 young were found in one termite nest. Similarly, Darwin reported six specimens of *Calomys laucha* were discovered in one burrow. The social and gregarious habits of *Phyllotis sublimis* were described by Pearson (1951).

From the patterns of trapping, it can be inferred that sigmodontines are mostly nocturnal. For example, the water rat *Nectomys squamipes* is primarily active just after sunset. Similarly, the rice rat *Oryzomys intermedius* remains sheltered during the day and becomes active at night. Several species, such as the long-nosed mouse *Oxymycterus nasutus* and the long-clawed mole mouse *Geoxus valdivianus*, are active both diurnally and nocturnally. Finally, other sigmodontines, such as the long-nosed mouse *Auliscomys boliviensis*, are primarily diurnal.

Sigmodontines use nests to shelter and to raise the young. *Nectomys squamipes* and *Oryzomys intermedius* use dry leaves and grasses to build nests that are egg-shaped, of about 6 in long and 4 in wide (15 and 10 cm), and lack an obvious entrance. Nests are usually placed at the end of tunnels of 4.0–12 in (10–30 cm) long inside or under fallen logs. Less com-

A white-footed mouse (*Peromyscus leucopus*) in Ohio, USA. (Photo by Gary Meszaros/Photo Researchers, Inc. Reproduced by permission.)

White-footed mouse (*Peromyscus leucopus*) young in nest. (Photo by Maslowski/Photo Researchers, Inc. Reproduced by permission.)

monly, some nests are located between rocks or exposed tree roots. *N. squamipes* nests closer to water courses than *O. intermedius*. Other species, such as *Thomasomys aureus*, build their nests in trees. At the same time, other sigmodontines take advantage of bird nests. This is the case of the red-nosed tree rat *Wilfredomys oenax* that in Uruguay uses abandoned nests of both the firewood-gatherer (*Anumbius annumbi*) and the golden-winged cacique (*Cacicus chrysopterus*) as diurnal shelter.

There are limited data on sigmodontine dispersal. Disperser individuals of *Akodon azarae* are in general smaller than those that do not disperse, but they neither differ with respect to sex nor with reproductive condition. The highest dispersal rate occurs in autumn. The water rat *Nectomys squamipes* only makes short movements and exhibits limited migration.

Several sigmodontines including, among others, the rice rats *Oryzomys couesi* and *O. palustris*, the water rats of the genera *Amphinectomys*, *Lundomys*, *Holochilus*, and *Nectomys*, the marsh rats of the genus *Scapteromys*, and the ichthyomyines are excellent swimmers and divers. By swimming and diving these sigmodontines are able to escape predators and to exploit surface and underwater resources. Other species, such as *Sigmodon hispidus*, are less skilled swimmers, swimming only on the water surface (Cook et al., 2001).

Grooming behavior has been studied in *Nectomys squamipes*. The water rat licks most reachable body parts, and grooms its face by circular movements of the forepaws.

Little is known on sigmodontine communication. High-pitched vocalizations have been reported, mostly in anecdotic terms, for a few sigmodontines species, including *Scapteromys aquaticus*, *S. tumidus*, and *Nectomys squamipes*. Dominance status in the hispid cotton rat *Sigmodon hispidus* is communicated by urinary and fecal odors.

Feeding ecology and diet

Most of the information available on sigmodontine diet comes from analysis of stomach contents (in which, usually a small number of individuals were studied) and not from field observation or experimental studies. As expected from such a diverse group, sigmodontines show a large range of diets. Sigmodontines are omnivorous (e.g., *Zygodontomys brevicauda*), grassivorous (e.g., *Reithrodon typicus*), primarily frugivorous (e.g., *Thomasomys aureus*), primarily granivorous (e.g., *Eligmodontia typus*), and primarily animalivorous (e.g., *Oxymycterus nasutus*, *Rheomys mexicanus*); still others consume large amounts of fungus (e.g., *Chelemys macronyx*).

Mice and rats of the ichthyomyine tribe are among the most distinctive sigmodontines with regard to their diet because they feed on aquatic organisms (Voss, 1988). In much of the scientific literature ichthyomyines are referred to as the fish-eating sigmodontines. However, though ichthyomyines feed on fishes, they represent a relatively uncommon item of the ichthyomyine diet. Ichthyomyines primarily feed on arthropods, of which the vast majority is part of the stream benthic fauna, including crabs, amphipods, and several insect orders (larvae, ninphae, and adults). Other less common ichthyomyine food items are tadpoles and salamanders. *Ichthyomys* exhibits feeding plasticity: in the lowlands, crabs are an important food item, while in the highlands, where crabs are absent, it may be largely insectivorous.

After entering the water *Ichthyomys pittieri* uses its whiskers to explore the substrate, searching for, and identifying live prey. The rat attacks its prey when they move after being touched. Small prey (up to 0.8 in long; 20 cm) are seized with the forepaws and are usually eaten immediately, while sitting on its hindquarters in the shallow water. Larger prey are pinned to the bottom with forepaws, bitten repeatedly until moribund, and then carried out of the water where they are consumed.

The feeding behavior of the omnivorous water rat *Nectomys squamipes* was studied by observations of captive animals (Ernest and Mares, 1986). The rat picks up immobile items (e.g., leaves) with the incisors, then sits back on its haunches and holds the food in the forepaws, to bite and chew the food. Mobile items (e.g., cockroaches, Blattidae) are caught on the ground by jumping on it with the forepaws. Flying insects are caught close to the ground and eaten head first, and entirely. The water rat takes mobile prey in the water (e.g., tadpoles) with the forepaws. After the prey is secured, it is eaten like the immobile items.

Combining analyses of stomach contents and cafeteria tests, Castellarini and collaborators (1998) established that the vesper mouse *Calomys venustus* is omnivorous, and that it shows a tendency to folivory in spring and autumn and to granivory in summer. *C. venustus* does not consume the leaves that are abundant in the habitat, or consume them in low proportions, rather, it shows a high preference for seed consumption under conditions of equal food availability.

Reproductive biology

Information on sigmodontine reproduction comes primarily from observations recorded during specimen collections (e.g., external measurements, testes position, presence of vaginal closure membranes, and number of embryos). From these observations, inferences on the part of the year where species are reproductively active, number of estrous cycles per year, and litter size, are made. There are species that seem to breed throughout the whole year; for example *Zygodontomys brevicauda* reproduce continuously, even in habitats with marked seasonality (e.g., dry and wet season). Litter size ranges from one to 11, averaging 4.5. Similarly, *Sigmodon hispidus* also breeds, at least in the warmer parts of its distribution, during the whole year. It has one to 15 young per litter. Other sigmodontine species restrict reproduction to one or two specific parts of the year (seasonally active). *Reithrodon auritus* concentrates breeding in spring and early summer. Litter sizes vary from one to eight, with a mean of 4.5 embryos. Sigmodontines are in general short-lived, and in several species at least one sex reaches sexual maturity in the same season of birth. This is the case of *Reithrodon auritus* females. *Eligmodontia typus* rarely live longer than 9 months; it reaches sexual maturity at approximately 45 days (Pearson et al., 1987).

Sumichrast's harvest mouse (*Reithrodontomys sumichrasti*) is a natural predator of the monarch butterfly (*Danaus plexippus*). (Photo by Gregory G. Dimijian, M.D./Photo Researchers, Inc. Reproduced by permission.)

Information on the patterns of sigmodontine copulatory behavior is sparse. *Calomys*, however, is a relatively well known genus in this regard. There is information on three of the 11 species of the genus. They display intravaginal penile thrusting and multiple ejaculations, in combination with single or multiple pre-ejaculatory intromissions. Locks are either rare or absent. In addition, *C. musculinus*, a non-monogamous species, undergoes a stereotyped precopulatory behavior composed mostly of agonistic behaviors in which the female and the male play the aggressive and submissive roles, respectively (Laconi and Castro-Vasquez, 1998).

A remarkable aspect of sigmodontine population dynamics is the massive population irruptions or outbreaks recorded in several parts of South America since the sixteenth century. These explosive increases in sigmodontine population abundance or density during a relatively short period have been called ratadas. Starting in 1522, 63 ratadas are well-documented in literature; these have occurred in Argentina, Brazil, Chile, and Peru. The outbreak estimated densities of some sigmodontines are as follows: *Oryzomys xantheolus* (range = 250–259 individuals per 2.5 acres [1 ha]), *Abrothrix olivaceus* (52–237), *Phyllotis darwini* (30–225), *Oligoryzomys longicaudatus* (46–154), and *Akodon azarae* (115). As ratadas involve one to four species

simultaneously, the total combined sigmodontine density may be even higher. Naturalists noted that massive flowering and subsequent massed seeding of bamboos preceded several rodent irruptions, so sigmodontine outbreaks became associated with bamboo blooming. Later, it was shown that several ratadas are associated with rainfall peaks, some of which are caused by El Niño Southern Oscillation disturbances. Both types of ratadas occur with approximately equal frequency and appear geographically located. Brazil, southern Chile, and southern Argentina are affected mainly by bamboo-associated rodent outbreaks, while Peru, northern Chile, and northern Argentina are affected by rainfall-associated outbreaks. Functionally, ratadas are the result of a population closely tracking changes in the environment. However, as it was shown in studies of the leaf-eared mouse *Phyllotis darwini*, a species that undergoes ratadas in semi-arid Chile, intrinsic factors such as density-dependence variables and competitors or predators also play a key role in shaping the demographic dynamics of these species. This evidence underscores the interplay of different phenomena regulating reproduction and demography in natural populations.

Finally, it is interesting to note that in nine species of *Akodon* (*azarae*, *boliviensis*, *kofordi*, *mollis*, *montensis*, *puer*, *subfuscus*, *torques*, and *varius*) there are females with a XY pair of sexual chromosomes (and not XX as is typical in mammals; XY females also occur in the arvicolines *Dycrostonix torquatus*, *Microtus cabrearae*, and *Myopus schisticolor*). The prevalence in wild populations of these heterogametic females ranges from 30 to 60%. These females are fertile. XY sex reversed females are assumed to occur due to a deficient expression of the Y chromosome linked gene Sry, resulting in the developing of ovaries instead of testes.

Conservation status

In April 2003 the IUCN Red List of Threatened Species listed 54 sigmodontine species. Three sigmodontines, *Nesoryzomys darwini*, *N. indefessus*, and *Oryzomys nelsoni*, are considered to be extinct; four other species, *Nectomys parvipes*, *Oryzomys gorgasi*, *Rhagomys rufescens*, and *Sigmodontomys aphrastus*, are listed as Critically Endangered. Ten sigmodontines species are considered Endangered, 13 Vulnerable, one species Near Threatened, and 19 to be at Lower Risk. Data are deficient to evaluate the status of four species. For the sole fact that the understanding of species limits of most sigmodontine genera is far from being settled, these figures are subject to change. For instance, instead of subsuming *Oryzomys galapagoensis* under *O. bauri*, Dowler et al. (2000) recognize both forms as distinct Galápagos endemic species. This classificatory scheme implies that another sigmodontine species, *O. galapagoensis* that has not been collected since 1835, should be regarded as extinct.

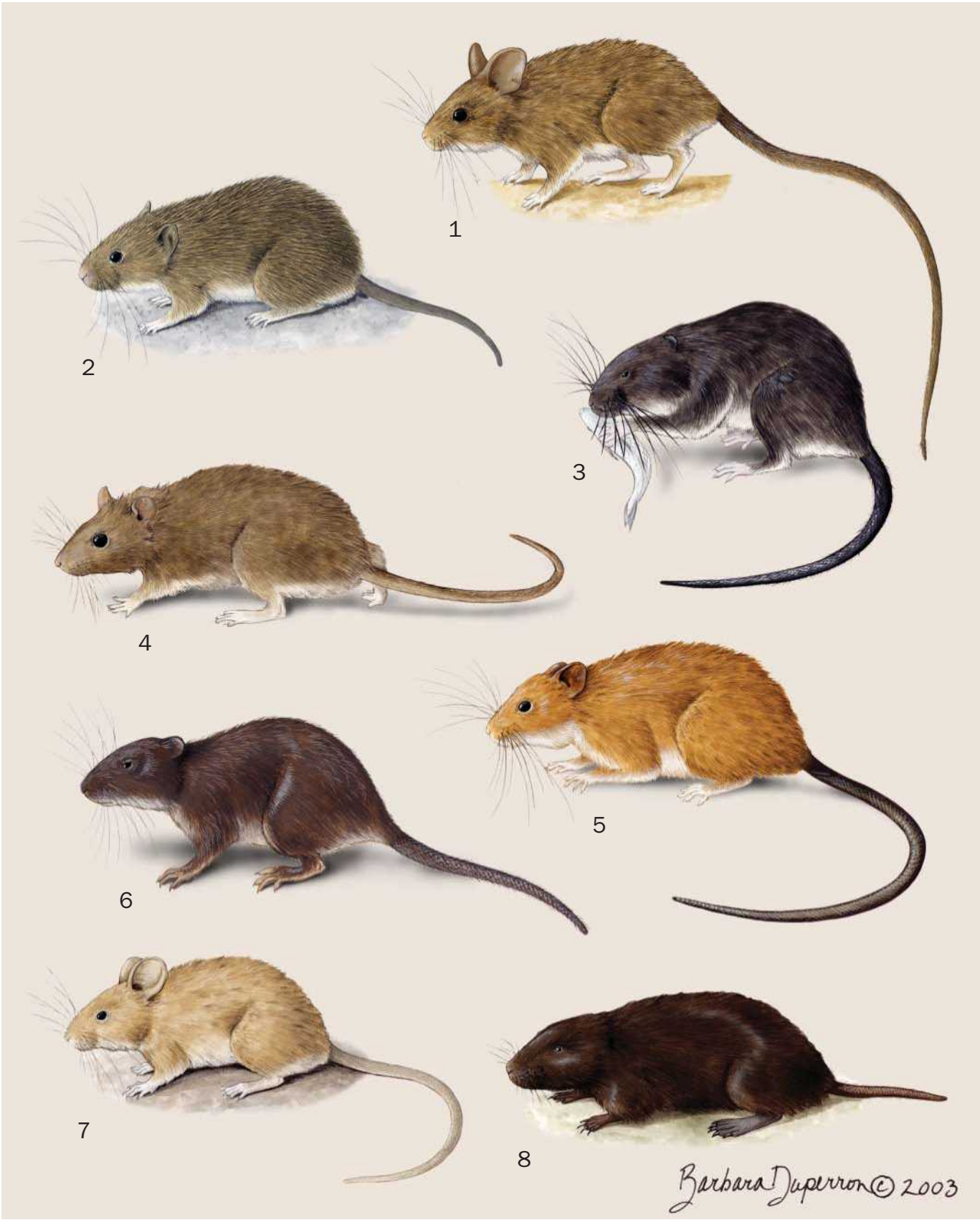
One of the major sigmodontine threats is habitat destruction due to land conversion for urbanization and agricultural and logging expansion. Another important threat is the introduction of exotic fauna. For instance, the most likely cause of the extinction of the Galápagos endemic *Nesoryzomys darwini* and *N. indefessus* is the introduction of black rats (*Rattus rattus*), either through the introduction of pathogens to which native species were susceptible, or through direct competition. Similarly, *Megaroyzomys*, another Galápagos endemic, became extinct presumably in historic times, through predation by introduced dogs, cats, pigs, and *Rattus*. Hunting pressure may be considered as a minor threat affecting sigmodontine conservation. Mann (1945) suggested that in some Chilean areas extensive trapping may have seriously reduced the populations of *Chinchillula*.

Significance to humans

The importance of sigmodontines to humans cannot be overstated. Some species cause much damage to agricultural lands and stored foods. For example, in Formosa Province, Argentina, the water rat *Holochilus chacarius* is reported to damage banana, mandioca, and sugar cane plantations. Similarly, in the Mexican state of Veracruz, the cotton rat *Sigmodon hispidus* and rice rat *Oryzomys couesi* are plagues on sugar cane plantations of such important magnitude that eradication plans are being designed. It is estimated that a single individual of *Calomys laucha* or *Akodon azarae*, which consume stored foods in farm and village structures, can eat 2.2 to 4.4 lb (1–2 kg) of food per year.

Other sigmodontines are the reservoirs of the etiological agents of a number of human diseases. In South America, all hantaviruses known to cause Hantavirus Pulmonary Syndrome are associated with species of sigmodontine rodents, including different long-tailed mice of the genus *Oligoryzomys*, the field mice *Necromys benefactus* and *Akodon azarae*, the vesper mouse *Calomys laucha*, and the cotton rat *Sigmodon alstoni*. In addition, the vertebrate reservoir of the Machupo virus, the etiological agent of the Bolivian hemorrhagic fever, is a non described species of vesper mouse (*Calomys*). Similarly, the reservoir of the Junin and Guanarito viruses, which cause the Argentine and Venezuelan hemorrhagic fevers, are, respectively, the vesper mouse *Calomys musculinus* and the cane mouse *Zygodontomys brevicauda*. Finally, it has been shown that the forest mouse *Akodon montensis*, the long-tailed mouse *Oligoryzomys nigripes*, the subterranean mouse *Thaptomys nigrita*, and the rice rat *Oryzomys russatus* are reservoirs of *Borrelia*-like spirochetes which cause a Lyme disease simile.

On the other hand, many sigmodontines species are beneficial to man by the role played in ecosystems. Some are keystone species in maintaining the vigor of ecosystems, through their role in dispersing seeds (e.g., *Oryzomys intermedius*) and/or being prey of many medium- and large-sized vertebrates (e.g., owls, snakes, and other carnivores). Other species are directly exploited by man. For example, the chinchilla mouse *Chinchillula* is trapped for its thick, soft, and silky fur. Trimmings and robes are made of these skins. Remarkably, one of these robes may contain more than 150 skins. Zooarcheological work indicates that during the Holocene period, sigmodontines did not represent a food item for the indigenous peoples that lived in the areas that are now known as the Argentinean Patagonia and Pampas. However, present Mbyá Guaraníes from Misiones, Argentina hunt and eat sigmodontines. Finally, some species play an increasing role as "domestic animals" used in medical research; this is the case of *Calomys laucha* and *C. musculinus*.



1. Chilean tree mouse (*Irenomys tarsalis*); 2. Hispid cotton rat (*Sigmodon hispidus*); 3. Water mouse (*Chibchanomys orcesi*); 4. Marsh rice rat (*Oryzomys palustris*); 5. Rio de Janeiro rice rat (*Phaenomys ferrugineus*); 6. Kemp's grass mouse (*Deltamys kempi*); 7. Andean mouse (*Andinomys edax*); 8. Brazilian shrew mouse (*Blarinomys breviceps*). (Illustration by Barbara Duperron)

Species accounts

Rabbit rat
Reithrodon auritus

TAXONOMY
Reithrodon auritus (Fischer, 1814), Buenos Aires Province, Argentina. Tribe Reithrodontini.

OTHER COMMON NAMES
Spanish: Rata conejo.

PHYSICAL CHARACTERISTICS
Total length 8.3–10.6 in (212–269 mm), tail length 3.3–4.0 in (84–103 mm), ear length 0.6–1.1 in (15–29 mm). Weight 0.7–4.1 oz (20.5–116 g). Pelage color varies from dark brown to pale buffy gray dorsally, and from white to brownish ochreous ventrally. Eyes and ears are large. It has four pairs of mammary glands. Hind legs are very long. Upper incisors have two frontal grooves. Molars are markedly high.

DISTRIBUTION
Patagonian region of Argentina, from Tierra del Fuego and southern Chile to 36ºS. North of 36ºS is restricted to a few high-altitude (> 6,562 ft; > 2,000 m) localities in central and northern Argentina. There is an unconfirmed record from Malvinas Islands.

HABITAT
Most common in steppes and prairies. However, the rabbit rat inhabits a wide range of environments, including beech forests, sparse shrub lands, bunchgrass prairies, dense grasslands, cultivated fields, overgrazed pastures, sandy coasts, and stony hills.

BEHAVIOR
Active both diurnally and nocturnally year-round. Activity begins in the evening and lasts until the early hours of the morning. *Reithrodon* excavates tunnels of 1.6–2.8 in (4–7 cm) in diameter. It also uses tunnels made by other animal such as those of tuco-tucos (*Ctenomys*).

FEEDING ECOLOGY AND DIET
The diet consists only of grasses.

REPRODUCTIVE BIOLOGY
Females reach reproductive maturity at about two months of age. Males reach maturity later than females. Specimens reproductively active have been collected in spring and summer (September to March). Most gravid females were found in spring. Litter size ranges from one to eight. Juveniles were found in spring and in higher numbers during summer and autumn.

CONSERVATION STATUS
Not threatened. Populations are protected in several Argentinean and Chilean national parks and reserves.

SIGNIFICANCE TO HUMANS
In the Argentinean Province of Buenos Aires the rabbit rat is considered a pest because it eats large amounts of grass. ◆

Kemp's grass mouse
Deltamys kempi

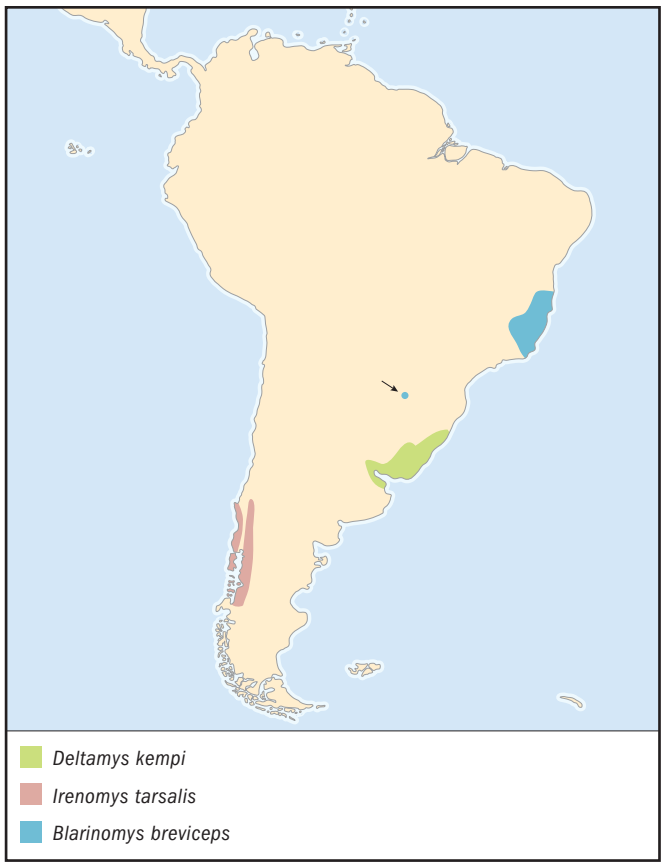
TAXONOMY
Deltamys kempi Thomas, 1917, Isla Ella, Delta of the Parana River, Argentina. Tribe Akodontini.

OTHER COMMON NAMES
Spanish: Ratón aterciopelado.

PHYSICAL CHARACTERISTICS
Measurements of the holotype. Total length 6.9 in (174 mm), tail length 3.3 in (85 mm), ear length 0.5 in (13 mm), length of foot without claws 0.9 in (22 mm). Eyes are small and barely visible, ears are narrow. The soft pelage is blackish brown dorsally and dull brownish gray ventrally. Tail is faintly bicolored.

DISTRIBUTION
Small area of southeastern South America, from northeast Buenos Aires Province and southern Entre Ríos Province in Argentina, throughout south, central east, and northeast Uruguay, to the Atlantic coast of the Rio Grande do Sul State in Brazil.

HABITAT
Marshy areas, especially edges of wetlands, flooded grasslands, and places with reeds and straws. In Uruguay also inhabits, although less abundantly, some woodlands. In



Argentina it has also been collected in tall grass coastal areas and gallery forest.

BEHAVIOR
Probably fossorial. It rests under grasses and leaves.

FEEDING ECOLOGY AND DIET
Mostly carnivorous. Insect remains have been recorded in stomachs of Argentinean and Uruguayan specimens. In addition, seeds and remains of green plants have been found in stomachs of specimens collected in Uruguay.

REPRODUCTIVE BIOLOGY
Little is known on reproductive aspects of Kemp's grass mouse. Litter size may be three since that numbers of young were found in one nest in Argentina and another in Uruguay.

CONSERVATION STATUS
In Argentina it is considered rare and at lower risk. Uruguayan populations are considered not threatened. The status of Brazilian populations is not known.

SIGNIFICANCE TO HUMANS
None known. ◆

Marsh rice rat
Oryzomys palustris

TAXONOMY
Oryzomys palustris (Harlan, 1837), near Salem, New Jersey, United States. Tribe Oryzomyini.

OTHER COMMON NAMES
Spanish: Rata arrocera, coludo.

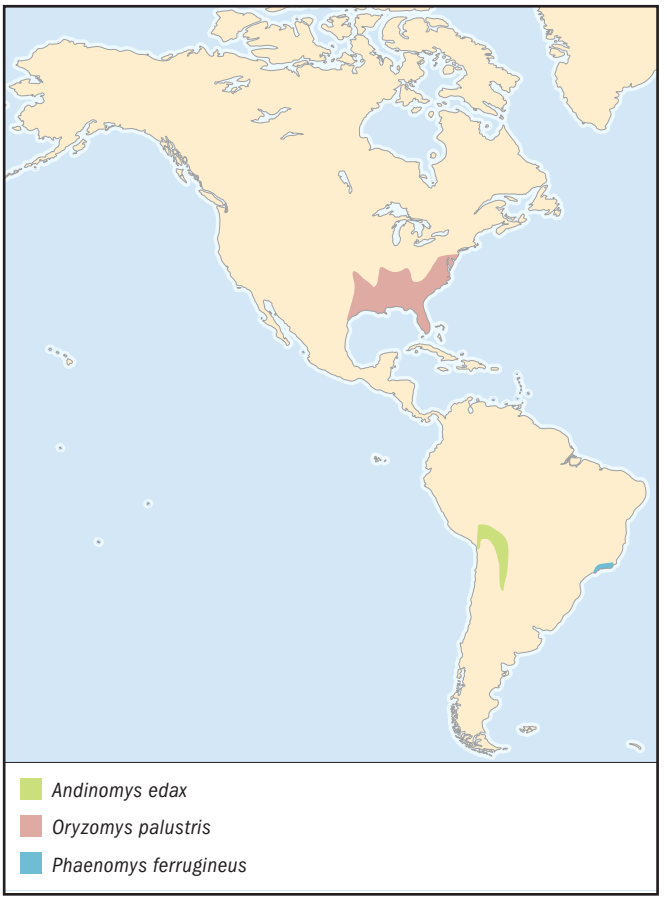
PHYSICAL CHARACTERISTICS
Total length 8.9–12.0 in (225–305 mm), tail length 3.9–6.9 in (100–175 mm), hindfoot length 1.1–1.5 in (28–37 mm). Weight 1.4–3.0 oz (40–85 g). Generalized rat-like appearance. Dorsal coloration range varies from grayish brown to gray. The venter is much lighter. The underfur is water repellent. Eight pairs of mammary glands. The forefoot and hindfoot have four and five toes, respectively. Tail is scaly, long, and nearly naked.

DISTRIBUTION
Endemic to the United States, ranging from southeastern Pennsylvania and southern New Jersey to the tip of Florida and westwards to eastern Texas. There are records from southern Kentucky and Illinois, southwestern Missouri, and southeastern Oklahoma.

HABITAT
Common in wetlands, including marshes at the Atlantic and Gulf coasts. It also inhabits swamps, meadows, and prairies.

BEHAVIOR
Semiaquatic, being good swimmers and divesr. Primarily nocturnal. High-pitched squeaks were associated with agonistic behavior upon females by males in captivity. It constructs spherical grassy nests to sleep in during the day.

FEEDING ECOLOGY AND DIET
Carnivorous, but also feeds on seeds, succulent plant parts, and fungus. Food items may vary seasonally upon resource avail-



ability. Animal items vary, but insects, fiddler crabs, snails are the most common; other animal items are fishes, clams, eggs, and young of long-billed marsh wrens.

REPRODUCTIVE BIOLOGY
Breeding may occur throughout the year, although it may be low during hot summer months. Gestation period lasts between 21 and 28 days. Different average litter size has been reported, 3.6, 4.8, and 5. Newborn weigh around 0.1 oz (3.5 g). Weaning occurs at age 11–20 days. Sexual maturity is reached between 40 and 45 days of age. Life expectancy is generally less than one year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Reservoir of the Bayou hantavirus, a pathogenic virus associated with human pulmonary syndrome. ◆

Chilean tree mouse
Irenomys tarsalis

TAXONOMY
Irenomys tarsalis (Philippi, 1900), Fundo San Juan, Valdivia Province, Chile. Formerly placed in the phyllotine tribe.

OTHER COMMON NAMES
Spanish: Ratón arbóreo, laucha arbórea.

PHYSICAL CHARACTERISTICS
Total length 10.6–12.8 in (270–326 mm), tail length 3.5–7.7 in (90–196 mm), hindfoot length 1.1–1.3 in (28–32 mm), ear length 0.8–1.0 in (20–25 mm). Weight 1.1–2.4 oz (30–67 g). Dorsal coloration is grayish cinnamon. The venter is washed with pinkish cinnamon buff. Ears are brownish black. Tail is blackish brown, and it may be paler on the ventral side; it ends in a penciled tip. Upper incisors are grooved.

DISTRIBUTION
Although vernacularly known as the Chilean tree mouse, *Irenomys tarsalis* is not endemic to Chile, it also has populations in Argentina. In Chile it ranges from Chillán (VII Región) south to Puerto Ibañez (XI Región), including Chiloe Island and the Guaitecas Islands. In Argentina distributes in along the western side of Neuquen, Río Negro, and Chubut Provinces.

HABITAT
Generally confined to humid, temperate forested habitats, especially bamboo stands or shrubby areas, although it is also present in the interface between forest and steppe.

BEHAVIOR
Nocturnal. It appears docile when removed from traps. After release it often climbs bamboo or trees, although it may run across the forest floor.

FEEDING ECOLOGY AND DIET
Granivorous and frugivorous, although also eats green vegetation, fungi, and seeds.

REPRODUCTIVE BIOLOGY
Breeding occurs in spring but may extend into summer. Birth takes place in summer. Litter size ranges from three to six.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Brazilian shrew mouse
Blarinomys breviceps

TAXONOMY
Blarinomys breviceps (Winge, 1887), Rio das Velhas, Minas Gerais State, Brazil. Tribe Akodontini.

OTHER COMMON NAMES
Portuguese: Rato do Mato.

PHYSICAL CHARACTERISTICS
Total length 5.1–6.3 in (129–161 mm), tail length 1.2–2.0 in (30–52 mm), hindfoot length 0.6–0.8 in (16–21 mm), ear length 0.3–0.4 in (8–10 mm). Shrewlike; superficially resembles the North American insectivore genus Blarina, and hence its scientific generic name. Pelage is dark gray. Head is short and conical. Eyes extremely reduced. Claws well developed.

DISTRIBUTION
First known from the Brazilian states of Bahia, Espiritu Santo, Minas Gerais, and Rio de Janeiro States; it has also been recovered from owl pellets in the Argentinean province of Misiones.

HABITAT
Montane forest.

BEHAVIOR
Primarily fossorial.

FEEDING ECOLOGY AND DIET
Carnivorous. Stomachs of two specimens contained arthropods of six different orders, mostly insects (90%) but also arachnids.

REPRODUCTIVE BIOLOGY
Little is known. Males with scrotal testes were collected in January and February. Pregnant females were trapped in September, January, and February. Observed number of embryos has been one or three.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Andean mouse
Andinomys edax

TAXONOMY
Andinomys edax Thomas, 1902, El Cabrado, Potosi Department, Bolivia. Formerly placed in the phyllotine tribe.

OTHER COMMON NAMES
Spanish: Rata andina.

PHYSICAL CHARACTERISTICS
Total length 10.1–12.4 in (257–315 mm), tail length 4.2–6.3 in (107–160 mm), hindfoot length 1.2–1.3 in (30–32 mm), ear

length 0.9–1.1 in (22–27 mm). Heavy-bodied. Pelage soft, lax, upperparts and sides drab, underparts gray. The tail is thinly haired and sharply bicolored. Feet are well developed.

DISTRIBUTION
High-altitude regions of northwestern Argentina, Bolivia, northern Chile, and southern Peru.

HABITAT
It lives in the puna in dense vegetation near water courses and bushy thickets.

BEHAVIOR
Nocturnal; terrestrial, but may also be scansorial. It nests inside round holes carpeted with fine straw.

FEEDING ECOLOGY AND DIET
Feeds on green herbs.

REPRODUCTIVE BIOLOGY
Breeds at the end of the dry season. A female collected by O. Pearson on December 18 had three well-developed embryos.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Water mouse
Chibchanomys orcesi

TAXONOMY
Chibchanomys orcesi Jenkins and Barnett, 1997, Las Cajas, Azuay Province, Ecuador. Tribe Ichthyomyini.

OTHER COMMON NAMES
Spanish: Rata acuática.

PHYSICAL CHARACTERISTICS
Total length 8.3–9.0 in (211–229 mm), tail length 4.3–4.8 in (108–122 mm), hindfoot length 0.8–0.9 in (19–24 mm), ear length 0.4–0.6 in (9–14 mm). Weight 1.2–1.4 oz (35–40 g). Pelage is soft, dense, and woolly, dark brownish gray dorsally, and light gray ventrally. Ears and eyes are reduced. The tail is longer than head and body.

DISTRIBUTION
Known only from three localities in the Las Cajas Plateau, Ecuador.

HABITAT
High altitude páramo (10,170–13,100 ft; 3,100–4,000 m), close to fast-flowing streams.

BEHAVIOR
Semiaquatic.

FEEDING ECOLOGY AND DIET
Primarily an aquatic insectivore, but also eats fish.

REPRODUCTIVE BIOLOGY
Nothing is known. It appears to be a scarce páramo inhabitant.

CONSERVATION STATUS
Not known, but Barnett (1997) noted that the Las Cajas Plateau, the only place from where *C. orcesi* is known, may become severely impacted by human activities in the near future.

SIGNIFICANCE TO HUMANS
None known. ◆

Rio de Janeiro rice rat
Phaenomys ferrugineus

TAXONOMY
Phaenomys ferrugineus (Thomas, 1984), Rio de Janeiro, Brazil. Formerly placed in the Thomasomyine tribe.

OTHER COMMON NAMES
Portuguese: Rato do mato ferrugíneo.

PHYSICAL CHARACTERISTICS
Measurements of the holotype: total length 13.2 in (335 mm), tail length 7.4 in (187 mm), hindfoot length 1.3 in (34 mm), ear length 0.7 in (17 mm). Pelage is dorsally rust-colored, cheeks and sides are lighter, and the underparts are whitish. Ears are small and well furred. The tail is unicolored, dark gray.

DISTRIBUTION
Known only from three localities in the Brazilian states of Rio de Janeiro and San Pablo.

HABITAT
One specimen collected in 1998 was trapped in herbaceous vegetation in an area that is considerably altered for agriculture and pasture. The collection site is in a valley surrounded by forested hills that have been selectively logged.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Hispid cotton rat
Sigmodon hispidus

TAXONOMY
Sigmodon hispidus Say and Ord, 1825, St. Johns River, Florida, United States. Tribe Sigmodontini.

OTHER COMMON NAMES
Spanish: Rata de campo; rata algodonera.

PHYSICAL CHARACTERISTICS
Total length 8.8–14.4 in (224–365 mm), tail length 3.2–6.5 in (81–166 mm), hindfoot length 1.1–1.6 in (28–41 mm), ear length 0.6–0.9 in (16–24 mm). Weight 3.5–8.0 oz (100–225 g). Pelage is grizzled with blackish or dark brownish hairs. Underparts are pale to dark grayish. Tail is dark. Female possesses five pairs of mammae; however, females with six and four pairs have also been found.

DISTRIBUTION
Inhabits the three Americas; from southeast United States (south Nebraska, central Virginia, southeast Arizona, peninsular Florida), through interior and east Mexico through Central America, to northern Colombia and Venezuela.

HABITAT
Usually an inhabitant of grass dominated landscapes.

BEHAVIOR
Both diurnal and nocturnal, and is able to swim.

FEEDING ECOLOGY AND DIET
Feeds primarily on grasses. There are data showing that it selects food items and combines them into a nutritious diet. It does not hoard food.

REPRODUCTIVE BIOLOGY
Breeding is through the year; however, differences exist in relation to latitude. Gestation lasts approximately 27 days. Litter size varies from one to 15, with animals from northern populations having larger litters. Neonates are well developed at birth; their eyes open within 36 hours after birth and are weaned in 10–15 days. Males reach reproduction maturity in two or three months; females reach it earlier, even in 10 days and in an average of 30–40 days. Females normally produce several litters per year.

CONSERVATION STATUS
The subspecies *S. h. eremicus* and *S. h. insulicola* are considered at Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Sigmodon hispidus has been used as a biomonitor to assess environmental contamination. *Sigmodon hispidus* is the reservoir of two strains of hantavirus called Black Creek Canal virus and Muleshoe viruses; these are pathogenic viruses associated with human pulmonary syndrome. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Allen's woodrat *Hodomys alleni*	Long, narrow head. Upperparts are reddish brown to dusky brown. Underparts are white to buff. Tail from dusky to white. Head and body length 14.5–17.5 in(36.8–44.5 cm), tail length 6.2–8.1 in (15.8–20.6 cm).	Dry wooded slopes, tropical deciduous forest, rocky outcrops to dense scrub. Little known of reproductive habits. Females produce one to two offspring.	Southernmost Sinaloa to Oaxaca; interior Mexico along basin of Rio Balsas to central Puebla.	Coco-oil seeds along with other types of seeds, crabs.	Lower Risk/ Near Threatened
White-throated woodrat *Neotoma albigula* German: WÏstenratte	Coloration is brownish gray, underside is white to gray. Tail is brownish gray on top, lighter on bottom. Feet are white. Head and body length 12.9 in (32.8 cm), weight 7.6 oz (215 g).	Desert habitats, where they build nests in rocky areas, under shrubs, small trees, or cacti. Breeding season from January to August, two or more litters per season. Nocturnal, solitary, and territorial.	Extreme southeastern California to southern Colorado to western Texas, United States, south to northeastern Michoacan and western Hidalgo, Mexico.	Mainly cacti.	Not threatened
Bushy-tailed woodrat *Neotoma cinerea* German: Buschschwanzratte	Coloration varies across range, from buff to darker. White coloration around the feet. Average male weight 14.3 oz (405 g), female weight 9.5 oz (270 g)	A variety of habitats, from boreal woodlands to deserts. Litter size is usually three offspring. Build constructs called middens, do not hibernate.	Southeast Yukon and westernmost Northwest Territories, south through British Columbia and western Alberta, Canada, to northwestern United States, as far south as northern New Mexico and Arizona and east to western Dakotas.	Consists mainly of vegetable matter, such as woody plants, and arthropods.	Not threatened
Eastern woodrat *Neotoma floridana*	Coloration is brown around base of neck to dark brown and black on rump. Nasal area is pink. Body is small, compact.	Wooded marshes, grasslands, and coastal plains. Litter size ranges from two to seven offspring. Breeding season varies with geographic location. Nocturnal and solitary, except during breeding season.	South-central and eastern United States from east-central Colorado to eastern Texas, eastwards along Appalachians to western Connecticut, and along Gulf-Coast states to southern North Carolina and central Florida.	Leaves, bark, fruits, and seeds.	Not threatened
Dusky-footed woodrat *Neotoma fuscipes*	Coloration is cinnamon with tints of buff and pink. Ears are thin, large, rounded, and broad. Claws are short. Head and body length 15.2–17.4 in (38.5–44.3 cm), weight 8.1–10.6 oz (230–300 g).	On hillsides, valleys, and close to water. Avoid open grassland and open oak woods with little underbrush. Nocturnal, uses branches for travel.	Western Oregon through western and central California, United States, to northern Baja California, Mexico.	Seventy-two different types of plants.	Not threatened
Golden mouse *Ochrotomys nuttalli*	Coloration of fur is gold, underparts are white, tail is cream. Cheeks contain thick folds of enamel. Head and body length 2–4.5 in (5.1–11.5 cm), tail length 2–3.8 in (5–9.7 cm).	Thick woodlands, swampy areas, among vines, and within small trees and shrubs. Reproduces all year; nocturnal and solitary.	Southeastern Missouri across to southern Virginia, south to eastern Texas, the Gulf Coast, and central Florida.	Mainly seeds.	Not threatened
Southern grasshopper mouse *Onychomys torridus*	Fine, dense fur, gray or pinkish cinnamon in color. Underside of tail is white. Head and body length 3.5–5.1 in (9–13 cm), tail length 1.2–2.4 in (3–6 cm).	Found within burrow systems in the ground. Most reproductive activity between late spring and summer. Extremely aggressive, nocturnal, good climbers.	Central California, southern Nevada, and extreme southwestern Utah, United States, south to northern Baja California, western Sonora, and northernmost Sinaloa, Mexico.	Seeds, plants, and vegetables.	Not threatened
Big-eared climbing rat *Ototylomys phyllotis*	Coloration is gray and brown on dorsal side, white and gray on the ventral side. Hands and feet are pale. Tail is long, hairless, covered with scares, from dark gray/brown to a paler color on ventral surface. Eyes and ears are large and hairless. Head and body length 3.7–7.5 in (9.5–19 cm), tail length 3.9–7.5 in (10–19 cm).	Tropical forests, both dry and wet, with abundant rocks or rocky ledges. Nocturnal and arboreal.	Central Costa Rica north to Yucatán Peninsula, southern Tabasco, and northern Chiapas, Mexico; isolated record from north-central Guerrero, Mexico.	Fruits and leaves.	Not threatened

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Texas mouse *Peromyscus attwateri*	Coloration of dorsal side is brown with darker and blackish marks mixed in. Underside is lighter. Head and body length 7.8 in (19.8 cm), weight 0.9–1.2 oz (25–35 g).	Rocky areas including cliffs and limestone outcrops with woody vegetation. Breeding season from late September to winter. Four offspring per litter.	Edwards Plateau of north-central Texas, north through eastern Oklahoma, to south-eastern Kansas, south-western Missouri, and northwestern Arkansas, United States.	Seeds, fruits, flowers, nuts, and other plant products.	Not threatened
California mouse *Peromyscus californicus*	Coloration is yellowish brown or gray mixed with black dorsal coloring. Underparts are white. Fulvous throat patch and lateral line are present. Head and body length 8.7–11.2 in (22–28.5 cm), tail length 4.6–6.1 in (11.7–15.6 cm), weight 1.2–1.9 oz (33.2–54.4 g).	Dense chaparral and broad-sclerophyll woodland. Nocturnal, poor burrower, breeding occurs year-round.	Central and southern California, United States, excluding San Joaquin Valley, to northwestern Baja California Norte, Mexico.	Fruits, seeds, and flowers of shrubs.	Not threatened

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Guillermo D'Elía, PhD

△

Rats, mice, and relatives V

All other rats, mice, and relatives

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Muridae

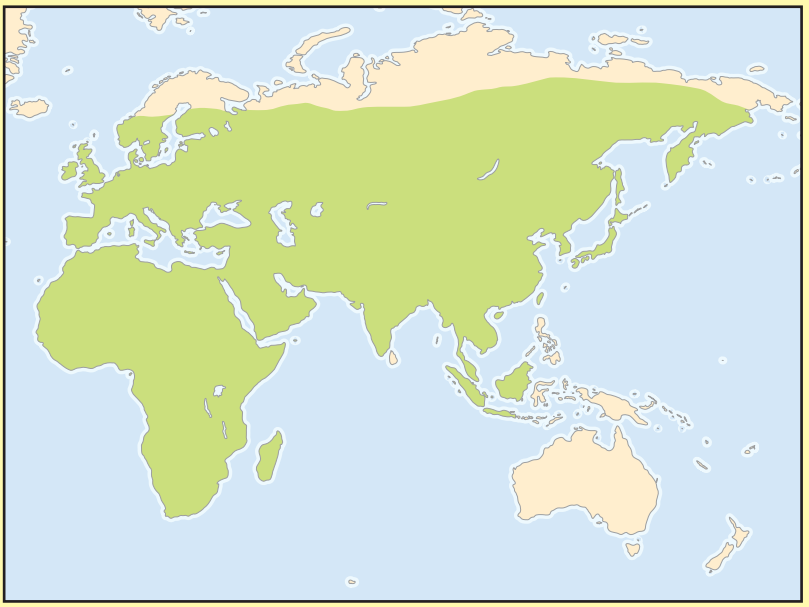
Thumbnail description
The 13 remaining subfamilies of Muridae are incredibly diverse ecologically, behaviorally, and morphologically

Size
The more than 213 species in the 13 remaining subfamilies of Muridae vary in size from small, mouse-sized animals to bamboo rats (Rhizomyinae), which can reach 8.8 lb (4 kg) in weight

Number of genera, species
47 genera; approximately 213 species

Habitat
Habitats range from deserts to dense, tropical forests; there are animals that specialize for burrowing underground, hopping across loose soils, and climbing in trees

Conservation status
Critically Endangered: 18 species; Endangered: 12 species; Vulnerable: 18 species; Lower Risk/Near Threatened: 27 species; Data Deficient: 1 species



Distribution
Found throughout Africa, Madagascar, and Asia, including Europe

Evolution and systematics

The rodent family Muridae is the largest mammalian family. Murids occur on nearly all landmasses, except for some arctic and oceanic islands, New Zealand, Antarctica, and parts of the West Indies. Morphological, ecological, behavioral, dietary, and taxonomic diversity in murids is truly astonishing. Murids range from solitary animals to highly social animals and from very common to very rare. Murid fossils are known from the Oligocene to recent in North America and Eurasia, from the Pliocene until recent in South America, and more recently in Africa, Madagascar, and Australia.

The relationships among all subfamilies of Muridae (including those not covered here: Murinae, Sigmodontinae, Cricetinae, and Arvicolinae) are poorly understood. Careful

The greater Malagasy bushy-tailed rat (*Eliurus tanala*) foraging. (Photo by Harald Schütz. Reproduced by permission.)

A red forest rat (*Nesomys rufus*) eating a mushroom. (Photo by Harald Schütz. Reproduced by permission.)

A white-throated wood rat (*Neotoma albigula*) foraging among the cactuses of Arizona, USA. (Photo by G. C. Kelley/Photo Researchers, Inc. Reproduced by permission.)

examination of morphological characters, especially cranial and dental characters, has not been able to elucidate patterns of relationship among the various subfamilies, although some affinities were identified. Carleton and Musser (1984), in their exhaustive morphological work, preferred to treat relationships among all murid subfamilies as unresolved.

Recent systematic work using molecular characters has helped to resolve patterns of evolutionary relationships among many murid subfamilies. Although some murid subfamilies (Lophiomyinae and Platacanthomyinae) have yet to be included in a molecular analysis, DNA sequences of representative members of all other subfamilies have been generated and analyzed within a systematic framework. Nearly all currently recognized murid subfamilies retain their rank as distinct lineages in these analyses. The fossorial lineages, Spalacinae and Rhizomyinae, appear to share a common ancestor with all of the remaining subfamilies. The remaining subfamilies form several groups of related lineages. A primarily African group (including Madagascar) includes Nesomyinae, Petromyscinae, Cricetomyinae, Dendromurinae, and Mystromyinae. Calomyscinae appears as its own lineage; the remaining subfamilies form two large lineages. A group made up mainly of Arvicolinae, Sigmodontinae, and Cricetinae includes the subfamily Myospalacinae. The final cluster is made up of the subfamilies Murinae (in-

Gerbils (*Meriones unguiculatus*) have a number of different coat colors. (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

An ice rat or Sloggett's vlei rat, (*Otomys sloggetti*) basking in the sun outside its burrow. (Photo by Peter Chadwick/Photo Researchers, Inc. Reproduced by permission.)

cluding Otomyinae), Acomyinae (previously included within Murinae), and Gerbillinae.

Physical characteristics

The murid species in these subfamilies vary widely in size and other physical features. Most species are small and mouse-sized, usually with moderately long tails and a generally brownish fur color. However, many species have adopted fossorial modes of life, becoming large and robust, with reduced eyes and ears, and teeth and limbs modified for digging. Others, in particular the gerbillines, have become adapted to a nocturnal existence in primarily arid landscapes. These species are capable of jumping locomotion as a result of enlarged and modified hind limbs. They also have greatly enlarged auditory bullae, resulting in an extraordinarily keen sense of hearing. Species in several of the subfamilies strongly resemble other murid rodents such as voles (Arvicolinae) and hamsters (Cricetinae), and members of other rodent families such as pocket gophers (Geomyidae), dormice (Gliridae), jumping mice (Zapodidae), and jerboas (Dipodidae), illustrating the evolutionary plasticity of these groups.

Distribution

These 13 subfamilies are found throughout Africa, Madagascar, and Asia, including Europe.

A male gerbil (*Meriones unguiculatus*). (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

Habitat

Murids in these subfamilies occupy a wide variety of habitats and niches. Most are terrestrial but some live underground, in trees, are semi-aquatic, or live in extreme environments. Most notable in this respect are the gerbillines, which have become adapted to extreme aridity. They avoid water loss and heat stress by being active at night, seeking refuge during the day in burrows, maintaining high relative humidity in their burrows, and producing concentrated urine. Gerbillinae is the most diverse of the 13 sub-

A large bamboo rat (*Rhizomys sumatrensis*) forages on the ground. (Photo by L. Bruce Kekule/Photo Researchers, Inc. Reproduced by permission.)

A Malagasy reed rat (*Brachyuromy betsileonensis*) foraging. (Photo by Harald Schütz. Reproduced by permission.)

families, illustrating how successful this suite of adaptations has proven.

Behavior

Members of these 13 murid subfamilies vary widely in the social structures and behaviors. Many are solitary, but some species are highly social, with complex modes of communication. Most are active primarily at night, although some are active either throughout the day, or are diurnal.

Feeding ecology and diet

Dietary diversity in these groups ranges from animals that eat mainly invertebrates to those that eat all kinds of plant matter, and some that eat vertebrates. The typical diet is made up of primarily seeds, but includes fruits, shoots, leaves, and animal matter. The fossorial subfamilies Rhizomyinae, Spalacinae, and Myospalacinae eat mainly roots and other underground plant parts, rarely venturing aboveground. The diversity in dental patterns in these groups, particularly of the cheek teeth, reflects this dietary breadth.

Reproductive biology

Reproductive patterns and behavior in these groups are quite variable. Breeding can occur seasonally or throughout the year and the number of offspring can range from one to many. In general, multiple young are born on a seasonal basis and the young develop quickly, achieving both independence and sexual maturity at an early age. However, there are exceptions. Males are typically not involved in raising young.

A western Malagasy bushy-tailed rat (*Eliurus myoxinus*) feeding on a tree trunk. (Photo by Harald Schütz. Reproduced by permission.)

A jird or gerbil (*Meriones unguiculatus*) found in Mongolia. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Very little is known about the specifics of mating behaviors in the majority of species.

Conservation status

Many species in this diverse set of subfamilies are abundant and may be human commensals and agricultural pests. However, habitat destruction or human persecution threatens many species. Animals that are restricted to small ranges or particular habitats may be especially vulnerable. For example, members of the Petromyscinae tend to be restricted to small, relict distributions and are vulnerable to habitat changes. Especially notable in this regard are the members of the Nesomyinae, which are all restricted to portions of Madagascar. This rodent radiation is truly unique and nearly all of the species in this group are critically threatened by profound, human-induced habitat destruction throughout Madagascar. Although the Gerbillinae is the most diverse of the 13 subfamilies, many species within this particular subfamily are threatened or Endangered.

Significance to humans

Species within this very diverse group include human commensals, agricultural pests, food animals, research animals, and pets. More importantly, almost all of the species in these 13 subfamilies are important members of the ecosystems in which they live. Many small rodents in this group are among the most abundant small mammals in their communities, forming an important prey base for small and large predators. Many species are also important in nutrient cycling and seed dispersal. Finally, research on the incredible array of evolutionary trajectories and adaptations found in these subfamilies will continue to yield rich and valuable insights into evolutionary processes and patterns of animal diversity. Murid rodents are some of the primary animal models used in the analysis of human diseases and genetics, and a better understanding of murid evolution and ecology directly impacts society's ability to solve problems related to human health and well-being.

1. Mouse-like hamster (*Calomyscus bailwardi*); 2. White-tailed mouse (*Mystromys albicaudatus*); 3. Pygmy rock mouse (*Petromyscus collinus*); 4. Sundevall's jird (*Meriones crassus*); 5. Gray climbing mouse (*Dendromus melanotis*); 6. Malagasy giant rat (*Hypogeomys antimena*); 7. Gambian rat (*Cricetomys gambianus*). (Illustration by Brian Cressman)

1. Malabar spiny dormouse (*Platacanthomys lasiurus*); 2. Angoni vlei rat (*Otomys angoniensis*); 3. Crested rat (*Lophiomys imhausi*); 4. Siberian zokor (*Myospalax myospalax*); 5. Palestine mole rat (*Nannospalax ehrenbergi*); 6. Large bamboo rat (*Rhizomys sumatrensis*). (Illustration by Brian Cressman)

Species accounts

Mouse-like hamster
Calomyscus bailwardi

SUBFAMILY
Calomyscinae

TAXONOMY
Calomyscus bailwardi Thomas, 1905, Iran.

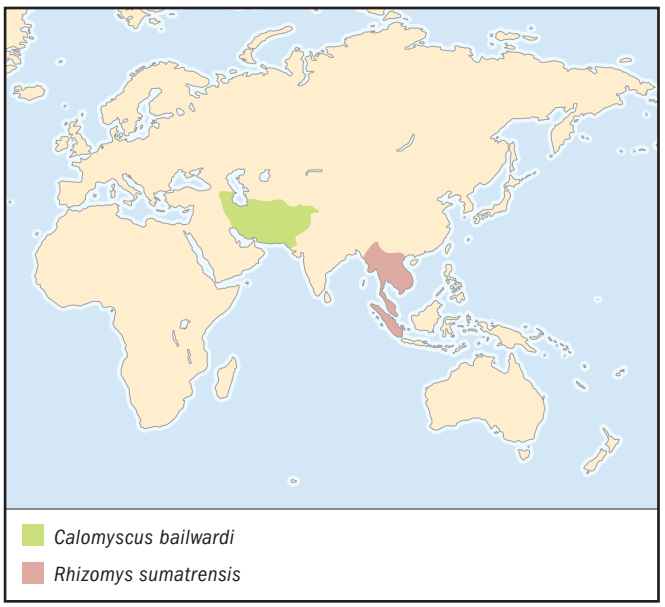
OTHER COMMON NAMES
English: Asian hamster mouse.

PHYSICAL CHARACTERISTICS
Head and body length 2.4–3.8 in (61–98 mm); tail 2.8–4 in (72–102 mm); weigh 0.5–1 oz (15–30 g). The fur is fine and soft, a sandy brown above and creamy white on the belly and feet. Tail is furry, and tufted at the end; dark above and white below. The ears are large and rounded, and whiskers are long. They have four-rooted molar teeth.

DISTRIBUTION
Central Asia, including Iran, Caucasus, Turkmenistan, Afghanistan, and Pakistan.

HABITAT
Found in a variety of habitats, from barren hillsides to wet forests, and from 1,310 to 11,480 ft (400–3,500 m) elevation. They build nests in rock crevices and other protected areas; nests are woven of grasses and other soft materials, including wool.

BEHAVIOR
Not highly social animals, but they can be found sheltering together in the wild and they huddle together in captivity. They are active at night during summer, but may extend activity into the dawn and dusk hours during spring and fall.



FEEDING ECOLOGY AND DIET
Eat primarily seeds, but also eat flowers, leaves, and animal foods when available.

REPRODUCTIVE BIOLOGY
Breeding may occur twice yearly, with a peak of reproduction in spring and then a late season breeding period; this may vary regionally and depend on food availability. Young are born hairless and with their eyes closed; they develop quickly and reach adult size at 6–8 months old.

CONSERVATION STATUS
There is very little known on the status of this calomyscine mouse, or other species in this genus. Two species are listed as Vulnerable in Russia. They may be locally abundant. *Calomyscus hotsoni*, of Pakistan, is considered endangered.

SIGNIFICANCE TO HUMANS
Where *Calomyscus* species are abundant and live near human habitations, they may act as agricultural pests or harbor disease agents. However, they are more likely to have little to no effect on humans, except in their role as members of healthy ecosystems. ◆

White-tailed mouse
Mystromys albicaudatus

SUBFAMILY
Mystromyinae

TAXONOMY
Mystromys albicaudatus (Smith, 1834), South Africa, eastern Cape Province.

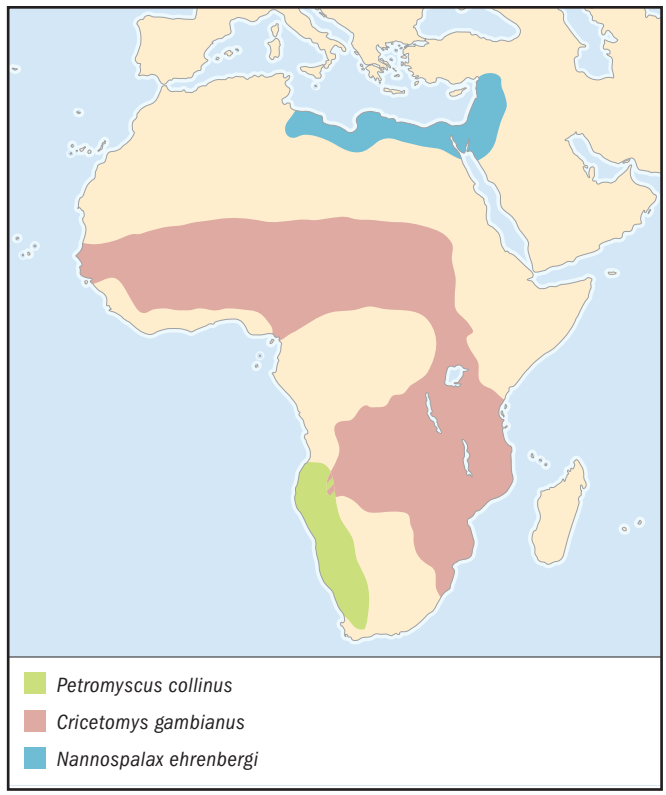
OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Critical differences, including their lack of check pouches, in the single species in this subfamily led to their elevation to the subfamily level, though their affinities remain obscure. Head and body length 3.3–4.1 in (84–105 mm); weigh 2.6–3.9 oz (75–111 g); tail 1.9–3.8 in (50–97 mm). The fur is soft and long, buffy gray above with black-tipped hairs; this darker dorsal coloration gradually lightens along the sides to the entirely white belly. The thick tail is covered with stiff bristles and the ears are large and rounded. The incisors are pale yellow and ungrooved, and the cheek tooth laminar pattern is unique.

DISTRIBUTION
Found in the uplands and Cape region of South Africa and Swaziland.

HABITAT
Found in grassy and sandy areas, they live in holes in the ground and the burrows of other mammals.

BEHAVIOR
Active mainly at night and may be especially active during wet weather. They do well in captivity, becoming tame and playful. Little is known about their social behavior.



FEEDING ECOLOGY AND DIET
Seeds seem to be their primary diet, though grasses and insects are also sometimes taken.

REPRODUCTIVE BIOLOGY
Have an unusual method of raising young: soon after birth, the young attach themselves to their mother's mammae and remain attached for about three weeks. The female drags them about during this time. They continue to suckle intermittently for another 2–3 weeks. The survival rate of young is high for rodents, as the mother can provide direct protection for her young. Sexual maturity is reached at about five months of age and litters can be produced as often as every 36 days. Mean litter size is 2.9 young. In captivity, they may live as long as six years; lifespan in the wild is unknown.

CONSERVATION STATUS
Little is known. Populations may be threatened by modifications to their habitat as a result of agriculture and grazing, and they are considered Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Although they may act as disease vectors and agricultural pests, it is most likely that they have a minimal effect on humans. They are important parts of the ecosystems in which they live, acting as seed dispersers and an important prey base for small predators. ◆

Gambian rat
Cricetomys gambianus

SUBFAMILY
Cricetomyinae

TAXONOMY
Cricetomys gambianus Waterhouse, 1840, River Gambia, Gambia.

OTHER COMMON NAMES
English: African pouched rat/mouse.

PHYSICAL CHARACTERISTICS
Fairly large: head and body length 9.4–17.7 in (240–450 mm); tail 14.3–18.1 in (365–460 mm); weight, males 6.1 lb (2.8 kg) and females 3 lb (1.4 kg). The fur is short and ranges from coarse to soft. They are generally dark or grayish brown with red tinges on their upperparts and creamy on the underparts. Their large ears and long, scaly tail are hairless and the tail is completely white for the last half of its length. There is a dark ring around each eye, making them appear masked. Some individuals are mottled with darker colors or may have an indistinct white line running across their shoulders. The head and face are long and narrow and the eyes are relatively small. They have cheek pouches into which they stuff food, bedding material, and found objects such as pebbles and metal trash, which they take back to their burrows. The incisors are ungrooved.

DISTRIBUTION
Found in appropriate habitat from Senegal and Sierra Leone in the west to Sudan and Uganda in the east and as far south as Zambia, Angola, and northern South Africa.

HABITAT
Prefer forests, thickets, and forest edge habitats, and are sometimes found in grasslands.

BEHAVIOR
Mainly nocturnal, though they are sometimes observed during daylight hours. Their relatively small eyes and their behavior during the daytime suggest that they rely mainly on their senses of smell and hearing. They can dig their own, simple

burrows, consisting of long passageways with side chambers for bedding and storage; however, they also use the burrows of other animals, termite mounds, or natural crevices such as rock crevices or hollow trees. Burrows usually have several openings that are camouflaged by dense vegetation. Burrow entrances are often plugged with vegetation from the inside. They can climb well and swim, and appear to be mainly solitary.

FEEDING ECOLOGY AND DIET
Omnivorous, eating all kinds of plant and animal matter, including insects, fruits, seeds, nuts, roots, leaves, snails, and crabs. They prefer palm fruits and kernels.

REPRODUCTIVE BIOLOGY
Breeding can occur throughout the year, depending on the nutritional status of females. In a captive study, a female had five litters in one year and it was estimated that as many as 10 litters per year could be produced. Gestation lasts from 27–36 days; an average of four young (with a range of 1–5) is born per litter. Young develop quickly and become sexually mature as early as 20 weeks old. One individual in captivity lived almost eight years.

CONSERVATION STATUS
Although common in some areas, they are less common in others. In South Africa, they are classified as Rare.

SIGNIFICANCE TO HUMANS
Often sold in the pet trade, Gambian rats were banned from import into the United States in 2003 in an effort to prevent the spread of monkeypox virus infection. They are also hunted as food by native peoples. ◆

Pygmy rock mouse
Petromyscus collinus

SUBFAMILY
Petromyscinae

TAXONOMY
Petromyscus collinus (Thomas and Hinton, 1925), Damaraland, Namibia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 2.7–3.5 in (70–90 mm); tail 3.1–3.9 in (80–100 mm). Small, mouse-sized rodents with broad, flattened heads and large ears. Their long tails are scaly and sparsely furred, and the pelage is soft and brown above and grayish below. Dental characteristics suggest they are related to members of the subfamilies Dendromurinae and Mystromyinae, but they are distinctive in other characters.

DISTRIBUTION
Found in the arid regions of southwestern Africa. *Petromyscus collinus* is found from southern Angola to western South Africa in the Namib Desert.

HABITAT
Found in areas of boulders and rock outcroppings in arid mountainous regions.

BEHAVIOR
Nocturnal, they shelter during the day in rock crevices and among loose boulders and forage in the same areas at night by creeping among the rocks. Very little is known about these animals.

FEEDING ECOLOGY AND DIET
Observations suggest they are omnivorous, taking advantage of many food types as they are available.

REPRODUCTIVE BIOLOGY
Breed once yearly, with births peaking in January, preceding the main rainy season. Litter size is estimated at 2–3 young.

CONSERVATION STATUS
Little is known about the population status. The areas they occupy are remote and little used by humans, though their limited distribution makes them potentially Vulnerable.

SIGNIFICANCE TO HUMANS
The remote areas they occupy do not support dense human settlements; it is unlikely that there are any direct effects of *Petromyscus* species on humans. ◆

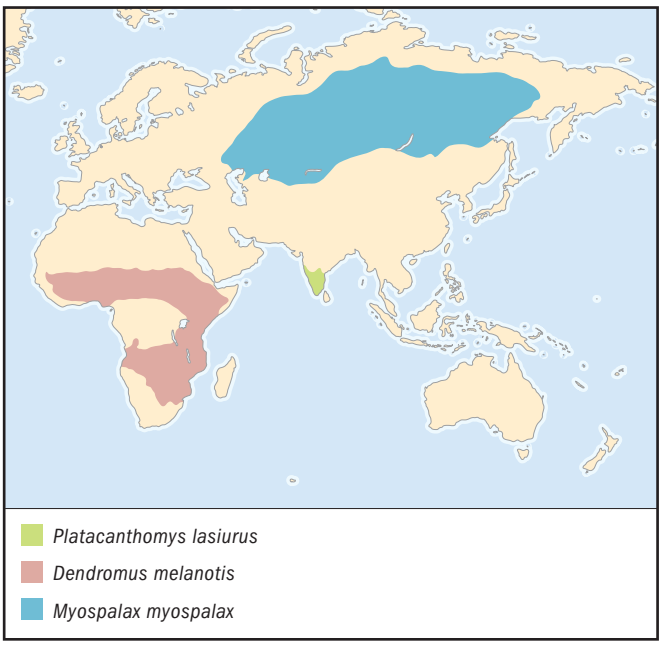
Gray climbing mouse
Dendromus melanotis

SUBFAMILY
Dendromurinae

TAXONOMY
Dendromus melanotis Smith, 1834, near Port Natal, South Africa.

OTHER COMMON NAMES
English: African climbing mouse, gerbil mouse, fat mouse, forest mouse.

PHYSICAL CHARACTERISTICS
Head and body length 1.9–3.9 in (50–100 mm); tail 2.5–5.1 in (65–132 mm); weight 0.2–0.7 oz (5–21 g). They have three digits on their forefeet, a characteristic unique to the genus; the rear feet have the normal number of digits. Their long,



prehensile tails are slightly bicolored, darker on the upper surface. The dorsal fur is soft and gray, with a darker stripe running down their midline, their underparts are lighter. The eyes are very large and often have darker fur surrounding them, making them look as if they have spectacles. Upper incisors are grooved.

DISTRIBUTION
Widely distributed in suitable habitats in Central Africa, from Guinea in the west to Ethiopia in the east and as far south as South Africa. Some other *Dendromus* species have very restricted ranges.

HABITAT
In general, found in a wide variety of habitats, from arid grasslands to dense, moist forests. *D. melanotis* is found mainly in dry, open grasslands, often in sparse vegetation on sandy soils, but also in swampy areas, coastal lowlands, low velds, moist upland, and montane areas. They make simple burrows underground, consisting of entrance and exit tunnels and a grass-lined nest chamber. Other *Dendromus* species build globular nests aboveground. Several *Dendromus* species, which occupy similar habitats, may build their burrows underground to escape the seasonal fires that are typical of the grasslands in which they live.

BEHAVIOR
There is variation in the degree of sociality among *Dendromus* species, but they are solitary and quite territorial. They are active at night and use their tails for climbing.

FEEDING ECOLOGY AND DIET
Omnivorous, eating seeds, fruits, insects, and small vertebrates.

REPRODUCTIVE BIOLOGY
The time of breeding may vary regionally, based on wet season timing and food availability, but they breed only once yearly. Gestation lasts 23–27 days, after which 2–8 young are born in the mother's nest. The young are cared for by their mother until they are 30–35 days old, after which they leave the nest.

CONSERVATION STATUS
Population information on most *Dendromus* species is unavailable. They may be locally abundant in suitable habitats, but some are Vulnerable to human disturbances of their habitat. *D. vernayi* of Angola is considered Critically Endangered by IUCN.

SIGNIFICANCE TO HUMANS
May act as disease vectors and agricultural pests of seed crops, but their impact on humans is likely to be minimal. ◆

Malagasy giant rat
Hypogeomys antimena

SUBFAMILY
Nesomyinae

TAXONOMY
Hypogeomys antimena Grandidier, 1869, Madagascar.

OTHER COMMON NAMES
English: Malagasy rat/mouse.

PHYSICAL CHARACTERISTICS
Large rodents: head and body length 11.8–19.6 in (300–500 mm); tail 8.2–19.6 in (210–500 mm). Their ears are quite large, reaching 2.3 in (60 mm) in length. They tend to sit back on their well-muscled haunches and long hind feet and are excellent jumpers and runners. The fur is coarse and short; their dorsal fur is gray, brown, or reddish, and the fur on their belly, feet, and hands is white. The dark tail is covered with stiff hairs.

DISTRIBUTION
West coast of Madagascar.

HABITAT
Found only in the sandy forests of western coastal Madagascar. They construct long, deep burrows in the sandy soil.

BEHAVIOR
Nocturnal, emerging from their burrows at nightfall to search for food.

FEEDING ECOLOGY AND DIET
Eat mainly fallen fruit.

REPRODUCTIVE BIOLOGY
Very little is known. They give birth to single young.

CONSERVATION STATUS
Threatened by habitat destruction as the virgin forests of Madagascar are cut and burned for agriculture by a burgeoning human population. Populations have decreased in number and range in recent years; they are listed as Endangered by IUCN.

SIGNIFICANCE TO HUMANS
Along with other nesomyine rodents, they are remarkable examples of an adaptive radiation into unoccupied niches on Madagascar. They are significant as a kind of natural experiment in murid evolution. They may also be important in dispersing seeds of native vegetation, though little research has been done on their ecosystem roles and ecology. ◆

Sundevall's jird
Meriones crassus

SUBFAMILY
Gerbillinae

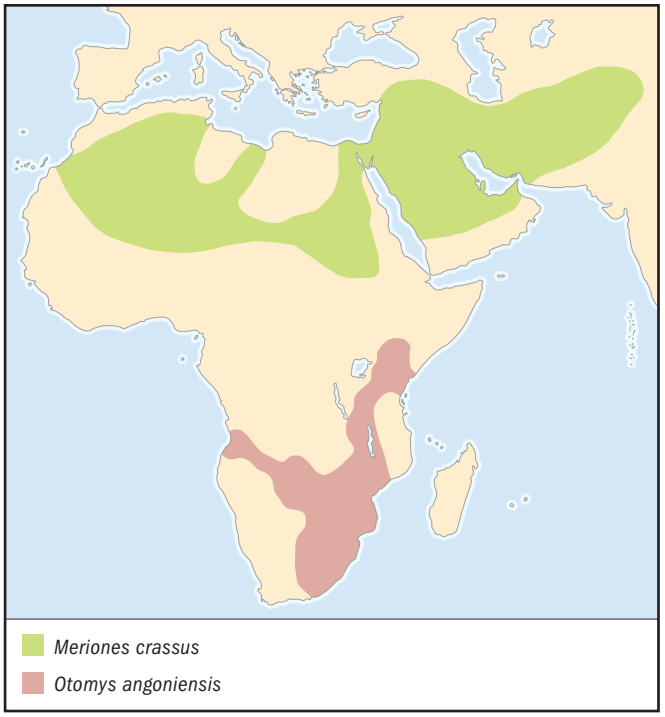
TAXONOMY
Meriones crassus Sundevall, 1842, Sinai, Egypt.

OTHER COMMON NAMES
English: Gentle jird, gerbil, sand rat.

PHYSICAL CHARACTERISTICS
Slightly larger than mouse-sized: head and body length 5.9 in (150 mm); tail 5.9 (150 mm); weight 1.6–2.1 oz (45–60 g). Tail is sparsely furred, with a brush-like tip. The fur is soft and fine, their undersides are entirely white, and their dorsal surfaces are gray to buffy.

DISTRIBUTION
Occur throughout the Arabian Peninsula, Iran, and Iraq, and into Turkey and Syria. Also found throughout much of Africa north of 20°N latitude, from Morocco to Sudan.

HABITAT
Prefer the most arid, hot, and open habitats throughout their range. Typically found in areas with sandy soils, but can also be found in rocky areas. They are well adapted to their arid



habitats; they have efficient kidneys that produce highly concentrated urine. They also defecate fecal material that is very dry. Maintain a high relative humidity in burrows, close to 100% in their deepest parts.

BEHAVIOR
Escape both the heat and aridity of the daylight hours and the diurnal predators by being mainly nocturnal, though their remains have been found in owl pellets. They are social animals, living in small colonies that occupy complex burrow systems.

FEEDING ECOLOGY AND DIET
Diet consists mainly of seeds, though fruits, and foliage; insects are also taken. Recorded eating *Acacia*, thistle, locust, and other plant seeds, melons, dates, and orthoperan insects (crickets and locusts). They shift to include more foliage in their diet during winter, possibly as a way of increasing moisture intake. Food is brought back to the burrow before being consumed, and parts of the burrow are used for food storage.

REPRODUCTIVE BIOLOGY
Capable of breeding at an early age, as early as two months old, and breeding can occur throughout the year. Courtship and mating behavior is relatively complex. Males display to females by foot-stomping and tail-beating. Mating occurs at night for several hours at a time, during which copulation occurs repeatedly. Females groom males during mating sessions. From one to eight young (average 3.5) are born in each litter. Young are born naked and helpless and are cared for by their mother in the burrow. They develop rapidly, becoming weaned after one month. Gestation is from 21 to 31 days in length, with a 4.5 day long estrus. The length of estrus and gestation is influenced by the mother's nutritional and reproductive state.

CONSERVATION STATUS
Fairly common throughout their range. They tend to occupy habitats that are undesirable to humans, and are therefore less disturbed. However, several other *Meriones* species are considered Endangered.

SIGNIFICANCE TO HUMANS
Several species are common in the pet trade and in medical and biological research. In the wild, they may be considered agricultural pests because they damage seed and fruit crops. Their burrowing activities may cause damage to structures such as irrigation canals. They are also critical natural components of the ecosystems in which they live. ◆

Angoni vlei rat
Otomys angoniensis

SUBFAMILY
Otomyinae

TAXONOMY
Otomys angoniensis Wroughton, 1906, Malawi.

OTHER COMMON NAMES
English: Vlei rats, whistling rats, karoo rats, groove-toothed rats.

PHYSICAL CHARACTERISTICS
Medium-sized, stocky rodents: head and body length 4.1–8.1 in (105–207 mm); tail 1.7–5.1 in (43–131 mm); weight 0.8–4.8 oz (25–138 g). Males and females are approximately the same size. The majority of this large amount of variation in size is distributed across regional populations. The blunt face and short ears give them an almost vole-like appearance. The fur is soft and long and is almost uniformly dark gray, brown, or reddish, with the underparts being slightly lighter. Tail is sparsely furred, dark above, and light below. Incisors are ungrooved and yellow.

DISTRIBUTION
Are found from southern Kenya to northeastern Cape Province, South Africa.

HABITAT
Found in the savannas and grasslands of central and southern Africa below 8,200 ft (2,500 m) in elevation. They are most common in moist, dense grasslands. They build nests in dense grass or in burrows, and runway systems through and under grasses and vegetation that form a dense canopy.

BEHAVIOR
Solitary animals, although congregations may occur near water and quality food sources. Throughout much of their range, they are active during the day, although they are primarily nocturnal in other areas. They swim across shallow water readily.

FEEDING ECOLOGY AND DIET
Herbivorous, eating mainly grasses, and reed shoots, roots, and rhizomes. Their hindguts are complex and elongated to accommodate their herbivorous diet. They also eat bark and seeds on occasion. Grass stems are cut off at their base and the tender parts eaten.

REPRODUCTIVE BIOLOGY
Reproduction is not well understood. They may begin breeding at four months old and breed several times in a year, with births peaking during wet seasons. Breeding is synchronized by photoperiod changes. Information on gestation period, number of young, and the development of young is unavailable. However, museum records indicate the litter size may be from one to five young. Young are born well developed, with a full coat of fur and their incisors, which they use to cling to their mother's nipples for a period of time.

CONSERVATION STATUS
Common throughout their range, they are not considered threatened. Their close relative *Otomys occidentalis* of Cameroon and Nigeria is considered Endangered.

SIGNIFICANCE TO HUMANS
Captured and eaten by humans in some areas. They are important parts of grassland ecosystems, involved in recycling nutrients and acting as an important and abundant prey base for small predators. ◆

Crested rat
Lophiomys imhausi

SUBFAMILY
Lophiomyinae

TAXONOMY
Lophiomys imhausi Milne–Edwards, 1867, Somalia.

OTHER COMMON NAMES
English: Maned rat.

PHYSICAL CHARACTERISTICS
Distinguished by a number of distinctive features. Head and body length 10–14.1 in (255–360 mm); tail 5.5–8.4 in (140–215 mm); weight 20.8–32.4 oz (590–920 g). Females are typically larger than males. The fur is long, dense and silky, except for an erectile crest of coarse fur along the back and onto the tail; this crest, or mane, is raised when the animal is startled. The fur on either side of the mane is shorter, and lighter in color, having the effect of emphasizing the mane. The fur is generally brown or black with a pattern of white stripes and spots extending from the head. Individual hairs are banded with dark and light color, giving them a frosted appearance. The underparts are dark in color and the feet are black; the tail is bushy and tipped in white. They have a blunt face and short, rounded ears; they resemble small porcupines. They have four digits on their hands and feet and a partially opposable thumb, making them well adapted to arboreal life. Their skulls are strangely modified; the temporal fossae are entirely covered in bone and the surface of the skull appears granulated.

DISTRIBUTION
Found in southern Sudan, Ethiopia, Somalia, Kenya, and Sudan.

HABITAT
There is some disagreement on what kinds of habitats they are found in They are generally believed to be restricted to montane forests, but are found from sea level to 10,825 ft (3,300 m) in Ethiopia in a variety of habitats.

BEHAVIOR
Nocturnal and solitary, they emerge from their burrows at dusk to begin foraging. They are arboreal and are adept at climbing, though they do so slowly. They emit hissing, snorting, and growling sounds.

FEEDING ECOLOGY AND DIET
Herbivorous, they use their hands to grasp leaves and shoots and eat them while sitting on their hindquarters.

REPRODUCTIVE BIOLOGY
Very little is known about their reproduction. They may have one to three young at a time, which develop quickly and are capable of feeding on their own at 40 days old. May live for a long time, reaching almost eight years old in captivity.

CONSERVATION STATUS
Information on populations is incomplete; they are not currently listed as threatened.

SIGNIFICANCE TO HUMANS
May be eaten by natives on occasion. ◆

Malabar spiny dormouse
Platacanthomys lasiurus

SUBFAMILY
Platacanthomyinae

TAXONOMY
Platacanthomys lasiurus Blyth, 1859, India.

OTHER COMMON NAMES
English: Malabar spiny mouse, and blind tree mice.

PHYSICAL CHARACTERISTICS
Head and body length 5.1–8.3 in (130–212 mm); tail 2.9–3.9 in (75–100 mm) long. They have a delicate, pointed muzzle, small eyes, and naked ears. Their dental formula is the same as other murids and they lack premolars. The underfur is dense and soft and is intermixed with a thick layer of flattened spines on the back and fewer, smaller spines on the underparts. The tail is long, sparsely furred, scaly, and is tipped with long hairs that form a distinct brush. Fur color is generally reddish brown on the back and head and grayish white on the belly and feet. The tail is darker than body color, but terminates in a light-colored tip.

DISTRIBUTION
Occur in southern India in habitats below 9,840 ft (3,000 m).

HABITAT
Typically found in forested habitats and rocky hillsides between 1,970–2,950 ft (600–900 m) in elevation. They construct nests of leaves and moss in trees and rock crevices.

BEHAVIOR
Arboreal, moving by climbing and leaping in trees. They are active at night.

FEEDING ECOLOGY AND DIET
Eat fruit, grains, seeds, and roots. They are called "pepper rats" because they eat large quantities of pepper fruits.

REPRODUCTIVE BIOLOGY
The specifics of reproduction are unknown.

CONSERVATION STATUS
Quite abundant and are not considered threatened.

SIGNIFICANCE TO HUMANS
Locally abundant, becoming agricultural pests in some areas, particularly on pepper crops. ◆

Siberian zokor
Myospalax myospalax

SUBFAMILY
Myospalacinae

TAXONOMY
Myospalax myospalax (Laxmann, 1773), Russia.

OTHER COMMON NAMES
English: Zokors.

PHYSICAL CHARACTERISTICS
Head and body length 5.9–10.6 in (150–270 mm); tail 1.1–3.7 in (29–96 mm). Stout, torpedo-shaped animals with powerful limbs and claws suitable for digging. Their eyes are very small and are often covered by the fur and there are no external ears, both adaptations for their fossorial lifestyle. The fur is soft, long, and lacks guard hairs. Color varies among different shades of brown and gray, with the underparts being slightly lighter than the upper parts. Individual hairs are often darker at the tips.

DISTRIBUTION
Found in Russia and Kazakhstan.

HABITAT
Found in forested and agricultural areas with soils suitable for their digging activities. They live almost entirely underground, digging long tunnels very rapidly. Their presence is easily determined by a characteristic mound pattern. Burrows are created in a similar manner and consist of nest chambers, food storage areas, a defecation chamber, and a series of tunnels. Burrows are generally at depths of 6.5 ft (2 m).

BEHAVIOR
Active throughout the year and throughout the day. They sometimes emerge from their underground tunnels to forage on the surface at night. Despite their much-reduced eyes, they seem sensitive to light. They squeal when disturbed.

FEEDING ECOLOGY AND DIET
Eat mainly roots and grains. They burrow underground to gain access to roots.

REPRODUCTIVE BIOLOGY
Not much is known about reproduction. Females with 2–6 young have been captured in spring, but reproduction could occur at other times.

CONSERVATION STATUS
Several zokor species, including Siberian zokors, are not considered threatened, but at least four are considered Vulnerable by IUCN.

SIGNIFICANCE TO HUMANS
Can be agricultural pests and are actively hunted to reduce population sizes. ◆

Palestine mole rat
Nannospalax ehrenbergi

SUBFAMILY
Spalacinae

TAXONOMY
Nannospalax ehrenbergi (Nehring, 1898), Jaffa, Israel.

OTHER COMMON NAMES
English: Blind mole rat.

PHYSICAL CHARACTERISTICS
Head and body length 5.9–10.6 in (150–270 mm); there is no external tail. Characterized by the lack of external openings for the eyes and ears. Small eyes are present below the skin and the ears are reduced to a small ridge. There are sets of whiskers along the face to aid in tactile sensation and it is thought that their sense of hearing is acute. They are robustly built, with a large head, powerful limbs, and a streamlined body. Their incisors are very large and project beyond the lips when the mouth is closed. The claws are small.

DISTRIBUTION
Found along the coasts of the Mediterranean Sea from Libya, through Egypt, Palestine, and Syria.

HABITAT
Prefer to occupy areas with sandy or loamy soils and are found in a variety of habitats. They do not occur in desert areas. They spend most of their lives in their underground burrow systems, which are complex and made up of multiple foraging tunnels, nest chambers, storage areas, and latrines. Burrow depth is influenced by weather, with burrows occurring deeper in the hot, summer months. Burrow systems may also include mounds, which are found aboveground. In the center of the mounds are sleeping chambers.

BEHAVIOR
Solitary and active throughout the day. Burrow systems are generally occupied by single animals.

FEEDING ECOLOGY AND DIET
Eat the underground parts of plants, including roots, tubers, stems, and seeds that can be obtained from below ground. Food is stored in underground chambers.

REPRODUCTIVE BIOLOGY
Apparently use an unusual form of locating mates, whereby males and females produce vibrations by drumming the top of their head against burrow ceilings. During the mating season, females construct elaborate, aboveground breeding mounds made up of tunnels and multiple chambers. The central chamber is the nest chamber. Males construct mounds surrounding the breeding mound of a female. Mating occurs once yearly from November–March and young are born from January–April. Litter size is one to five young. These young are born naked and helpless, but develop quickly, leaving the nest at 4–6 weeks old. Maximum lifespan in the wild is 4.5 years.

CONSERVATION STATUS
Not currently considered threatened, though, in general, they may be vulnerable to habitat modifications and persecution by humans.

SIGNIFICANCE TO HUMANS
Considered agricultural pests in some areas, but in other regions are not considered destructive. In Libya, it is believed that blindness results from touching a mole rat, so they are left unharmed. They have been instrumental in locating significant archeological sites by bringing buried items to the surface. ◆

Large bamboo rat
Rhizomys sumatrensis

SUBFAMILY
Rhizomyinae

TAXONOMY
Rhizomys sumatrensis (Raffles, 1821), Malacca, Malaysia.

OTHER COMMON NAMES
English: African mole rat, bamboo rat, root rat.

PHYSICAL CHARACTERISTICS
The largest species of bamboo rat: head and body length to 18.9 in (480 mm); tail to 7.8 in (200 mm); weight to 8.8 lb (4 kg). They have robust, streamlined bodies, with powerful limbs, strong claws, procumbent, orange incisors, and small eyes and ears. The fur is short and coarse, and is generally light gray. Individual hairs are tipped in white, giving them a frosted appearance. Their tails are scaled and without fur. Similar in appearance to American pocket gophers, but lack cheek pouches.

DISTRIBUTION
Found in Myanmar, Thailand, throughout Indochina, the Malay Peninsula, and Sumatra.

HABITAT
Live in bamboo forests at elevations between 3,937–13,123 ft (1,200–4,000 m). They spend much of their lives in their underground burrows among the bamboo roots. Individuals use both their teeth and powerful claws to dig several burrows, each of which has is made up of foraging tunnels and nest chambers.

BEHAVIOR
Not much is known about their behavior. They move slowly and can be fierce when cornered. They emit grunting and tooth-grinding noises when upset. They are probably solitary and active throughout the day.

FEEDING ECOLOGY AND DIET
Eat primarily bamboo roots, but will also forage aboveground at night, when they take stems, leaves, fruit, and seeds. They have been observed climbing bamboo stalks to cut sections that are then taken into the burrow.

REPRODUCTIVE BIOLOGY
Breeding occurs twice yearly, once from February–April and again from August–October. Litter size is one to five young. They are born naked and helpless in their mother's nest chamber, but develop quickly, being able to eat plant foods at one month old. They live for about four years.

CONSERVATION STATUS
Not currently threatened, though they may be vulnerable to habitat destruction and persecution by humans.

SIGNIFICANCE TO HUMANS
Sometimes are agricultural pests, especially of sugar cane and tapioca roots. They are captured as food by humans. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Setzer's hairy-footed gerbil *Gerbillurus setzeri*	Stocky, with hairy feet and long, well-furred tail. Light brown in color, with white underparts. Tail has brushy tip and a length of 4.4–5.8 in (11.3–14.5 cm). Head and body length is 8.5–10 in 21.7–26.3 cm).	Extremely arid and hot areas of the Namib Desert, most often on compacted, gravel plains, but sometimes colonize dune areas when population densities are high. They construct burrows, which guard them from the extremes of temperature and aridity in their habitat. Burrows are complex, branched, and tend to be longer and deeper than those of most gerbils. Characteristics of burrows, and the fact that these gerbils are more tolerant of conspecifics than are other gerbils, suggests that they are more social than most gerbil species.	Along the coasts of Angola and Namibia, in the Namib desert.	Information on diet is limited. Known to eat seeds, insects, and other plant material.	Not listed by IUCN
Bushveld gerbil *Tatera leucogaster* English: Large naked-soled gerbil	Sleek, short fur, large eyes, well-developed hindlimbs and long, bi-colored tails. Soles of the hindfeet are bare. Body length 3.5–7.9 in (9–20 cm) and tail length 4.5–9.7 in (11.5–24.5 cm).	Arid grasslands, plains, and woodlands with soils suitable for burrowing. Large burrow systems with multiple entrances and nest chambers. Active at night and generally move by walking, but are capable of large, bounding hops when they must make a rapid escape.	From Angola and Tanzania to South Africa.	Seeds, roots, bulbs, foliage, and insects.	Not listed by IUCN
Fat-tailed gerbil *Pachyuromys dupras*	Unusual member of the gerbil subfamily is relatively stocky and short-legged. Most notable feature is a short, thick tail, which appears somewhat club shaped and probably serves to store fat. Fur is soft and ranges from light yellow to buffy brown. Ears are short and white and the eyes are large. Full complement of whiskers along the nose. Head and body length is about 4 in (10.5 cm) and tail length is 1.5–2.5 in (4.5–6 cm).	Believed to be restricted to a particular desert habitat, hamadas, which are gravelly areas marked by perennial bushes.	Northern Sahara region, from Morocco to Egypt.	Insectivorous.	Not listed by IUCN
Fat mouse *Steatomys pratensis*	Thick-bodied, with short, round ears, and a thick tail. Four fingers and five toes and grooved upper incisors. Commonly brown above with white below, fur is soft and short. Length 2.5–5.8 in (6.5–14.5 cm) and tail length 1.3–2.3 in (3.4–5.9 cm).	Found in a variety of habitats, from arid areas to forests and agricultural areas. Active at night and construct burrows in loose soils. Burrows are deep but simple, consisting of entrance and exit tunnels and a main sleeping chamber. Solitary, except for mothers and their young.	Found throughout much of Africa, from Cameroon and Sudan in the north to Namibia and eastern South Africa in the south.	Seeds, grass bulbs, and insects. Known for their ability to accumulate layers of fat that enable them to remain underground and inactive during seasons when food is scarce. Because of their high fat content they are considered a delicacy by indigenous peoples.	Not listed by IUCN

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Delany's swamp mouse *Delanymys brooksi*	Reddish brown above, with white chin and buffy underparts. Similarities in the structure of their cheek teeth has resulted in them being classified with rock mice in the subfamily Petromyscinae, though they are not alike in external appearance. Small mice with an extraordinarily long tail. Body length is 1.9–2.5 in (5–6.3 cm) and tail length 3.4–4.4 in (8.7–11.1 cm).	Little is known about these mice. Limited distribution, high elevation marshes between 5,280 and 8,610 ft (1,700 and 2,625 m) elevation. Nocturnal and climb well, using tail to balance. Globular grass nests with two entrances in vegetation above the ground.	High altitude marshes of eastern Democratic Republic of the Congo (Zaire) and western Uganda.	Mainly seeds.	Not listed by IUCN
Bukovin mole rat *Spalax graecus*	Powerful rodents with solid, chunky bodies, short legs and no tail, making them very mole-like in appearance. Dense, soft fur moves in either direction, making it easier to move in tunnels. Fur varies from brown to gray, with a lighter belly. Stiff whiskers extend from the snout to the eye; may serve as touch sensors. Head and body length is 6.7–13.8 in (17–35 cm) and weight is 0.5–1.25 oz (21.5–7 g).	Live in soils suitable for digging that get at least 4 in (100 mm) of rainfall each year. Variety of habitats, from plains to hilly areas and cultivated fields. Construct elaborate burrows with an upper level for foraging and lower levels with nesting chambers, storage areas, and chambers for defecating. Burrow systems can be quite extensive and mole rats are active throughout the year. Active throughout the day but sometimes forage above ground during the night. Blind mole rats are solitary.	Romania and south-western Ukraine.	Primary diet is made up of underground parts of plants, including roots and tubers. Sometimes forage on grasses, seeds, and insects above ground.	Vulnerable
Chinese pygmy dormouse *Typhlomys cinereus*	Soft, dense fur that is deep gray, under-parts lighter in color. Long tail is moderately furred and scaly, with white, brush-like tip. Although not superficially similar to Malabar spiny dormice, their dental formulae and structure are the same. Body length 2.8–3.8 in (7–9.8 cm), and tail length 3.7–5.3 in (9.5–13.5 cm).	Montane cloud forests dominated by dwarfed trees and bamboo understory. Elevations between 4,000 and 6,890 ft (1,200–2,100 m). Little is known about this mammal, although indigenous people readily trap them.	Found in southern China and northern Vietnam.	Diet is unknown.	Critically Endangered
East African mole rat *Tachyoryctes splendens*	Compact and sturdily built fossorial mammals, resembling North American gophers. Eyes and ears are small but visible. Large incisors project from their mouth beyond the lips. Claws are not large, as in other fossorial murids, but the legs are powerful. Fur is thick, dense, and soft, and varies in color from very dark to pale grays and browns. Body length is 6.3–10.2 in (16–26 cm), tail length 2–3.7 in (5–9.5 cm), and weight 0.3–0.6 oz (160–280 g).	Prefer moist grasslands in upland areas and agricultural fields. Can be found at high elevations, up to 13,600 ft (4,150 m). Construct large and complex burrows, including foraging tunnels, nest chamber lined with grass, escape tunnel, and a chamber for defecation. In dry seasons may become less active and burrow deeper into the earth. They burrow mainly using their large incisors, periodically turning in the burrow to push accumulated soil out of the tunnel with cheeks and forepaws. Active throughout the day and appear to be solitary.	Eastern Africa, including Ethiopia, Somalia, Uganda, Burundi, Rwanda, Kenya, and northern Tanzania.	Underground parts of plants, roots and tubers, although sometimes forage for grasses and legumes at the surface.	Not listed by IUCN
Pouched mouse *Saccostomus campestris*	Gray to brown robust, hamster-like mice with large cheek pouches, short, dense, fine fur, and short legs and tail. Belly, limbs, and ventral tail are white. Head and body length 3.7–7.4 in (9.4–18.8 cm), tail length 1.2–3.2 in (3–8 cm), and weight 0.08–0.18 oz (40–85 g).	Savannas, scrub forest, agricultural areas, and sandy plains. Dig own simple burrows or use those of others. Active at night, move relatively slowly, and store seeds during summer for winter use.	Southern Africa, from Angola, Zambia, Malawi, and Mozambique to South Africa.	Omnivorous, eating seeds, grain, nuts, fruit, and insects.	Not threatened

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Tanya Anne Dewey

Scaly-tailed squirrels
(Anomaluridae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Anomaluridae

Thumbnail description
Squirrel-like animals with a flexible furred membrane between the fore- and hindlimbs (except in one genus); long, silky fur and very long whiskers; long tail with two rows of pinecone-like scales one-third of the way along the underside

Size
Anomalurus: Head and body 7.3–18.5 in (18.5–46 cm); tail 5.4–18.4 in (13.8–45); weight 7 oz.–4 lb (200–1,800 grams); *Idiurus* and *Zenkerella*: Head and body 2.5–9 in (6.5–23 cm); tail 2.7–6.6 in (7–17 cm); weight 0.5–7.8 oz (14–220 g)

Number of genera, species
3 genera; 7 species

Habitat
Open dry forest and rainforest

Conservation status
Lower Risk/Near Threatened: 4 species

Distribution
Africa

Evolution and systematics

Anomaluridae is an exceedingly ancient rodent family, with a lineage extending back some 30 million years (late Eocene). Formerly much more diverse, some 20 fossil genera have been identified. The external resemblance to squirrels is misleading and, instead, anomalures are thought to resemble closely the rodent stock from which today's porcupines, rats, and squirrels are descended. Anomalures are an evolutionary enigma, very ancient and yet at the same time highly specialized. The anomalure lineage is thought to have survived for so long because they have specialized in a substance that is easily found but that few other mammals can eat: tree bark. Their family name, means "the strange-tailed ones." All members use the furred membranes for gliding between trees, sometimes very adeptly. This ability is thought to have arisen originally for moving between the widely spaced trees of dry seasonal forests, not unlike today's *Brachystegia* "miombo" woodlands. A pliable fur-coated membrane extends between the legs and also extends between the hind legs and the tail. The presence of a similar membrane in 14 genera of flying squirrels (*Aeretes*, *Aeromys*, *Belomys*, *Biswamoyopterus*, *Eupetaurus*, *Glaucomys*, *Hylopetes*, *Iomys*, *Petaurillus*, *Petaurista*, *Petinomys*, *Pteromys*, *Pteromyscus*, *Trogopterus*) and the marsupial genus *Petaurus* is a remarkable example of convergent evolution.

The systematic position of this family has been much debated. In the past they have variously been grouped with Old World porcupines, the mouse-related rodents, and the squirrel-related rodents. Sometimes, they are included in the separate suborder, Anomaluromorphia, and superfamily, Anomaluroida. This also includes another family, the Zegdoumyidae, which is extinct. Unlikely as it may seem, the closest relative to the anomalures may well be the springhare (*Pedetes capensis*), a thoroughly terrestrial resident of southern Africa's semi-arid grasslands. It too has a very ancient lineage.

Physical characteristics

There are two major forms in this family, the large anomalures and the smaller flying mice (one of which cannot fly). With their roughly square gliding membranes extended, members of the former group may be larger than a tea tray, while in the same condition the latter are smaller than the cover of a paperback novel. A cartilaginous extension of the elbow keeps the flying membrane rigid, while allowing the

front limbs greater freedom for manipulative tasks. This strut is one of the anomalurids' unique features. The membrane, though thickly furred on top, is relatively sparsely furred on the underside. Eyes are large and forward facing, providing excellent biocular vision. Hearing is acute and may extend to ultrasonic frequencies. The two rows of spiked scales under the tail act as anti-skid devices on landing and also provide extra grip during climbing, or support while resting vertically on a trunk. For extra grip, claws are robust and sharp. The membrane is very flexi ble, and forms a loose folded extension of the flank when not in use. It does not hinder movement and all anomalurids can run along branches like the garden-familiar *Sciurus* squirrels. Anomalures do not come voluntarily to the ground. When placed on it they are clumsy, moving away in clumsy kangaroo-like hops.

Distribution

Anomalurids live in Africa south of the Sahara, but are absent from southern Africa.

Habitat

These animals live in the rainforests of West and Central Africa and the open drier woodlands of East Africa. The anomalures' distribution closely maps the distribution of five of the most preferred food trees: *Brachystegia* (miombo), *Cynometra* (ironwood), *Dialium* (velvet tamarind), *Julbernadia* (awoura), and *Pentaclethra* (owala oil).

Behavior

They are the only gliding mammals in Africa and fulfill a similar ecological role to gliding squirrels elsewhere. Anomalures remove small branches that obstruct their traditional gliding lines out from their denning tree. The long duration of the Anomalure lineage has led to some remarkable examples of coevolution with the tree species they feed on, including the deliberate gnawing off of the tops of any young non-food trees nearby, thus reducing competition with their food trees and favoring food tree growth. Anomalures and hornbills compete for dens/nest holes. Eagles are occasional predators. Scent is important in communication and large glands in the groin region produce a variety of strong-smelling secretions. Field studies of anomalures have been made difficult by the remoteness of their habitat and by the fact that they are sensitive to the red light biologists usually use to observe nocturnal animals. Anomalures are not rare, but they are hard to find. Recent population estimates in the Foret des Abeilles, central Gabon, indicate that there may be up to 500 anomalures (of three species) per 1.2 mi^2 (1 km^2).

Feeding ecology and diet

The large anomalures gnaw bark and small branches from more than a dozen types of tree. They may also eat gum and insects. The smaller ones (flying mice) are believed to eat insects and gum almost exclusively. Bark is a low-nutrient food source. To compensate, anomalures have long guts, allowing the extraction of the maximum nutrients. These comprise half the weight and much of the body volume of an adult anomalure. Gut contents regularly exceed 12% of body weight. In order that they may still glide effectively, the anomalure skeleton is very lightweight.

Reproductive biology

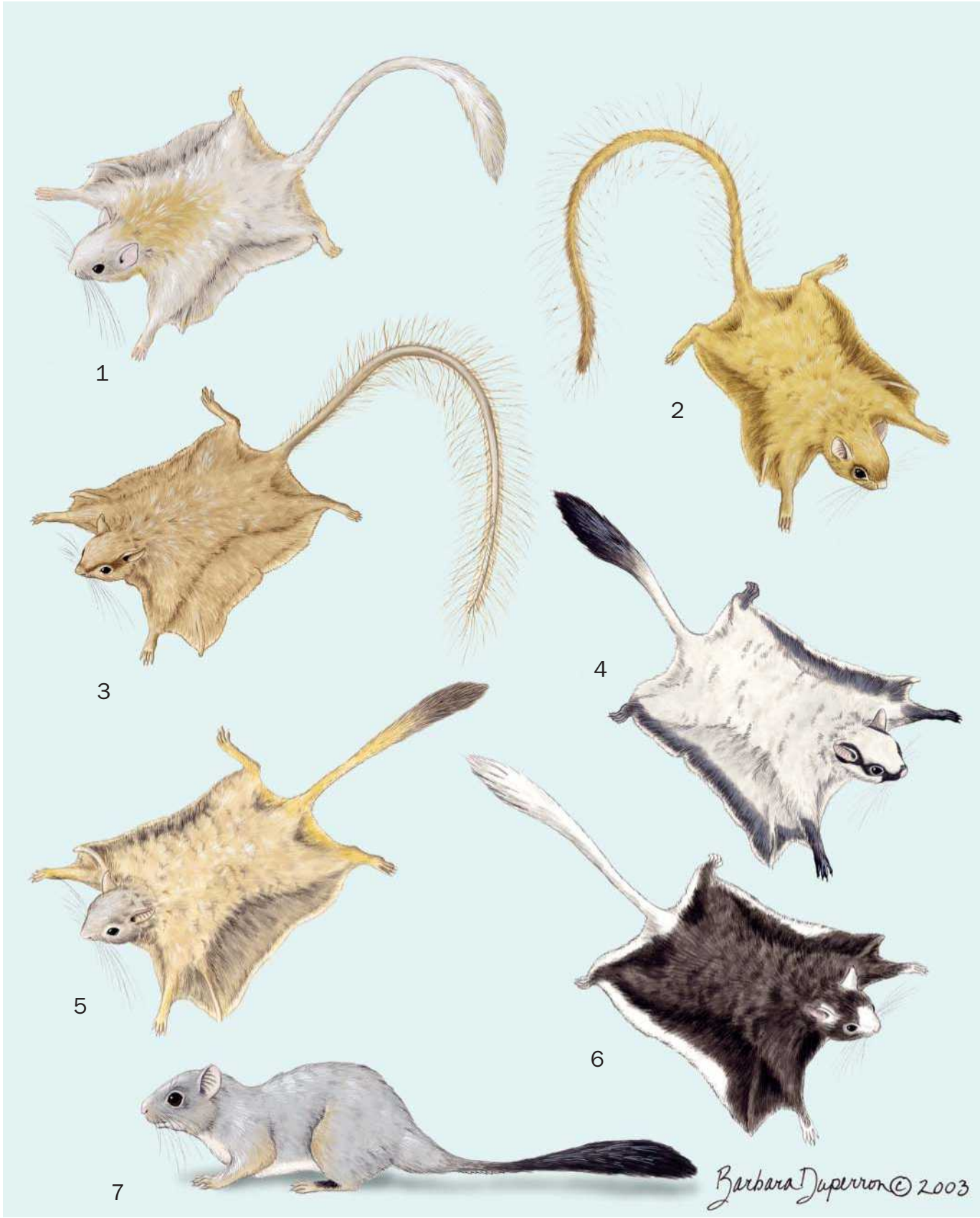
The young are born with thick fur and open eyes (precocial). Litter size may be up to three. They are weaned onto solid food via finely chewed food held in the parents' cheek pouches.

Conservation status

Four species are Lower Risk/Near Threatened (*Anomalurus pelii*, *Idiurus zenkeri*, *I. macrotis*, and *Zenkerella insignis*). The remaining three species are not threatened.

Significance to humans

Occasionally accused of robbing oil palms for their nuts, but not regarded as a major pest. The large anomalures are highly dependent on particular species of tree and require tall trees, with a clear sub-canopy and enough old trees to provide an abundance of holes. Hence they are vulnerable to habitat disturbance. Many of their food tree species are valued commercially for timber.



1. Beecroft's anomalure (*Anomalurus beecrofti*); 2. Zenker's flying mouse (*Idiurus zenkeri*); 3. Big-eared flying mouse (*Idiurus macrotis*); 4. Lord Derby's anomalure (*Anomalurus derbianus*); 5. Lesser anomalure (*Anomalurus pusillus*); 6. Pel's anomalure (*Anomalurus pelii*); 7. Cameroon scaly-tail (*Zenkerella insignis*). (Illustration by Barbara Duperron)

Species accounts

Lord Derby's anomalure
Anomalurus derbianus

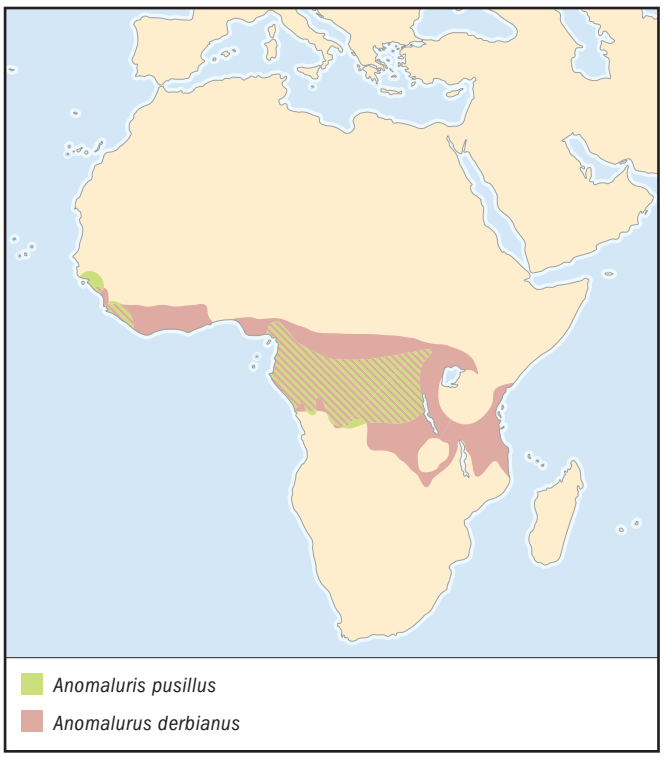
SUBFAMILY
Anomalurinae

TAXONOMY
Pteromys derbianus (Gray, 1842), Sierra Leone. One of the subspecies of *A. derbianus* in the Congo, is occasionally given species rank as *A. fraseri*. Sixteen subspecies.

OTHER COMMON NAMES
English: Lord Derby's scalytail; French: Ecureuil volant de Derby; German: Gemeines Dornschanz-hornchen.

PHYSICAL CHARACTERISTICS
Physical characteristics vary geographically over its range, with the dorsal fur varying from gray to rich russet grizzled with silver. The subspecies, though all share the characteristic facial pattern of white snout, forehead, and cheeks, with a black band above the nose, around the eyes and back of the head. Head fur is dense and velvety, body fur long (to approximately 1 in [or 25 mm] or more) and silky. The tail is shorter than the head and body. The last half of the tail is generally black. The ears are naked and pink. There are six pairs of tail scales.

DISTRIBUTION
Widely distributed from western Sierra Leone to west Kenya and, more sparsely, from north Angola to northern Mozambique.



HABITAT
From sea level to 7,875 ft (2,400 m) in moist rainforests and seasonally dry woodlands, wherever forest provides food trees, refugia, and denning holes. Studies in the rainforests of Gabon found that most roosting trees were hollow with both basal and high holes. The high hole was often only just big enough to squeeze an anomalure body through. There was no preference in tree species.

BEHAVIOR
Up to eight animals may share a den, and individuals show fidelity to a particular den for many seasons. Social behavior of *A. derbianus* remains to be studied. Den may be up to 130 ft (40 m) up, always in a hollow in an old tree. Used holes may vary in diameter from 1 to 8 ft (0.3–2.5 m). In the den, humidity varies little (90–95%) and temperature is also fairly constant (66–77°F [19–25°C]).

Although predominantly nocturnal, anomalures enjoy sunbathing in the early morning and, to a lesser extent, in the late afternoon. Vocalizations include a variety of social purrs and twitters and a series of defensive growls and hisses. Long-distance movement is by gliding, with speed checked before alighting by a final upturn to induce a stall. *A. derbianus* has been reliably measured as having glided 820 ft (250 m). An adult female, radio-tracked in a Gabonese rainforest, traveled an average of 1,770 ft (540 m) per night, with most glides being less than 328 ft (100 m). The total home range was less than 8.6 acres (3.5 ha). A male averaged 3,480 ft (1,060 m) per night and used an area of 22.8 acres (9.25 ha).

FEEDING ECOLOGY AND DIET
Diet consists of the bark of a dozen species of trees, leavened with fruits, flowers and nuts. Occasional insectivory also recorded. Thick bark from large limbs and the main trunk is preferred. *A. derbianus* will maintain several simultaneous feeding sites. At each, it will remove a single narrow strip adjacent to that from the previous night's feeding. Action at a particular site is curtailed when damage gets too extensive (beyond about 5.9 in [15 cm] wide). Feeding sites are initiated at natural bark wounds caused by growth splits and falling branches and by elephant damage. The trees are physiologically adapted to the rodent's depredations and grow replacement bark. In the rainforests of Gabon, an individual of the subspecies *fraseri* was found to have substantial volumes of termites in its stomach. Bark is sometimes scraped away and just the oozing phloem sap licked up while the bark is ignored. Such wounds may be revisited for the insects they attract.

REPRODUCTIVE BIOLOGY
Reproduction is seasonal for dry-forest subspecies, but not so for those inhabiting rainforests. Females may move to a special nursery den. Young are large and capable of coordinated movement soon after birth, but they remain in the nest until almost fully grown. After weaning, they are fed chewed-up food, brought in the cheek pouches of their parents. Females have also been observed gliding in the forest in the company of nearly full-grown young. Three animals were once observed gliding repeatedly between trees and chasing each other as if in play.

CONSERVATION STATUS
Despite its specializations, the species is widely spread enough not to be threatened. Population in Ghana are on CITES Appendix III.

SIGNIFICANCE TO HUMANS
None known. ◆

Pel's anomalure
Anomalurus pelii

SUBFAMILY
Anomalurinae

TAXONOMY
Pteromys (Anomalurus) pelii (Schlegel and Muller, 1845), Dubacrom, Ghana.

OTHER COMMON NAMES
English: Pel's scaletail; French: Ecureuil volant de Pel; German: Pel Dornschwanz-hornchen.

PHYSICAL CHARACTERISTICS
The largest anomalure, Pel's all-black back and pure white belly are quite distinctive. The fur on the head is black, and the snout and fur at the bases of the ears is white. The tail is white and as long as the head and body, with a thickened brush of fur on the last half. The gliding membranes are black in some subspecies and white in others. There are six pairs of tail scales. They are especially well developed in this species.

DISTRIBUTION
Liberia to Ghana, West Africa.

HABITAT
Lowland moist rainforests only, with a preference for forests with palms and tall emergent trees.

BEHAVIOR
Dens may contain up to six animals. Highly nocturnal, *A. pelii* emerges only well after sunset, and is aggressive, using deep hoots as contact calls. Defensive noises include growls, hisses and tooth-chatterings, which the den hole may serve to amplify.

FEEDING ECOLOGY AND DIET
Supplements diet of bark with palm fruits. Observed eating leaves, twigs, and flowers of *Antiaris toxicaria*, an important timber tree in Ghana.

REPRODUCTIVE BIOLOGY
Litter size of three. Two litters a year.

CONSERVATION STATUS
The IUCN considers the species to be Lower Risk. Population in Ghana is on CITES Appendix III.

SIGNIFICANCE TO HUMANS
Sometimes blamed for damage to oil palm crops. ◆

Beecroft's anomalure
Anomalurus beecrofti

SUBFAMILY
Anomalurinae

TAXONOMY
Anomalurus beecrofti Fraser, 1853, Bioko, Equatorial Guinea. This species is sometimes placed in its own genus *Anomalurops*, which means "closely resembling Anomalurus." It was named for John Beecroft, an Englishman who was made Governor by the Spanish of their colonial possession of Fernando Po.

OTHER COMMON NAMES
English: Narrow-snouted scalytail; French: Ecureuil volant de Beecroft; German: Beecroft Dornschwanz-hornchen.

PHYSICAL CHARACTERISTICS
Snout, and head generally, markedly narrower than other anomalures. Tail proportionately much shorter and narrower than other species of anomalure. Tail has nine pairs of tail scales. A species with a wide range and corresponding geographical variation. Dorsal colors range from gray to rich red or orange. The belly is always some shade of orange-yellow and the head always has a white spot (of variable size) in the middle of the forehead.

DISTRIBUTION
Southern Senegal to eastern Democratic Republic of the Congo.

HABITAT
Rainforest, from sea level to 8,200 ft (2,500 m). Also cultivated palm groves and disturbed land if some big trees remain.

BEHAVIOR
Probably a species that, in undisturbed forest, makes use of natural tree falls and the palms that grow up in them. Much less dependent on deep forest than the other anomalures, this species can occur in agricultural areas. Quite often active during the day. Females with young build nests of leaves in tree holes. Males and non-reproducing females may hide during the day beneath large branches or at the basal junction of a palm's frond and trunk, or may crouch flat against a trunk. Members of this species may take palm nuts back to the den to peel and eat.

FEEDING ECOLOGY AND DIET
Less dependent on bark than other anomalures. Though eaten, bark is less important than fruits (especially those of palms). Some leaves and insects are also eaten.

REPRODUCTIVE BIOLOGY
Not known. A female with a single embryo has been collected.

CONSERVATION STATUS
Not considered to be threatened. Population in Ghana is on CITES Appendix III.

SIGNIFICANCE TO HUMANS
Occasionally blamed for loss of palm fruits, but not hunted punitively. ◆

Lesser anomalure
Anomalurus pusillus

SUBFAMILY
Anomalurinae

TAXONOMY
Anomalurus pusillus Thomas, 1887, Democratic Republic of the Congo.

OTHER COMMON NAMES
English: Dwarf scalytail; French: Ecureuil volant de pygmlbée; German: Zwergdornschwanz-horchen.

PHYSICAL CHARACTERISTICS
The smallest anomalure, the coloration of *A. pusillus* varies from a mottled light gray and tan to very dark gray. The underside is usually a yellow-washed gray. Head is generally gray with no facial pattern. There are seven named subspecies. The tail, one-third the length of the body, generally has a black hinder third.

DISTRIBUTION
Three isolated populations in Senegal, Sierra Leone/Liberia and Cameroon/Gabon/Congo.

HABITAT
Deep primary lowland rainforest.

BEHAVIOR
Little studied. Known to roost in hollow trees.

FEEDING ECOLOGY AND DIET
Bark and fruit.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Naturally rare, but not categorized as a species of concern by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Zenker's flying mouse
Idiurus zenkeri

SUBFAMILY
Zenkerrinae

TAXONOMY
Idiurus zenkeri Matschie, 1894, Yaunde, southern Cameroon.

OTHER COMMON NAMES
English: Dwarf flying mouse; French: Ecureuil volant de Zenker; German: Zenker Gleitbilch.

PHYSICAL CHARACTERISTICS
With a head and body less than 3.9 in (10 cm) long, this is the smallest member of the family. Weight: less than 0.5 oz (15 g). The body is buff-colored above, a gray-white below. The tail, 50% longer than the head and body, has an underside fringed with two rows of stiff hairs. Long, scraggly sparsely distributed hairs emerge from the tail's upper surface. The snout is conspicuously upturned and the oddly notched upper incisor teeth are especially long and protrude beyond the lips.

DISTRIBUTION
Central Africa, Cameroon, and Democratic Republic of the Congo.

HABITAT
Primary moist lowland rainforest.

BEHAVIOR
Strictly nocturnal and little known. Recorded roosting in hollow trees in groups from three to over 100. Small colonies may also roost under bark. Believed to travel many miles (kilometers) a night in search of food. Zenker's flying mouse is an exceptionally agile glider, capable of glides exceeding 164 ft (50 m) and of intricate spirals and of S-shaped glides close to trunks. Shrill mouse-like squeaks have been reported.

FEEDING ECOLOGY AND DIET
Oil palm pulp, insects, and nectar.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Big-eared flying mouse
Idiurus macrotis

SUBFAMILY
Zenkerrinae

TAXONOMY
Idiurus macrotis Miller, 1898, Efulen, Cameroon. Now believed to include the species *I. kivuensis*.

OTHER COMMON NAMES
French: Anomalure nain; German: Grosshargleitbilch.

PHYSICAL CHARACTERISTICS
A larger animal with darker, grayer fur than *I. zenkeri*. The ears are longer and black compared to the pale brown of *zenkeri*. The tail is only 25% longer than the head and body.

DISTRIBUTION
Two isolated populations. Sierra Leone, Liberia, Ivory Coast, Ghana; Cameroon, Gabon, Congo, and north eastern Democratic Republic of the Congo. No records from Nigeria.

HABITAT
Primary lowland rainforests, but also uses areas where local small plantations have thinned the canopy.

BEHAVIOR
Recorded sharing hollow tree roosts with *I. zenkeri*, other anomalures, and bats. In Gabon, prefers trees with a single large basal hole. Groups of animals may use the same den for several years in a row. An adult male, equipped with a radio collar, moved through an area of 7.4 acres (3 ha) in 48 hours, traveling an average of 2,590 ft (790 m) each night. Nocturnally active, the male began moving around 15 minutes after sunset and ending at dawn. On emerging, the colony members will spend some 30 minutes running up and down the trunk of the home tree before gliding out to forage. Though always seen resting in groups, *I. macrotis* appears to forage alone.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Five female *I. macrotis* were collected in June and August in eastern Democratic Republic of the Congo. Each had a single embryo.

CONSERVATION STATUS
Lower Risk/Near Threatened. Populations in Ghana are on CITES Appendix III. The species is on the country Red List in Sierra Leone and Ivory Coast.

SIGNIFICANCE TO HUMANS
None known. ◆

Cameroon scaly-tail
Zenkerella insignis

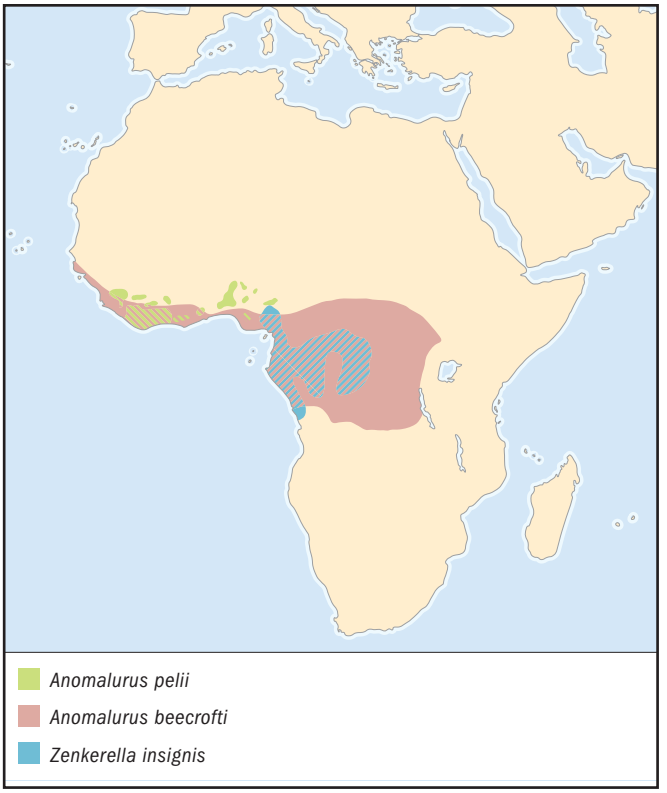
SUBFAMILY
Zenkerrinae

TAXONOMY
Zenkerella insignis Matschie, 1898, Yaunde, Cameroon. This rodent shares its generic name, *Zenkerella*, with a genus of African tree from the pea family.

OTHER COMMON NAMES
English: Flightless dwarf anomalure; German: Dornscgwanzbilch.

PHYSICAL CHARACTERISTICS
Strong resemblance to a very soft-furred dormouse. Large eyes, pink ears. Long ashy gray fur washed with dull yellow, especially on the lower limbs and cheeks. The underparts are a paler gray. Whiskers are long and shiny black. The tail is thick, with long black hairs. No flight membrane is present between limbs, but tail has the family's characteristic bark-gripping scales. There are 13 scales, one line of six and one of seven. Very little is known about this animal—less than two dozen have been caught and examined by scientists.

DISTRIBUTION
Known only from the western part of Central African rainforests; Cameroon, Equatorial Guinea, Gabon, Congo, and from Bioko Island (formerly Fernando Po) in the Gulf of Guinea.



HABITAT
Tolerates climates ranging from relatively dry (rainfall, 59 in [1,500 mm] per year) to very humid (394 in [10,000 mm] of rain per year). Most records from lowland rainforest, with a few from seasonally deciduous forest and treed savannas.

BEHAVIOR
Probably a day-active high-canopy specialist that has abandoned flight for a more scuttling progression. Very long, dense fur might cushion short leaps between trunks or branches. Must on occasion descend to the ground since has been caught in traps set for terrestrial rodents. Ankles have a brush of stiff hairs with flattened "spoon-like" tips. Associated with a patch of glands, they may serve to broadcast territorial scents, but the exact mechanism is uncertain. Rests by leaning against the interior wall of a hollow tree. Sometimes found roosting in the company of other anomalurids. Considered rare, though this may be an artifact of the remoteness of its habitat and the difficulty of studying small mammals in the rainforest canopy. In some parts of its range, the species may be nocturnal; the Bubi forest people of Bioko, who do not hunt at night, were unaware of this species.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Basically unknown. A male collected in the dry season had fully developed testes.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

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Adrian A. Barnett, PhD

Springhares
(Pedetidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Pedetidae

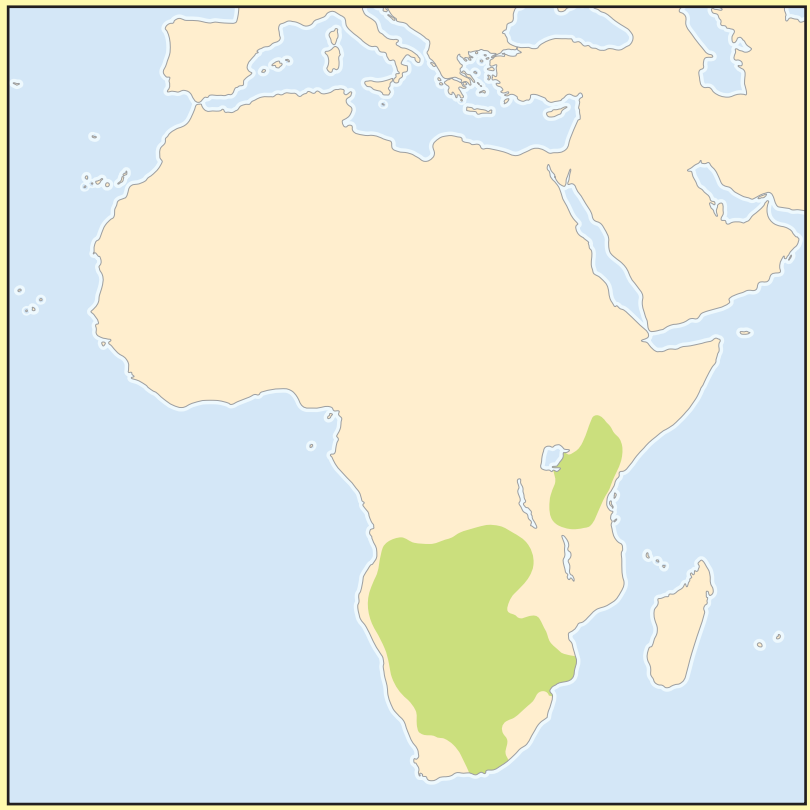
Thumbnail description
Short front limbs, powerful hind legs; long vibrissae and eyelashes; front paws clawed for burrowing; bushy tail with a black tip; soft pelage on the body with pinkish brown to gray upperparts and brownish white underparts

Size
Head and body length 10.7–16.7 in (27.2–42.4 cm); tail length 1.8–18.4 in (30–46.8 cm); weight up to 8.8 lb (4 kg)

Number of genera, species
1 genus; 1 species

Habitat
Scrub and grassland

Conservation status
Vulnerable



Distribution
Angola, Botswana, Congo, Kenya, Mozambique, Namibia, South Africa, Tanzania, Zambia, and Zimbabwe

Evolution and systematics

The earliest known fossil of the Pedetidae was recorded from the early Miocene at Elizabethfeld in Namibia as *Parapedetes namaquensis* while a larger form of the modern springhare (*Megapedetes*) appeared later in the Miocene in East Africa. The fossil record may be traced via the early Pliocene site at Taung (*P. gracilis*) in the northwestern Cape Province of South Africa (where notable australopithecine remains were discovered) to Pleistocene deposits in Bulawayo, Zimbabwe (as *Pedetes capensis*).

Historical confusion about its taxonomic position, brought about in part by a lack of substantive palaeontological records, saw *Pedetes* placed initially in a subfamily of jerboas (Dipodidae). The family Pedetidae was positioned subsequently in the suborder Hystricomorpha before its reclassification within the suborder Sciurognathi. In the 1920s, the "Pedetini" were placed by some taxonomists in the family Anomaluridae considered by others to be part of the superfamily Anomaluroidea. The family Pedetidae has now been returned to the suborder Sciurognathi.

The taxonomy for this species is *Yerbua capensis* (Forster, 1778), Cape of Good Hope, South Africa.

Physical characteristics

Resembling a small kangaroo, the springhare has short, front limbs and powerful hind legs, the latter adapted to ricochetal locomotion. The front paws are clawed for use in digging. The hind feet have four long toes with straight claws. The heel, the sole of the foot, and the base of each toe are hairless. Its large eyes are set in a blunt, short head. It has long vibrissae and eyelashes and long, narrow ears, which are thinly haired at the tip and naked inside. A well-developed tragus keeps sand from the ears when the animal is burrowing

The bushy tail is roughly the same length as the head and body and is tawny in color. The distal third is dark brown to black and the tip is noticeably black

The pelage of the body is composed of long, straight hairs and is soft and well-furred. The hairs of the dorsal area are a pinkish brown to sand in color with black tips and dark gray roots. The ventrum is buffy-white with a similarly-colored strip running upwards in front of the thighs and on the

Springhare (*Pedetes capensis*). (Illustration by Joseph E. Trumpey)

A springhare (*Pedetes capensis*) in mid-leap. (Photo by Frans Lanting/Minden Pictures. Reproduced by permission.)

inside of the leg. The coloration of the springhare varies geographically: specimens from eastern South Africa are paler than those found further to the west.

Distribution

Springhares are widely distributed throughout southern and eastern Africa. Their range extends from South Africa north to Angola and the southern Congo and northeast to Kenya but excludes eastern Zambia, southeastern and western Tanzania, and eastern and northern Kenya. They are present in areas of higher elevation (e.g., in Natal) but are absent from some coastal regions of South Africa, Tanzania, and Kenya and from the coastal fringes of the Namib Desert in Namibia. Some reports state that they occur neither in the east nor the northeast of Zimbabwe and in Mozambique only from the Sabi River southwards to about 25°S but no further. Distribution patterns indicate that springhares avoid rocky ground. In Kenya, they are sometimes found on "black cotton" soil that has a high clay contents and becomes quite hard when dry.

A springhare (*Pedetes capensis*) sleeping in its burrow. (Photo by Animals Animals ©C.-Par Houghton, OSF. Reproduced by permission.)

Habitat

Springhares are found most commonly in arid and semi-arid country with scant cover. Open, sandy areas are also favored, especially if these support light woodland. Heavily wooded areas are avoided. *Pedetes* is rarely documented in tall grass land but may enter these to feed on rhizomes. Heavily grazed areas are known to provide a useful food source because where the upper layers of grasses have been removed by larger ungulates, springhares will feed on the more succulent lower stems, often digging for roots when the above-ground plant growth has been consumed.

Behavior

The springhare is terrestrial and nocturnal, although individuals are occasionally observed during daylight hours. Although usually solitary, springhares may form male-female pairs. They are well equipped for burrowing and excavate one or more burrows with a diameter of 7.8–9.8 in (20–25 cm) up to 3 ft (0.9 m) below ground level, preferably in firm, sandy soil. They commence their emergence at dusk with a

The springhare (*Pedetes capensis*) uses its powerful hindlegs to jump short distances. (Photo by Gregory G. Dimijian/Photo Researchers, Inc. Reproduced by permission.)

A springhare (*Pedetes capensis*) emerges from its burrow. (Photo by W. T. Miller. Bruce Coleman, Inc. Reproduced by permission.)

powerful leap into the air to avoid the threat posed by potential predators waiting outside the entrance to the burrow.

Certain feeding areas may be favored and the springhare will return to these on a nightly basis, although established paths to the areas are not created. During feeding, *Pedetes* will move on all fours and will sit up, using its tail as a support, when consuming food. When proceeding at full speed, the species hops using only the rear legs in the same manner as kangaroos. Although a distance of 2.2 yd (2 m) (some sources suggest leaps of up to 9.8 yd [9 m]) may be covered in a single bound, springhares avoid moving at speed downhill due to their ricochetal gait.

Pedetes capensis has keen senses of hearing, smell, and vision and will run away at the least sign of danger due to its limited fighting abilities. When sleeping, *Pedetes* will sit on its haunches with head and forelimbs buried between the thighs and the tail coiled around the body.

Although usually silent, the species may occasionally emit low grunts.

A newborn springhare (*Pedetes capensis*). (Photo by John Visser. Bruce Coleman, Inc. Reproduced by permission.)

Feeding ecology and diet

The diet of the springhare incorporates stems and rhizomes of grasses (particularly fine leaf couch grasses), bulbs, and grain. In areas of cultivated land, maize (corn), barley, wheat, peanuts, and oats may be consumed. Beetles, locusts, and other insects may supplement the diet, when several miles per night need to be covered in the search for food. Feeding at some sites may damage commercial crops.

Reproductive biology

Young may be born at any time of the year, a possible reason for which may be the continuous availability of the rhizomes and shoots of couch grasses. The young are born in bare chambers in the burrows. One offspring is produced, although in very rare circumstances pregnant females may carry twin fetuses. Accurate data are lacking on the gestation period but this is believed to be in the region of two months. It has been suggested that the period between conceptions is on the order of 101 days, that the average interval between parturition and conception is 24 days, and that 3.6 is the mean number of pregnancies per year. At birth, the young weigh 9.8–10.6 oz (280–300 g), are well haired and open their eyes on the second day. Juveniles are suckled in the burrow by their mothers, who have two pairs of pectoral mammae, until they reach a weight of 2.75 lb (1,250 g) at six to seven weeks. When they emerge, they are weaned rapidly on a diet of grasses. Spermatogenesis occurs in males when they attain a body weight of 5.5 lb (2,500 g).

The springhare (*Pedetes capensis*) is listed as Vunerable. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Although a nocturnal species, the springhare (*Pedetes capensis*) is occasionally active during the day. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

Conservation status

Although relatively abundant throughout its range, *Pedetes capensis* is classified as Vulnerable, largely, it is presumed, on account of the decline in the quality of its habitat and its exploitation by humans. Its natural predators are birds of prey and the larger carnivores. Humans hunt springhares both as pests and as food.

Significance to humans

Owing to the damage they can inflict on commercial crops by destroying both planted seeds and established root systems, humans hunt springhares, while to indigenous people they represent a favorite source of food. It is estimated that the total number of springhares falling prey to hunters in a single year in Botswana was in excess of 2.5 million (of which 2.2 million were accounted for by pest hunters).

Springhares are known hosts of numerous parasites and, accordingly, play a role in the transmission to humans and cattle of bubonic plague, rickettsiasis, babesiasis, theileriosis, and toxicosis paralysis.

Resources

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Malcolm Pearch, PhD

Gundis
(Ctenodactylidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Ctenodactylidae

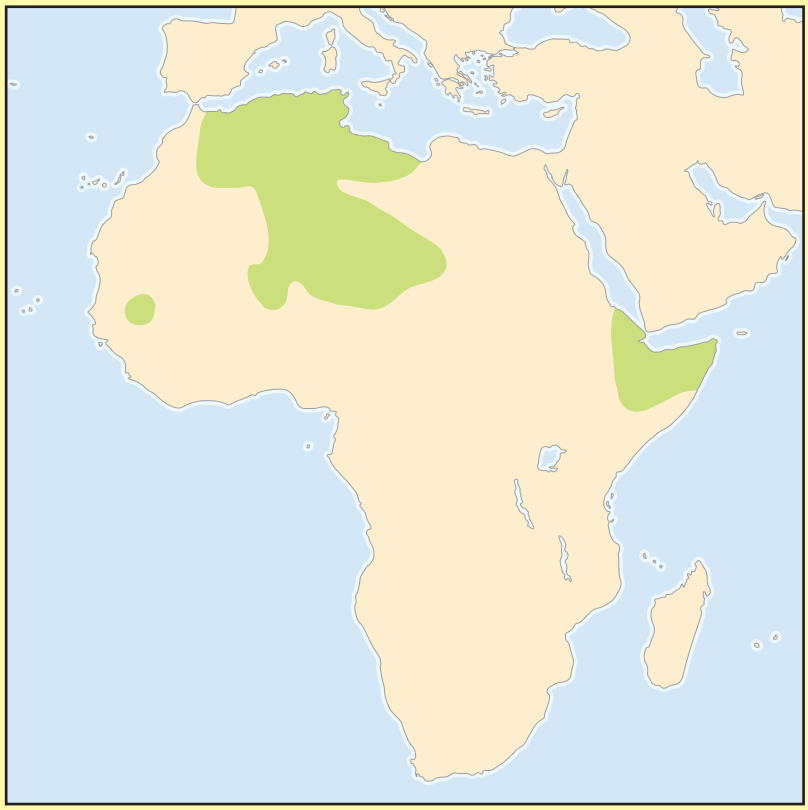
Thumbnail description
Small, thickset rodents with soft, thick fur, large, blunt heads, short, rounded ears, large eyes, short legs and short, furry tails.

Size
Body 5.5–9.5 in (14–24 cm); tail 0.4–2.4 in (1–6 cm); 6.0–10.2 oz (170–290 g)

Number of genera, species
4 genera; 5 species

Habitat
Rocky areas in deserts or semidesertic ranges.

Conservation status
Vulnerable: 1 species



Distribution
Northern Africa, from Mauritania and Morocco east to Eritrea and Somalia.

Evolution and systematics

The gundis (family Ctenodactylidae) are usually classified within the suborder Hystricomorpha but they may have affinities with the Paramyids from the Eocene and, as the sciurid rodents, may also be descended from the Paramyids. The gundis could perhaps be placed in a separate superfamily (Ctenodactyloidea) within the Sciuromorpha (where they are included here) rather than the Hystricomorpha.

The family contains five species in four genera: *Pectinator*, *Felovia*, *Massoutiera*, and *Ctenodactylus*.

Hartenberger, in 1985, concluded that the Ctenodactylidae might be one of the oldest rodent families, having diverged from other rodent taxa in the early Eocene. Molecular data analysis of amino acid myoglobin sequences performed by Beintema et al. in 1991 provided supporting evidence for the hsytricognathous rodents and the Ctenodactylidae being early offshoots of the order Rodentia, although it proved impossible to decide whether they share a common ancestor.

The earliest fossils assigned to the Ctenodactylidae date from the middle Eocene of Asia. There are also Oligocene remains from central Asia and Miocene and Pleistocene remains from Asia, Sardinia, Sicily, and North Africa. The four living genera originated in Africa, where they are known only from the Recent period.

Physical characteristics

Gundis are small, stocky rodents with short, furry tails and short legs. They resemble guinea pigs (*Cavia*) in external appearance. Females are on average larger than males.

The head is large and blunt, the eyes large and the vibrissae long. The ears are short and rounded, and in some species have a protective fringe of hairs around their inner margin. In the mzab gundi (*Massoutiera mzabi*) the ears are flattened against the head and do not move.

The hind feet are longer than the forefeet. Each foot has four digits and on the hind feet the two inner digits have stiff bristles that form a comb: the family name translates as "comb-fingered." All digits have small, sharp claws. The two *Ctenodactylus* species have very small wispy tails but the other three species have longer, fan-like tails.

The fur is soft, silky, and dense. In Speke's pectinator (*Pectinator spekei*) the skin is thin and easily torn. Crouched on a rock with the wind blowing through their fur, gundis look like powder puffs. The cuticular scales on the hairs are unusual, being narrow and petal-like.

Gundis vary in color from grayish or buff to chestnut or yellowish red, with paler (usually whitish) underparts. The color of each species matches the rocks in which it occurs.

The skull is flattened, with broad frontals and relatively well-developed supraorbital ridges. The jugals have horizontal and vertical branches, and the vertical reaches the enlarged lacrimal. The bullae and mastoids are inflated, and the skull appears to broaden posteriorly. The dental formula is i1/1, c0/0, pm1/1 or 2/2, m3/3 = 20 or 24. The cheek teeth are flat-surfaced and ever-growing. Gundis have a flexible ribcage that allows them to squeeze into crevices.

The family is unusual in that females have a cervical pair of mammae in addition to the pair placed laterally on the anterior thorax.

Distribution

Gundis are confined to northern Africa. Speke's pectinator occurs from Eritrea and Ethiopia east to Somalia, while the other four species occur further west, in the Sahara region. The mzab gundi is confined to the central Sahara from Algeria and Mali to Libya and Chad, while the felou gundi (*Felovia vae*) occurs in Mauritania and Mali. The two *Ctenodactylus* species have overlapping ranges, the desert gundi (*C. vali*) ranging from Morocco through Algeria to Libya, while the North African gundi (*C. gundi*) also extends into Tunisia.

Habitat

Gundis are found on rocky outcrops, screes, hills, cliffs, and mountains in desert, subdesert, or desert edge habitats between sea level and 8,200 ft (2,500 m). Geologically, the rocks may be of any age and of any type from recent lava flows to ancient folded sandstone. In some areas, road building sites have also been occupied. Rocks must not be too large, and fissures, crevices, and caves are essential for permanent and temporary shelters, while ledges, flat rocks, and boulder tops are used for sunbathing. Gundis often favor a site with an easterly aspect, exposed to the morning sun, and ideally some part of the site should also catch the evening sun.

Behavior

Gundis do not excavate burrows but live in natural rock crevices or caves. They are gregarious, living in colonies that vary in density from the mzab gundi's 0.12 per acre (0.3 per ha) to over 40 per acre (100 per ha) for Speke's pectinator. Density is related to food supply and the nature of the terrain. Colony size varies from 16,150–21,500 sq ft (1,500–2,000 sq m) in Speke's pectinator to 26,900 sq ft (2,500 sq m) in the desert gundi.

Within colonies there are family territories occupied by a pair and their juveniles or by several females and offspring. Gundis do not make nests, and shelters are often temporary. Permanent shelters may be occupied for many years. Characteristically, a shelter retains the day's heat through the cold night and provides cool conditions in the heat of the day.

The large eyes might suggest nocturnal habits, but gundis are diurnal, moving rapidly from bright sunlight to deep shade in rock crevices. They often move slowly but can run quickly, with the belly almost touching the ground. They are shy and wary, and rely mainly on speed and agility to squeeze into crevices and holes to escape from predators. Rough friction pads on the soles of the feet assist in climbing on rocks, and gundis can ascent almost vertical surfaces, keeping the body pressed close to the rock face. All gundis thump with their hind feet when alarmed. Their flat ears allow them good all-round hearing and the hearing is acute.

When the weather is cold, wet, or windy, activity is restricted and the animals may not emerge at all. In winter, gundis pile on top of one another for warmth, with juveniles shielded by their mother or draped across the back of her neck. Gundis are not known to hibernate or estivate.

Gundis normally emerge at first light and remain active for up to five hours. Activity declines during the hot part of the day but increases again in the 2–4 hours before dusk.

The three species with fan-like tails use the tail for balance, while in Speke's pectinator the tail is also used in social displays.

Grooming is a common activity. The combs on the hind feet are used for grooming and scratching, and the rapid circular scratch of the rump with a hind foot is characteristic of gundis. The fur does not repel water and in wet weather it sticks together in tufts. The animals take particular care to ensure that the fur remains loose.

Vocalizations are varied, and each species has its own repertoire. Calls vary from the infrequent chirp of the mzab gundi to the relatively complex chirps, whistles, and chuckles of Speke's pectinator. In their habitat their low-pitched calls carry well. Short, sharp calls warn of predatory birds and cause all nearby gundis to take cover. Longer calls warn of ground predators and inform the predator it has been spotted. The felou gundi's harsh "chee" call continues as long as the predator remains in the vicinity.

Long complex chirps or whistles serve for recognition or greeting. The two *Ctenodactylus* species, whose ranges overlap, have very different calls that aid in species recognition: the North African gundi chirps, the desert gundi whistles.

Gundis "play possum," exhibiting an immobile, trancelike state when threatened by a predator such as a snake, lizard, fox, jackal, or cat, most of which hunt by sight. The gundi lies flat and completely immobile, and may stop breathing for up to a minute. Gundis do not bite when handled.

For small desert mammals, gundis are unusually active in the daytime. In the early morning they stretch out flat on their stomachs to sunbathe until the temperature rises above 20°C (68°F), when they forage. After feeding, they again flatten themselves on the warm rocks to keep their bodies warm

and to speed digestion: a way of making the best use of scarce food. When the temperature reaches 32°C (90°F) the gundis take shelter under rocks and do not emerge until the temperature drops in the afternoon. When long foraging expeditions are necessary, gundis alternate feeding in the sun with cooling off in the shade. In extreme drought, gundis eat at dawn when plants contain the most moisture.

Gundis have communal dunghills, some of which may have been in use for many years, and finding such a latrine may be the easiest way to ascertain the animals' presence in an area.

Feeding ecology and diet

These animals are entirely herbivorous. Their diet includes the leaves, stalks, flowers, and seeds of almost any desert plant, including grasses and acacia trees. Preferred plants include those in the families Cruciferae and Compositae. Gundis are not adept at gnawing and their incisors lack the hard orange enamel characteristic of most rodents.

Food is often scarce and gundis may forage over great distances, sometimes traveling 0.6 mi (1 km) in a morning. Regular foraging is essential because food is not stored and fat reserves are not accumulated in the body.

Most gundis do not drink but obtain all the water they need from plants; their kidneys have long tubules for absorbing water and under extreme conditions their urine can be concentrated, although this emergency response can only be sustained for a limited period.

Reproductive biology

Most species produce young between January–March and June, with the anestrus period extending for 6–8 months thereafter. The estrus cycle is 23–25 days and the gestation period 55–56 days. The litter size is 1–3 and most species apparently produce only one litter per year. The one exception to this seasonal cycle is Speke's pectinator, which appears to be a more opportunistic breeder, captive females being in anestrus only in July.

The young are born fully furred with their eyes open and are brought out into the open within a few hours of birth. They are left in a rock shelter while the mother forages and their continuous chirruping helps the mother relocate them in their temporary shelter. The female has been observed to carry small young in her mouth by the skin of their necks.

There are few opportunities to suckle, and young are fed chewed leaves from the start. They are weaned at about 4 weeks of age. Weaning probably starts early because the mother can produce little milk in the dry heat of the desert. Sexual maturity is attained at 8–12 months.

Longveity in the wild is estimated at 3–4 years; in captivity longevity of 10 years is recorded for Speke's pectinator.

Conservation status

The felou gundi is classed as Vulnerable because of a decline in its overall range and habitat. Other gundis are not globally threatened, although some may be locally threatened by hunting for food, disturbance from close human settlements, and predation by domestic cats and dogs.

Significance to humans

Gundis are well known to local people and "gundi" is their Arabic name, although it is also applied to other rodents of similar appearance. Twilight, in the common speech of Arabs, is known as "the hour when the gundi comes out." Gundis are hunted for food by some North African tribes. Although not regarded as pests, gundis could be potentially destructive to crops and gardens.

Species accounts

Speke's pectinator
Pectinator spekei

TAXONOMY
Pectinator spekei Blyth, 1856, Somalia.

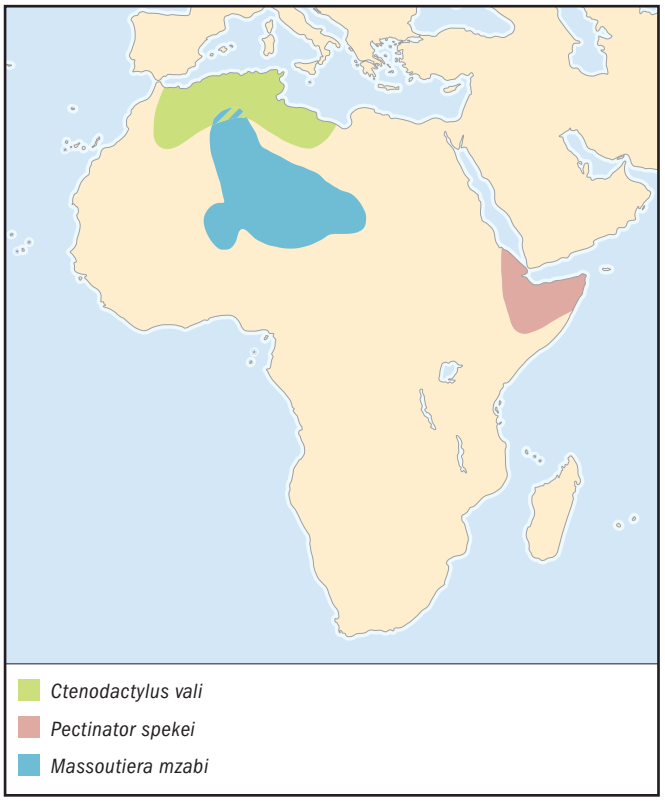
OTHER COMMON NAMES
English: Bushy-tailed gundi; French: Pectinator de Speke; German: Buschschwanzgundi.

PHYSICAL CHARACTERISTICS
Head and body length, 5.5–7.5 in (14–19 cm); tail 1.6–2.4 in (4–6 cm); and about 6.3 oz (178 g) for captive females. Gray, tinged brown or black; underparts grayish white; tail bushy.

Pectinator spekei

DISTRIBUTION
Eritrea, eastern and southern Ethiopia, Djibouti, and northeastern Somalia.

HABITAT
Rocky cliffs and outcrops in desert or semidesert, often with hyrax *Procavia*; occurs from sea level to 5,900 ft (1,800 m).



BEHAVIOR
Shelters in rock crevices. Diurnal, emerging to feed in early morning, peak activity 2–4 hours after dawn. It often basks in the sun. Vocalisations are a relatively complex range of chirps, chuckles and whistles; utters a whistling call on the approach of a predator; the normal call is described as a long, drawn-out "whee whee." Colonies of 16,150–21,500 ft^2 (1,500–2,000 m^2) with well-defined boundaries have been recorded; may occur at densities of over 40 individuals/acre (100/ha). Bushy tail used in social displays.

FEEDING ECOLOGY AND DIET
Eats only plant material, including dry grass stalks and seeds, the leathery green leaves of *Cadaba rotundifolia* bushes, and the leaves of *Acacia senegal* and the long-spined *A. seyal*.

REPRODUCTIVE BIOLOGY
Young born August–September. Captive females in anestrus only in July; possibly a more opportunistic breeder than *Ctenodactylus* and *Massoutiera*. Estrus cycle averages 22.7 days; litter size in captivity one, occasionally two. Life span in captivity 10 years.

CONSERVATION STATUS
Not globally threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Mzab gundi
Massoutiera mzabi

TAXONOMY
Ctenodactylus mzabi (Lataste, 1881), Ghardaia, northern Algeria.

OTHER COMMON NAMES
English: Lataste's gundi; French: Goundi du Sahara; German: Langhaargundi.

PHYSICAL CHARACTERISTICS
Head and body 6.7–9.5 in (17–24 cm); tail 1.4 in (3.5 cm); captive males averaged 6.05 oz (172 g), females 6.85 oz (194 g). Various shades of yellow, brown or buff; ears round and flat; tail bushy.

Massoutiera mzabi

DISTRIBUTION
Central Sahara Desert in Algeria, northern Niger, northwestern Chad, northeastern Mali, and southwestern Libya.

HABITAT
Rock outcrops and mountains in desert; occurs up to 7,875 ft (2,400 m) above sea level.

BEHAVIOR
Lives in rock crevices, using many temporary shelters. Diurnal; emerges to feed in early morning; peak activity one to four hours after dawn, but active for much of the day, except during hottest periods. Does not emerge in cold or wet weather; often sunbathes and grooms. Utters an infrequent chirp. In colonies, occurs at a density of 0.12/acre (0.3/ha). Lives in family groups with close social ties; females help other females during pregnancy and when giving birth.

FEEDING ECOLOGY AND DIET
Eats leaves, stems, flowers and seeds, preferring Cruciferae (especially *Moricandia arvensis*), Compositae, and Graminae.

REPRODUCTIVE BIOLOGY
Young recorded March to June; females also pregnant in April–May. Estrus cycle in captive females averages 24.9 days; estrus period October to March. Litter size in captivity two to three; newborn young 2.8–3.2 in (7–8 cm), and approximately 0.7 oz (20 g). Sexually mature in eight to 12 months.

CONSERVATION STATUS
Not globally threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Desert gundi
Ctenodactylus vali

TAXONOMY
Ctenodactylus vali Thomas, 1902, north of Tripoli, Libya.

OTHER COMMON NAMES
English: Sahara/Val's gundi; French: Goundi du Sahara; German: Sahara-Gundi.

PHYSICAL CHARACTERISTICS
Head and body length is about 6.3–6.7 in (16–17 cm); tail 0.4–0.6 in (1–1.5 cm); average mass 6.2 oz (175 g). Buff to chestnut, with whitish underparts; tail small, not bushy.


Ctenodactylus vali

DISTRIBUTION
Southern Morocco, western Algeria, and northwestern Libya.

HABITAT
Rocky outcrops in desert, from sea level to 8,200 ft (2,500 m).

BEHAVIOR
Shelters in rock crevices. Diurnal, emerging soon after dawn; activity peaks two hours after dawn, and there is often a small amount of activity for two to four hours before dusk. Sunbathes frequently. Has whistling calls. Family groups occupy territories in colonies; one colony covered approximately 26,900 ft^2 (2,500 m^2).

FEEDING ECOLOGY AND DIET
Feeds entirely on vegetation, preferring Cruciferae (especially *Eremophyton chevallieri*), Compositae (especially *Amberboa leucantha*), and Graminae (especially *Cymbopogon* and *Aristida*); also eats acacia leaves.

REPRODUCTIVE BIOLOGY
Semicaptive females produced young mainly in March–April, but breeding season may extend from February to June. Estrous cycle averages 23.4 days; anestrus from May to December. Gestation period 56 days; litter size one to three. Young weigh about 0.7 oz (20 g) when born; nurse for several weeks; fully grown and sexually mature in nine to 12 months. Apparently only one litter per year. Longevity five years in captivity.

CONSERVATION STATUS
Not globally threatened. Locally threatened by hunting, human settlement and predation by domestic cats and dogs.

SIGNIFICANCE TO HUMANS
Some are hunted for food. ◆

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Barry Taylor, PhD

Dormice
(Myoxidae)

Class Mammalia
Order Rodentia
Suborder Sciurognathi
Family Myoxidae

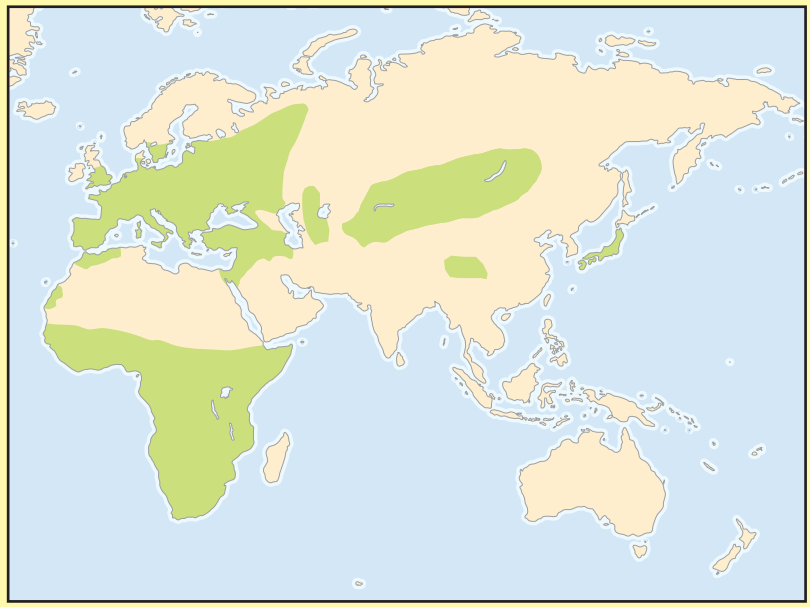
Thumbnail description
Variable in size; thick fur on body and bushy tail (except for *Myomimus*), large eyes, short, curved claws

Size
Body 2.4–7.5 in (6.1–19 cm); tail 1.6–6.5 in (4–16.5 cm); weight 0.5–7 oz (15–200 g).

Number of genera, species
8 genera; 26 species

Habitat
Woodland and forest, steppe and rocky areas.

Conservation status
Critically Endangered: 1 species; Endangered: 4 species; Vulnerable: 5 species; Lower Risk/Near Threatened: 5 species.



Distribution
Europe; Africa; central and western Asia; Japan.

Evolution and systematics

The earliest fossil remains of this family were discovered in Europe and date from the Eocene era (about 40 million years ago). Pleistocene fossils of *Leithia*, a giant dormouse, have been found in Sicily and Malta.

Phylogenetically, dormice have been grouped with the mountain beaver, Aplodontidae, and squirrels, Sciuridae: in appearance and behavior, dormice most closely resemble squirrels.

Taxonomically, this family is made up of three subfamilies, 8 genera, and 26 species. The largest subfamily, Graphiurinae, consists of a single genus *Graphiurus*, the so-called African dormice, whose 14 species are all found in sub-Saharan Africa. The subfamily Leithiinae has four genera; forest dormice *Dryomys*; garden dormice *Eliomys*, mouse-tailed dormice *Myomimus*, and desert dormice *Selevinia*. The latter genus, consisting of a single species, *Selevinia betpakdalaensis*, has been the subject of some taxonomic debate. This naked-tailed rodent has been placed either within the Muridae, in a distinct family, or as a subfamily of the Myoxidae. Holden (1993) believed it was most closely related to the mouse-tailed dormice and put it within the same subfamily.

Physical characteristics

In appearance, dormice have a squirrel or sometimes chipmunk-like shape. They vary considerably in size between species: an edible dormouse (*Myoxus glis*) is nearly two and a half times the length of a Japanese dormouse (*Myoxus japonicus*), for example. Most dormice are highly adapted to a predominantly arboreal existence—only mouse-tailed dormice appear to live exclusively on the ground. The feet are well adapted to grasping on to trees. On the soles, they have cushioned pads for gripping, and the four toes on the front feet and five toes on the hind feet all have strong, curved claws. The hind feet can be turned backwards, like those of a squirrel, enabling the animal to hang head-first from a branch to feed on the lowest fruit, and to run down stems with some dexterity.

The fur is generally soft and thick and in most species, the tail is bushy and long. Its primary function appears to be in assisting with balance, since it is not prehensile. Dormice will readily shed their tails to escape from predators. Ground-dwelling mouse-tailed dormice have thin, naked tails.

Adaptations for a largely nocturnal existence usually include large eyes, sensitive vibrissae, and an acute sense of hearing; the rounded ears are not, however, especially large.

Distribution

This Old World family is found through most of Europe apart from far northern parts; North Africa and the rest of the continent south of the equator; and western and more patchily, central Asia. The single species in the Far East is the Japanese dormouse, found only, as its name suggests, on islands of Japan. The two Balearic dormice species in the *Hyp-*

Edible dormice (*Myoxus glis*) hibernating in Germany. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

nomys genus are probably extinct, extirpated from these western Mediterranean islands by human settlers and their animals about 5,000 years ago.

Habitat

Most dormice occupy forest, woodland, or scrub habitat. True to their name, forest dormice are among the most arboreal, living in dense forests at up to 8,200 ft (2,500 m) in altitude. Hazel dormice (*Muscardinus avellanarius*) are also reluctant to come to ground, preferring to stay in the canopy of largely deciduous woodland. They may remain high in tall trees for several days at a time, or spend long periods feeding on low-hanging fruits close to the ground.

Edible dormice inhabit deciduous or mixed woodland. Both this species and the garden dormouse (*Eliomys quercinus*) are also found in orchards. The latter species, also called the orchard dormouse, is also able to live on the ground, since small numbers are discovered in fields, swamps, steppe, and even places where there are no trees. However, their title is something of a misnomer, since most live in forest habitat.

African dormice live in a wide range of forested habitats, ranging from thick forest where they may even be diurnal, to thinly wooded riverbanks of mountainous, rocky areas. The desert dormouse lives in desert scrub. Only the little-studied mouse-tailed dormice appear to live on or under the ground. In southeastern Europe, Roach's mouse-tailed dormouse (*Myomimus roachi*) has been trapped in a variety of open habitats, but never in forest.

Behavior

Dormice live at lower densities than most rodents of equivalent size. Outside the mating season, they appear to show little territoriality. Most species studied coexist in small groups, with juveniles typically making up half their number. Artificial nest boxes are often found with several inhabitants of both sexes inside. Families tend to stay together through winter hibernation; but a wild male, probably leaves a female after mating, in order to pursue other estrous females.

Home feeding ranges are very variable. At one extreme, hazel dormice rarely venture more than 230 ft (70 m) from their daytime nest. African dormice range far wider, and, in common with most species, males travel greater distances than females. In spectacled dormice (*Graphiurus ocularis*), the male occupies an average of 34.3 acres, (13.9 ha) while the female roams over 21 acres (8.5 ha).

At the start of the mating season, males exhibit territorial aggression towards each other. The hazel dormouse flicks its tail like a squirrel as a warning sign to intruders. Edible dormice mark their space with glandular secretions and fight with great savagery. Garden dormice share sleeping and feeding sites. Males adopt a dominance hierarchy shortly after the animals emerge from hibernation.

All species studied communicate using a range of calls. Five or six separate calls have been identified for forest dormice, including an alarm squeak. Other calls have sexual or aggressive functions.

During periods of inactivity, dormice seek a variety of places in which to shelter. Day nests are often constructed in

An edible dormouse (*Myoxus glis*) climbs down a tree. (Photo by B. Brossette/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

Hazel dormice (*Muscardinus avellanarius*) have a largely vegetarian diet. (Photo by Animals Animals ©M. Hamblin, OSF. Reproduced by permission.)

tree hollows, with the animal weaving a round ball of vegetation, consisting of leaves, grass, moss, lichen, and shredded bark, bound together with saliva, and lined with hair or feathers. Sometimes, a ball nest is made in the branches of a tree; at other times the animal will use a bird or squirrel nest as a foundation for its own nest, or it will tuck the nest behind the bark of the tree. Garden and African dormice in particular also use rock crevices. Artificial nestboxes are adopted readily by many species.

Ironically, it is during the period of sustained inactivity that dormice are most likely to come into contact with humans. Their search for a secure, enclosed hibernation site with stable temperatures leads them into some bizarre places. While hazel dormice make their winter nests in tree stumps or on the ground, rather than in trees where temperatures fluctuate and desiccation is a threat, edible dormice may also choose woodpecker holes, artificial nest boxes, and barns. Japanese dormice are known to select cottage roofs and birdhouses while African dormice sometimes winter inside house furniture.

Most species undergo periods of hibernation in response to food shortages and low temperatures. Hibernation in Europe may extend from September until May. The animal curls itself into a ball, with the tail covering the mouth to reduce water loss. Although hibernation is thought to occur in most species, climactic variation means that in some milder areas such as Israel, dormice do not go into true hibernation, but have several hours of torpidity each day during the winter.

Feeding ecology and diet

Dormice are nocturnal and crepuscular foragers, with most species taking their food from trees. Although they are nominally omnivorous, they are the only rodent family lacking a cecum. Consequently, their consumption of low grade plant food is minimal.

Most species are specialized in taking advantage of seasonal food. Typically, buds and tree flowers are eaten in spring and early summer; insects and other arthropods, small rodents, birds' eggs and insects in summer; and fruit, berries, seeds, and nuts in late summer and the fall. The extent to which individual species depend on one source varies—edible and hazel dormice have a largely vegetarian diet, whereas garden, forest, and African dormice are predominantly carnivorous. Yet each species can alter its diet in response to particular needs. "Vegetarian" dormice eat insects in the summer period of

Edible dormice (*Myoxus glis*) near their nesting hole in a tree. (Photo by Animals Animals ©Gerard Lacz. Reproduced by permission.)

Two savanna dormice (*Graphiurus parvus*) eating seeds. (Photo by Rudi van Aarde. Reproduced by permission.)

A hazel dormouse (*Muscardinus avellanarius*) in hibernation. (Photo by Kim Taylor. Bruce Coleman, Inc. Reproduced by permission.)

shortages before fruits and seeds have ripened. "Carnivorous" dormice switch to nuts and seeds in the fall, so that their fat intake increases in preparation for hibernation. Only the desert dormouse is thought to be purely carnivorous.

Reproductive biology

Lengthy hibernation periods at either end of the year mean that for a number of species, the breeding season is very short. In temperate zones, it lasts typically from May to October with one litter producing on average four young. Hazel dormice sometimes attempt—usually unsuccessfully—a second litter. Forest dormice appear to be exceptional in raising three litters. Productivity in Africa, where breeding seasons are much longer, is largely unknown.

A hazel dormouse (*Muscardinus avellanarius*) foraging for berries. (Photo by Stephen Dalton/Photo Researchers, Inc. Reproduced by permission.)

The edible dormouse (*Myoxus glis*) is a European species. (Photo by Jacana/Photo Researchers, Inc. Reproduced by permission.)

A garden dormouse (*Eliomys quercinus*) eating a prickly pear. (Photo by J. C. Carton. Bruce Coleman, Inc. Reproduced by permission.)

Dormice become sexually active after their first hibernation and bouts of wakefulness towards the end of hibernation may be caused by hormone changes that trigger sexual activity. Vocal calls are important in courtship as each sex entices the other with a range of squeaks and whistles. Once mated, the female builds a globular nest and gives birth to pink, blind young weighing just 0.07 oz (2 g). At seven days, they gain gray fur. By 18 days, the fur is brown and the babies can both hear and see. Shortly after, the young are able to accompany their mother on foraging trips. They reach independence after four to six weeks. Longevity is up to about 5.5 years in the wild. A captive garden dormouse lived for five years and six months.

Conservation status

A number of factors conspire to make more than half of all dormouse species at risk under IUCN criteria. The exclusively forest-dwelling species have poor mobility and this makes them highly vulnerable to habitat loss and fragmentation. Furthermore, a nocturnal, arboreal existence makes both survey and research work difficult. The little-understood

An African dormouse (*Graphiurus* sp.) living in West Africa. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Roach's mouse-tailed dormouse was only discovered in Europe in the mid-twentieth century. Despite years of concentrated research, scientists in the United Kingdom only discovered at the end of the twentieth century that hedges were an important habitat for the hazel dormouse.

Dormice may be adversely affected by climate change, which causes habitat alteration and temperature fluctuations. Arousal from hibernation during mild winters forces an animal to expend considerably greater amounts of energy than if it maintained consistently low internal temperatures.

Concerted efforts to understand the complex ecology and difficulties of protecting this vulnerable family have led to a series of international dormouse conferences, where scientists have been able to share information on the appealing but enigmatic Myoxidae.

Significance to humans

The ability of dormice to store reserves of fat in their bodies has made them desirable to humans as food. Their appeal dates back millennia—the Romans kept edible dormice in darkened enclosures called glisaria. Dormouse eating is well documented in southern Africa, Slovenia, and Yugoslavia and there is good reason to suppose it has taken place wherever humans have come into contact with these mammals.

Dormice are also famous for their sustained periods of hibernation and torpor. Indeed, the name comes from the French *dormir*—to sleep. The hazel dormouse—known in rural England as the sleep-mouse—gained wider notoriety when it was portrayed in Lewis Carroll's book *Alice in Wonderland* and in the Disney movie nearly a century later.

1. Chinese dormouse (*Dryomys sichuanensis*); 2. Hazel dormouse (*Muscardinus avellanarius*); 3. Spectacled dormouse (*Graphiurus ocularis*); 4. Japanese dormouse (*Glirulus japonicus*); 5. Garden dormouse (*Eliomys quercinus*); 6. Edible dormouse (*Myoxus glis*); 7. Desert dormouse (*Selevinia betpakdalaensis*); 8. Forest dormouse (*Dryomys nitedula*); 9. Roach's mouse-tailed dormouse (*Myomimus roachi*). (Illustration by Gillian Harris)

Species accounts

Spectacled dormouse
Graphiurus ocularis

SUBFAMILY
Graphiurinae

TAXONOMY
Graphiurus ocularis (Smith, 1829), Cape Province, South Africa.

OTHER COMMON NAMES
French: Graphiure spectaculaire; German: Brillenschläfer.

PHYSICAL CHARACTERISTICS
Head and body length 2.7–6.5 in (7–16.5 cm), tail 1.9–5.3 in (5–13.5 cm); weight 0.6–1 oz (18–30 g). Color is grayish with markings on the face, paler underneath.

DISTRIBUTION
Cape Province and southwestern Transvaal, South Africa.

HABITAT
Wooded rocky areas, generally near water.

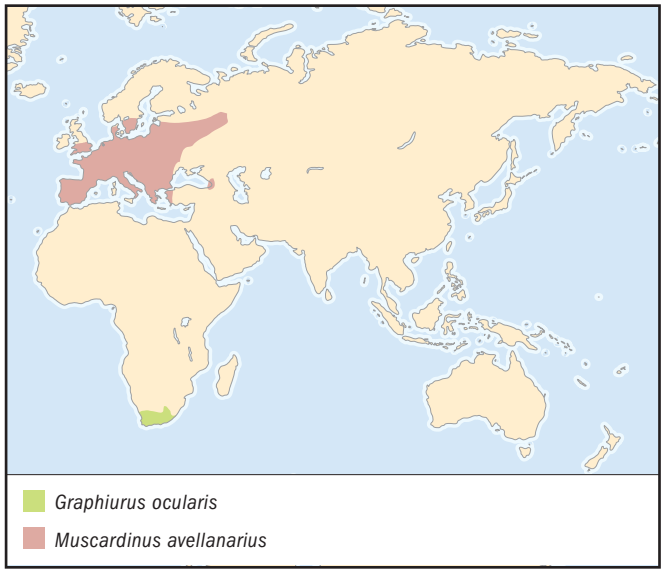
BEHAVIOR
Territorial pairs and their young occupy sizeable areas of up to 34.5 acres (14 ha).

FEEDING ECOLOGY AND DIET
Seeds, nuts, fruits, grain, insects, eggs, and small vertebrates.

REPRODUCTIVE BIOLOGY
Breeds in spring or summer with 4–6 young per litter.

CONSERVATION STATUS
Classified as Vulnerable on the IUCN Red List and declining.

SIGNIFICANCE TO HUMANS
Formerly more common around human habitation and eaten. Now largely absent because of competition with rats. ◆



Forest dormouse
Dryomys nitedula

SUBFAMILY
Leithiinae

TAXONOMY
Dryomys nitedula (Pallas, 1778), lower Volga River, Russia. Fifteen subspecies.

OTHER COMMON NAMES
French: Lerotin; German: Baumschläfer; Spanish: Muscardino balcanico.

PHYSICAL CHARACTERISTICS
Head and body length 3.1–5.1 in (8–13 cm), tail 2.35–4.5 in (6–11.3 cm); weight 0.6–1.2 oz (18–34 g). Color is grayish to yellowish brown, buffy white underneath.

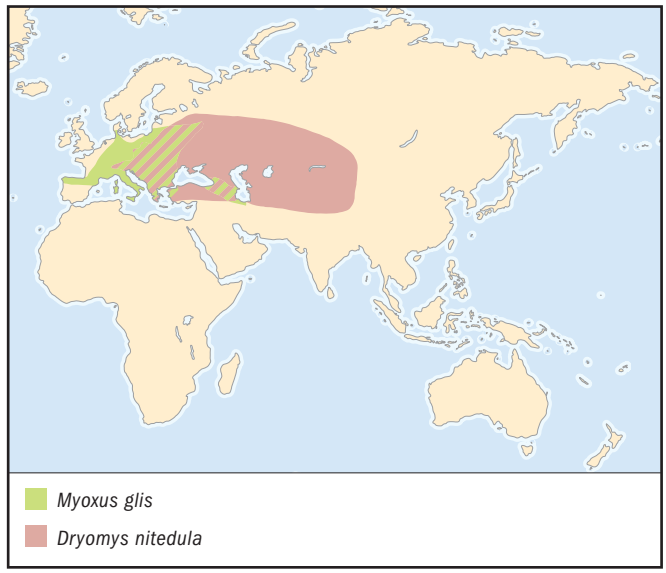
DISTRIBUTION
Central Europe and western Asia to Tien Shan mountains.

HABITAT
Forests and shrubs in gardens and fields.

BEHAVIOR
Arboreal and highly agile—able to leap distances of up to 6.6 ft (2 m) between trees.

FEEDING ECOLOGY AND DIET
Carnivorous in summer, eating spiders and other small invertebrates, eggs, and young birds. Otherwise subsists on seeds, buds, and fruit.

REPRODUCTIVE BIOLOGY
Nests colonially, either in one tree or in adjacent trees. Three litters south of its range and one litter of usually 2–5 young in temperate areas.



CONSERVATION STATUS
Classified as Lower Risk/Near Threatened on the IUCN Red List. Loss of forest habitat has caused declines in central Europe.

SIGNIFICANCE TO HUMANS
Causes damage to crops in apple orchards. ◆

Chinese dormouse
Dryomys sichuanensis

SUBFAMILY
Leithiinae

TAXONOMY
Dryomys sichuanensis (Wang, 1985), north Sichuan Province, China.

OTHER COMMON NAMES
French: Lerotin du Sichuan.

PHYSICAL CHARACTERISTICS
Head and body length 3.5 in (9 cm), tail 3.6–4 in (9.2–10.2 cm); weight 0.8–1.2 oz (24–36 g). Color is grayish to yellowish brown, buffy white underneath.

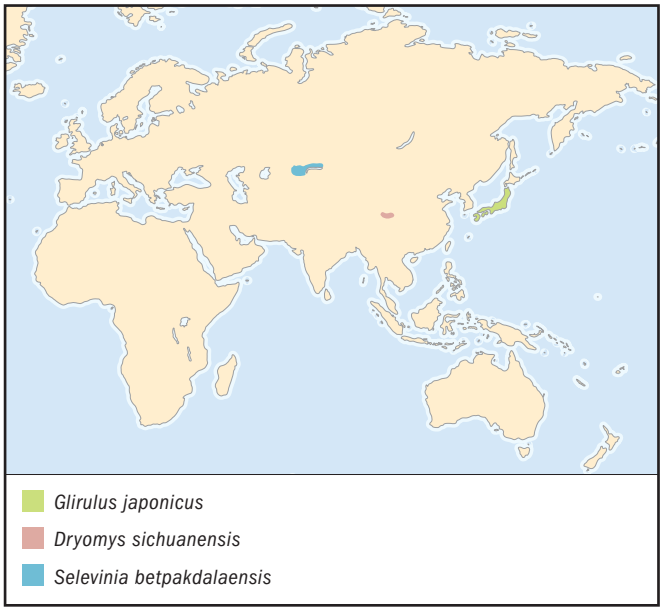
DISTRIBUTION
Northern Sichuan.

HABITAT
Subalpine mixed forests.

BEHAVIOR
Nocturnal; little other data available.

FEEDING ECOLOGY AND DIET
Thought to be largely gramnivorous.

REPRODUCTIVE BIOLOGY
Nests in small trees.



CONSERVATION STATUS
Classified as Endangered on the IUCN Red List.

SIGNIFICANCE TO HUMANS
None known. ◆

Garden dormouse
Eliomys quercinus

SUBFAMILY
Leithiinae

TAXONOMY
Eliomys quercinus (Linnaeus, 1766), Germany. Fourteen subspecies.

OTHER COMMON NAMES
English: Orchard dormouse; French: Lerot; German: Gartenschläfer; Spanish: Lirón careto.

PHYSICAL CHARACTERISTICS
Head and body length 3.9–6.9 in (10–17.5 cm), tail 3.5–5.3 in (9–13.5 cm); weight 1.5–4.2 oz (45–120 g). Color is gray to brown, cream to white underneath.

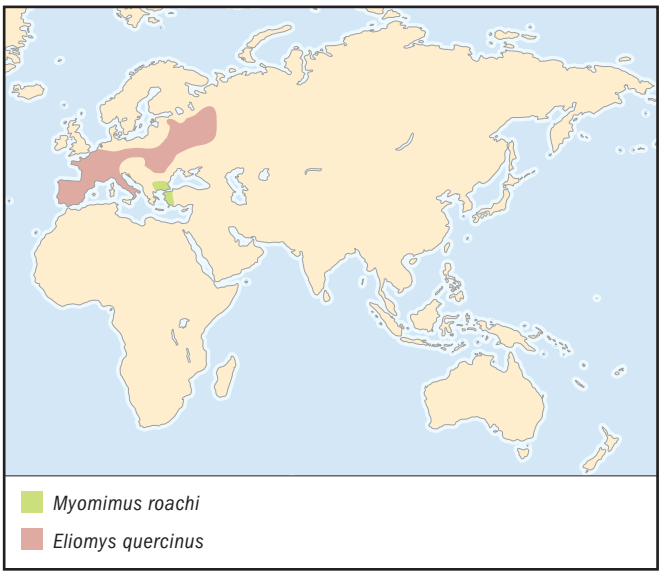
DISTRIBUTION
Europe from France to western Russia, south to southern Spain and Portugal.

HABITAT
Despite its name, the garden dormouse is most often found in forests. Also cultivated fields, rocky areas, and marshland.

BEHAVIOR
Although an agile tree climber, this species can also live without trees. Recorded feeding and sleeping together in groups.

FEEDING ECOLOGY AND DIET
Largely carnivorous, with insects making up to 89% of diet. Also fruit, especially in fall.

REPRODUCTIVE BIOLOGY
Highly vocal during courtship, with female attracting male using whistling calls.



CONSERVATION STATUS
Loss of forest habitat has meant this species is classified as Vulnerable on the IUCN Red List.

SIGNIFICANCE TO HUMANS
Historically, eaten for food by humans. ◆

Roach's mouse-tailed dormouse
Myomimus roachi

SUBFAMILY
Leithiinae

TAXONOMY
Myomimus roachi (Bate, 1937), Mount Carmel, Israel.

OTHER COMMON NAMES
English: Dormouse; French: Loir myomime, loir d'Ognev; German: Mausschläfer; Spanish: Lirón colipelado.

PHYSICAL CHARACTERISTICS
Head and body length 2.4–4.7 in (6.1–12 cm), tail 2–3.7 in (5.3–9.4 cm); weight 0.7–1.9 oz (21–56 g). Color is ocher and gray, white underneath.

DISTRIBUTION
Southern Bulgaria and western Turkey.

HABITAT
Open areas with trees, such as the edges of fields and gardens.

BEHAVIOR
Not a specialized tree dweller, this species appears to spend most of its time on the ground.

FEEDING ECOLOGY AND DIET
Seeds, nuts, fruits, grain, insects, eggs, and small vertebrates.

REPRODUCTIVE BIOLOGY
Seven pairs of mammae suggest large numbers of offspring. Breeding biology largely unknown.

CONSERVATION STATUS
Classified as Vulnerable on the IUCN Red List.

SIGNIFICANCE TO HUMANS
None known. ◆

Desert dormouse
Selevinia betpakdalaensis

SUBFAMILY
Selevinia

TAXONOMY
Selevinia betpakdalaensis Belusludov and Bashanov, 1939, south Kazakhstan.

OTHER COMMON NAMES
French: Loir du desert.

PHYSICAL CHARACTERISTICS
Head and body length 2.9–3.7 in (7.5–9.5 cm), tail 2.3–3 in (5.8–7.7 cm); weight 0.6–0.9 oz (18–25 g). Fur is grayish above and whitish underneath.

DISTRIBUTION
Kazakhstan.

HABITAT
Shrubby thickets in desert, especially wormwood and Spiriantes.

BEHAVIOR
Thought to emerge at twilight to feed, sheltering from the sun under cover, or possibly in a burrow by day. When threatened, moves in a succession of short jumps.

FEEDING ECOLOGY AND DIET
Probably wholly carnivorous, feeding on insects and spiders. Can eat three-quarters of its own body weight in one night.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Classified as Endangered on the IUCN Red List.

SIGNIFICANCE TO HUMANS
None known. ◆

Japanese dormouse
Glirulus japonicus

SUBFAMILY
Myoxinae

TAXONOMY
Glirulus japonicus (Schinz, 1845), Japan.

OTHER COMMON NAMES
French: Loir du Japon.

PHYSICAL CHARACTERISTICS
Head and body length 2.5–3.1 in (6.5–8 cm), tail 1.5–2.1 in (4–5.5 cm); weight 0.5–1.4 oz (14–40 g). Color is pale olive brown with a darker stripe along the spine.

DISTRIBUTION
Honshu, Shikoku, Kyushu Island.

HABITAT
Mountain forest.

BEHAVIOR
Arboreal and nocturnal. Known to hibernate in buildings and birdhouses.

FEEDING ECOLOGY AND DIET
Seeds, fruits, insects, and bird eggs.

REPRODUCTIVE BIOLOGY
An average of four young born in June–July after a month-long gestation.

CONSERVATION STATUS
Classified as Endangered on the IUCN Red List.

SIGNIFICANCE TO HUMANS
None known. ◆

Hazel dormouse
Muscardinus avellanarius

SUBFAMILY
Myoxinae

TAXONOMY
Muscardinus avellanarius (Linnaeus, 1758), Sweden. Six subspecies.

OTHER COMMON NAMES
English: Common dormouse; French: Muscardin; German: Haselmaus; Spanish: Muscardino.

PHYSICAL CHARACTERISTICS
Head and body length 2.35–3.5 in (6–9 cm), tail 2.1–2.9 in (5.5–7.5 cm); weight 0.5–1.4 oz (15–40 g). Color is yellowish brown or yellowish red, white to buff underneath.

DISTRIBUTION
Europe from southern England to western Russia, south to northern Turkey.

HABITAT
Largely deciduous woodland with varied canopy cover.

BEHAVIOR
Probably exclusively arboreal. In temperate areas, may hibernate for up to nine months of the year.

FEEDING ECOLOGY AND DIET
Flowers, fruit, nuts, and seeds. Insects in summer.

REPRODUCTIVE BIOLOGY
Long-lived species, normally producing a single annual litter of 4–5 young.

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened on the IUCN Red List.

SIGNIFICANCE TO HUMANS
Efforts to maintain populations have included reintroductions and nestbox schemes. ◆

Edible dormouse
Myoxus glis

SUBFAMILY
Myoxinae

TAXONOMY
Myoxus glis (Linnaeus, 1766), Germany. Nine subspecies.

OTHER COMMON NAMES
English: Fat dormouse; French: Loir, loir gris; German: Siebenschläfer; Spanish: Lirón (Castillian), lirón gris, rata durmidora (Catalan).

PHYSICAL CHARACTERISTICS
Head and body length 5.1–7.5 in (13–19 cm), tail 4.3–5.9 in (11–15 cm); weight 2.4–6.3 oz (70–180 g). Color is silvery gray, white underneath.

DISTRIBUTION
Europe, Iran, and Turkmenistan.

HABITAT
Deciduous and mixed forests, orchards.

BEHAVIOR
One of the most agile of arboreal dormice—recorded making tree-to-tree leaps of more than 23 ft (7 m).

FEEDING ECOLOGY AND DIET
Seeds, nuts, berries, and fruit. Insects in summer.

REPRODUCTIVE BIOLOGY
Apparently a territorial species, with males scent-marking boundaries. Male assists in raising of young and families may stay together through hibernation.

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened on the IUCN Red List.

SIGNIFICANCE TO HUMANS
Historically regarded as a food source, particularly as a delicacy. Considered a pest of fruit and vine crops. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Jentink's dormouse *Graphiurus crassicaudatus*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–6.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Liberia to Cameroon; perhaps Bioko Island.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Not listed by IUCN
Kellen's dormouse *Graphiurus kelleni*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–6.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Angola, Zambia, Malawi, and Zimbabwe.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Not listed by IUCN
Woodland dormouse *Graphiurus murinus*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–6.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Sudan and Ethiopia, south to South Africa; through Democratic Republic of the Congo (Zaire) to southern Angola.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Not listed by IUCN
Savanna dormouse *Graphiurus parvus*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–6.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Sierra Leone and Mali east to Nigeria; Sudan, Ethiopia, and Somalia south to Tanzania.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Not listed by IUCN
Stone dormouse *Graphiurus rupicola*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Namibia and north-western South Africa.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Not listed by IUCN
Silent dormouse *Graphiurus surdus*	Upperparts range from pale ashy gray to dark slaty gray, and from buffy to reddish brown, tinged with grayish. Underparts are white to grayish, often tinged with buff or reddish brown. Face has black and white markings. Head and body length 2.8–6.5 in (7–16.5 cm) and tail length 2.0–5.3 in (5–13.5 cm).	Forests and rocky areas near waterways. Nocturnal, though active during the day in dark forests.	Equatorial Guinea and southern Cameroon.	Grains, seeds, nuts, fruits, insects, eggs, and small vertebrates.	Data Deficient
Woolly dormouse *Dryomys laniger*	Upperparts grayish brown to yellowish brown; underparts buffy white. Head and body length 3.1–5.1 in (8–13 cm); tail length 2.4–4.4 in (6–11.3 cm); and weight 0.6–1.2 oz (18–34 g).	Lives in forests and thickets. Nocturnal and arboreal.	Southwestern Turkey.	Seeds, buds, fruits, arthropods, eggs, and young birds.	Lower Risk/Near Threatened
Asian garden dormouse *Eliomys melanurus*	Upperparts range through several gray and brown shades; underparts are creamy or white. Head and body length 3.9–6.9 in (10–17.5 cm); tail length 3.5–5.3 in (9–13.5 cm); and weight 1.6–4.2 oz (45–120 g).	Forest, swamps, rocky areas, cultivated fields, and steppe desert. Most active at night.	Southern Turkey and the Middle East, into northern Africa.	Acorns, nuts, fruits, insects, small rodents, and young birds.	Lower Risk/Near Threatened
Masked mouse-tailed dormouse *Myomimus personatus*	Upperparts are a combination of ochraceous and gray; underparts, insides of the limbs, and feet are white. Mouse-like tail. Head and body length (6.1–12 cm); tail length (5.3–9.4 cm); weight 0.7–2.0 oz (21–56 g).	Open areas with trees. Little is known of behavior.	Northeastern Iran, Turkmenistan, and Uzbekistan.	Seeds, nuts, fruits, grain, insects, eggs, and small vertebrates.	Vulnerable

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Setzer's mouse-tailed dormouse *Myomimus setzeri*	Upperparts are a combination of ochraceous and gray; underparts, insides of the limbs, and feet are white. Mouse-like tail. Head and body length (6.1–12 cm); tail length (5.3–9.4 cm); weight 0.7–2.0 oz (21–56 g).	Open areas with trees. Little is known of behavior.	Western Iran.	Seeds, nuts, fruits, grain, insects, eggs, and small vertebrates.	Endangered

Resources

Books

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Dormouse Hollow. <http://www.glirarium.org/dormouse>.

Dr. Paul W. Bright. <http://www.rhul.ac.uk/Biological-Sciences/bright/>.

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Derek William Niemann, BA

Dassie rats
(Petromuridae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Petromuridae

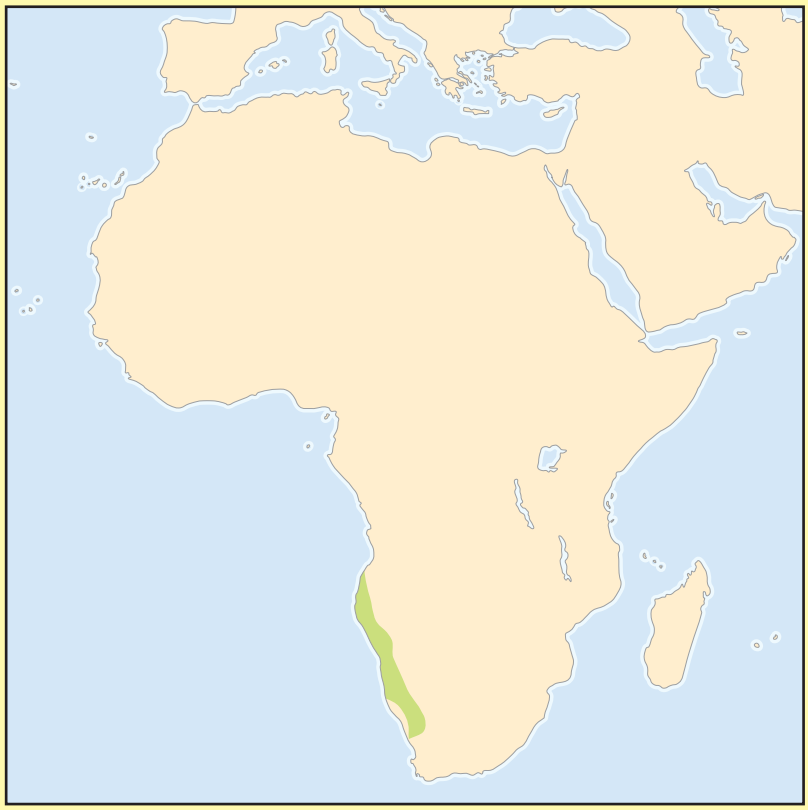
Thumbnail description
Squirrel-like, with less bushy tails and a scattered cover of long hair over the last three-quarters of the tail; pelage is soft and silky with no underfur; a yellow enamel layer on the front of the small, narrow and ungrooved incisors

Size
9.9–10.9 in (253–279 mm); 6.0–9.2 oz (170–262 g)

Number of genera, species
1 genus; 1 species

Habitat
Rocky areas in the South West Arid Zone of Africa

Conservation status
Not globally threatened



Distribution
Southern Angola, Namibia, and northwestern South Africa

Evolution and systematics

In 1939, Broom described a fossil form found at Taung (South Africa) as *Petromus minor*. Some 14 subspecies have been described, but Meester and co-workers (1964) feel that it is unlikely that 14 valid forms could occur in such a restricted range of the species. At present the family includes only one species, *Petromus typicus*. The name is derived from the Greek *petro*, "rock," and *mys*, "mouse." The species name refers to the Greek word *typicos*, "typical," i.e., a typical rat of the rocks.

The taxonomy for this species is *Petromus typicus* A. Smith, 1831, South Africa.

The dassie rat (*Petromus typicus*) is native to southwestern Africa. (Photo by John Visser. Bruce Coleman, Inc. Reproduced by permission.)

Physical characteristics

In external appearance this rodent is somewhat squirrel-like, although the tail is not bushy. It is shorter than the head body length and the last three quarters of it is covered with long hair, which do not fan out. They have short, blackish ears that are rather higher than broad. They have long black vibrissae. Data concerning size are meager with males: head and body length 10.9–14.0 in (27.9–36.0 cm); mass of

Dassie rat (*Petromus typicus*). (Illustration by Michelle Meneghini)

Due to its extremely flexible ribs, the dassie rat (*Petromus typicus*) has the ability to flatten itself to fit into tiny rock crevices. (Photo by Nigel Dennis/African Imagery.com. Reproduced by permission.)

The dassie rat (*Petromys typicus*) requires very little water. (Photo by Gerry Ellis/Minden Pictures. Reproduced by permission.)

two sub-adults 6.0 and 7.4 oz (170 and 212 g), and females: head and body length 9.9–14.0 in (25.3–35.8 cm); mass of two adult females 8.8 and 9.2 oz (251 and 262 g). Colors are geographically variable, and normally come in shades of brown, gray, or buff, with yellowish to dirty underparts. The front feet have four clawed toes with a short and rudimentary thumb. The five toes of the hind feet have short curved claws. The soles of the feet are naked with well-developed pads for moving on rocky substrates. They have a remarkable ability to flatten their bodies, due to flexible ribs and unusually flat skulls. The dental formula is (I1/1 C0/0, P1/1, M3/3) $\times$ 2 = 20.

Distribution

They have a fairly restricted distribution in the South West Arid Zone of Africa, stretching from the southwestern parts of Angola throughout the central and western parts of Namibia to the northwestern parts of the Northern Cape Province in South Africa.

Habitat

They are confined to rocky areas where they occupy crevices or take cover under piles of boulders. They may be scattered throughout different types of vegetation and shelter seems to be more important than the available vegetation type.

When startled, the dassie rat (*Petromus typicus*) emits a whistle to warn others. (Photo by © Janine Pestel/Visuals Unlimited, Inc. Reproduced by permission.)

Behavior

Dassie rats are diurnal and occur singly, in pairs, or in family groups. Because of the flat skull and the manner in which they can flatten the body they can squeeze into very narrow crevices when threatened. They can utilize crevices too narrow even for small hyraxes. Their rock shelters have lookout points, sunbathing platforms and are linked to suitable feeding grounds. They are a docile species with activity noticeable during early morning and late afternoons. Although they will defecate anywhere within the home range, they tend to have latrines where they urinate, causing the rocks to become whitish stained. They love to sun and dust-bathe themselves near their shelters. When threatened they run with great speed for shelter, jumping from rock to rock. They have low water requirements and probably get most of their water from the food they eat.

Feeding ecology and diet

They are vegetarian feeding on grasses, twigs, and shrubs. They will climb trees to plug leaves. Flowers of the many species of Compositae growing in their immediate vicinity are also sought after. Grass and leaves may be taken to their shelters where it is either eaten, or used for nest-building. Apparently they are unique in that they may regurgitate food back to the mouth where it is then masticated and reswallowed. They are coprophagous and sometimes eat some of their own pellets.

Reproductive biology

Data meager. Gravid females were found during the spring months (September-November) in Namibia. The number of young varies from one to two. Young are born in an advanced stage of development. Females have three pairs of teats, two laterally situated pairs below the shoulders with the third pair, often non-functional, further back.

Conservation status

In 1996 they were listed as Lower Risk/Least Concern, a the IUCN Red List. During 2002 they were globally listed as Lower Risk/Least Concern. Nationally they could be regarded as Vulnerable, but due to the small area of occupancy and the current inferred stability it is down rated to Lower Risk/Near Threatened.

Significance to humans

None known.

Resources

Books

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Bate, D. M. A. "An Extinct Reed-rat *Thryonomys arkelli* from the Sudan." *Annual Magazine of Natural History* 14, no. 11: 65–71.

Broom, R. "The Fossil Rodents of the Limestone Cave at Taungs." *Annuals of the Transvaal Museum* 19 (1999): 315–317.

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Mac van der Merwe, PhD

Cane rats
(Thryonomyidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Thryonomyidae

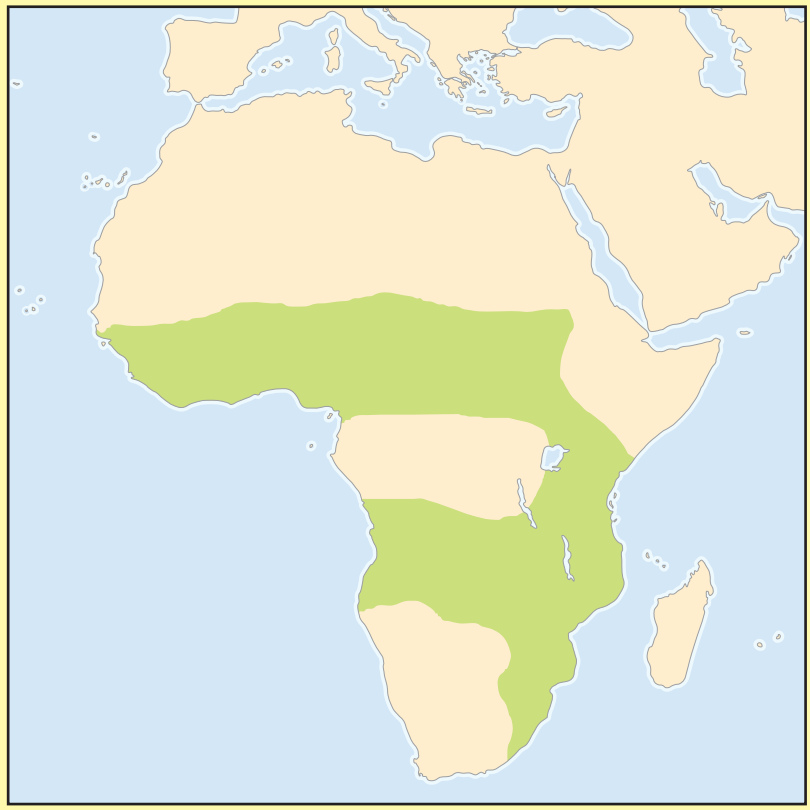
Thumbnail description
Robust rodents with stocky bodies, small ears, and short tails; body covered with sharply pointed, but pliable, spiny hairs; broad, heavily built orange-colored chisel-shaped incisors, with the upper ones grooved longitudinally at the front

Size
1.3–2.6 ft (40.9–79.3 cm); 3.1–14.3 lb (1.4–6.5 kg)

Number of genera, species
1 genus; 2 species

Habitat
Wooded savanna and grassland

Conservation status
Not threatened



Distribution
Common throughout Africa south of the Sahara in humid and sub-humid areas where dense grass or reeds are found

Evolution and systematics

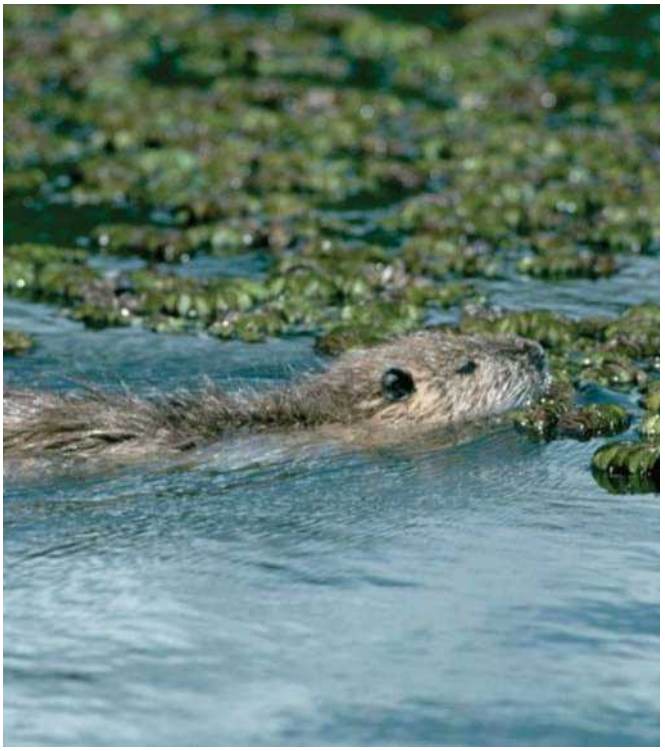
The fossil record indicates that the genus *Thryonomys* existed in the central Sahara during the Pleistocene. Romer and Nesbit (1930) described fossil forms collected approximately 497 mi (800 km) from the Niger River as *T. logani*. Bate (1947) described another fossil form, *T. arkelli*, from Pleistocene deposits in Sudan. Walker (1975) mentioned that they occurred in Africa from the Upper Miocene to the recent era.

The African cane rats (family Thryonomyidae) includes only one genus *Thryonomys* and, although many varieties have been described, there are probably only two species, the greater cane rat (*Thryonomys swinderianus*) and the lesser cane rat (*Thryonomys gregorianus*). The name comes from the Greek *thryon*, which means rush, and *mys*, which means mouse. It makes reference to its common association with vegetation along waterways. Cane rats are more closely related to porcupines than to rats. At present, no subfamilies or subspecies are recognized.

Physical characteristics

Except for size and mass, there is a great similarity in the external features between the two cane rat species. The description here concentrates mainly on the greater cane rat for which more information is available. They are heavily built with a head that looks small for the body, including small ears and a squarely cut muzzle. The muzzle is used as a pad when they butt each other. When panicking in captivity, they will also ram the walls of the enclosure with the muzzle. The body is covered with spiny hairs that are firm, sharply pointed yet supple, and varies in color from a speckled yellowish brown to a speckled grayish brown. The lips, chin, and throat are predominately white, with a brown pellage mottled with white on the ventral surface. The skin is very weak and tears easily, however, it also heals easily. The dark-brown tail tapers and is covered with short, bristly hair. When caught by the tail, it can easily be broken off. In adults, the genital area is an orange color. The legs are strong, the feet well padded. The front feet have five digits, the first one being rudimentary and the fifth one small. The hind feet have four larger digits, the first one being absent and the fifth one small. All the available digits are strong and possess strong, powerful, and fairly straight claws.

Cane rats are the second largest rodents in Africa, surpassed in size and mass only by the porcupine *Hystrix*



The greater cane rat (*Thryonomys swinderianus*) is an excellent swimmer. (Photo by Yann Arthus-Bertrand/Cobris. Reproduced by permission.)

africaeaustralis (26.4–28.6 lb; 12–13 kg). Cane rat males are much larger than females. The greater cane rat is about twice the size of the lesser cane rat.

The dental formula is (I1/1 C0/0 P1/1 M3/3) × 2 = 20. The two upper and two lower incisor teeth are broad, heavily built, and chisel shaped. The bright orange enamel layer covers only the incisors on the front, while the rest is dentine. The upper incisors are deeply grooved longitudinally on the outer surface. Regardless of the enormous incisors, there is no record of people being bitten by wild cane rats when handling them. They will rather make frantic efforts to escape, a process in which they may injure themselves badly.

Distribution

The greater cane rat is much more widespread in Africa than the lesser cane rat, and although there are overlaps in their distribution, they occupy different ecological niches. They occur in grassland or in wooded savanna areas of Africa south of the Sahara. Because of specialized habitat requirements, their distribution is discontinuous. They do not inhabit rainforest, arid regions, or deserts. The only exception being forests where there are clearings with a grassland invasion. Cane rats (or "grasscutters" as they are known in West Africa) can be found in virtually all countries of west, east, and southern Africa, as far south as the eastern Cape, South Africa.

Habitat

Cane rats can be found in swampy low-lying areas along river banks and streams where there are reed beds or areas of dense tall grass, as well as the higher altitudes on the eastern tropical escarpment where they are able to utilize drier terrain. They are good swimmers and will easily take to the water when threatened.

Behavior

Cane rats are predominantly nocturnal in the wild and travel through trails in the reeds and grass. They appear to live in small groups of up to 12 animals. In captivity, greater cane rats exist as family groups of one male and from one to seven females. The dominant male will not tolerate the presence of another mature male. The same behavior is anticipated in the wild where a family group will consist of a dominant male, few females, and their offspring. When alarmed, they stamp their hind feet on the ground, making a booming sound. They also make a loud whistling sound, as a stress or warning sound. When relaxed and eating, they make soft grunting noises. In the reed beds or grass runs, waste products of feeding and scattered piles of feces can be found. Although they have well-developed claws, they do not appear to burrow. Where there appears to be a lack of cover, they make use of existing holes, dug by other animals or caused by water erosion alongside river banks.

Feeding ecology and diet

They are vegetarian and eat the roots, shoots, and stems of various grasses. They cut the grass stems at the base with their powerful incisors, and then while sitting in an upright position, they manipulate the grass stem or other foodstuff with their front paws while pushing it into the mouth and chopping it into small pieces with the incisors. Grasses are their principal food, including elephant grass, *Pennisetum purpureum*, and buffalo or guinea grass, *Panicum maximum*. They consume the soft parts of the grasses and shrubs, and the drier sections and leaves are often discarded. They can become severe agricultural pests in some areas where crops, such as peanuts, maize, sorghum, wheat, cassava, and sugar cane grow in close proximity to their habitat. They are very fond of kikuyu grass and will raid lawns. They scratch the soil aside to expose vegetables such as potatoes and sweet potatoes or, in certain grasses, to expose the succulent underground stems or roots. Fermentation of food occurs mainly in the caecum and the animals are coprophagous. They produce two kinds of feces, hard pellets that are excreted and soft pellets that are reingested.

Reproductive biology

In captivity, cane rats are polygynous and the same is expected for the wild. The gestation period is 156 days (range is 137–172 days). It is possible for them to have two litters per annum, with litter sizes ranging from one to five young and even eight. Newborn young are precocial, meaning fully furred with open eyes. Mass at birth varies from 2.7 to 7.2 oz (75–204

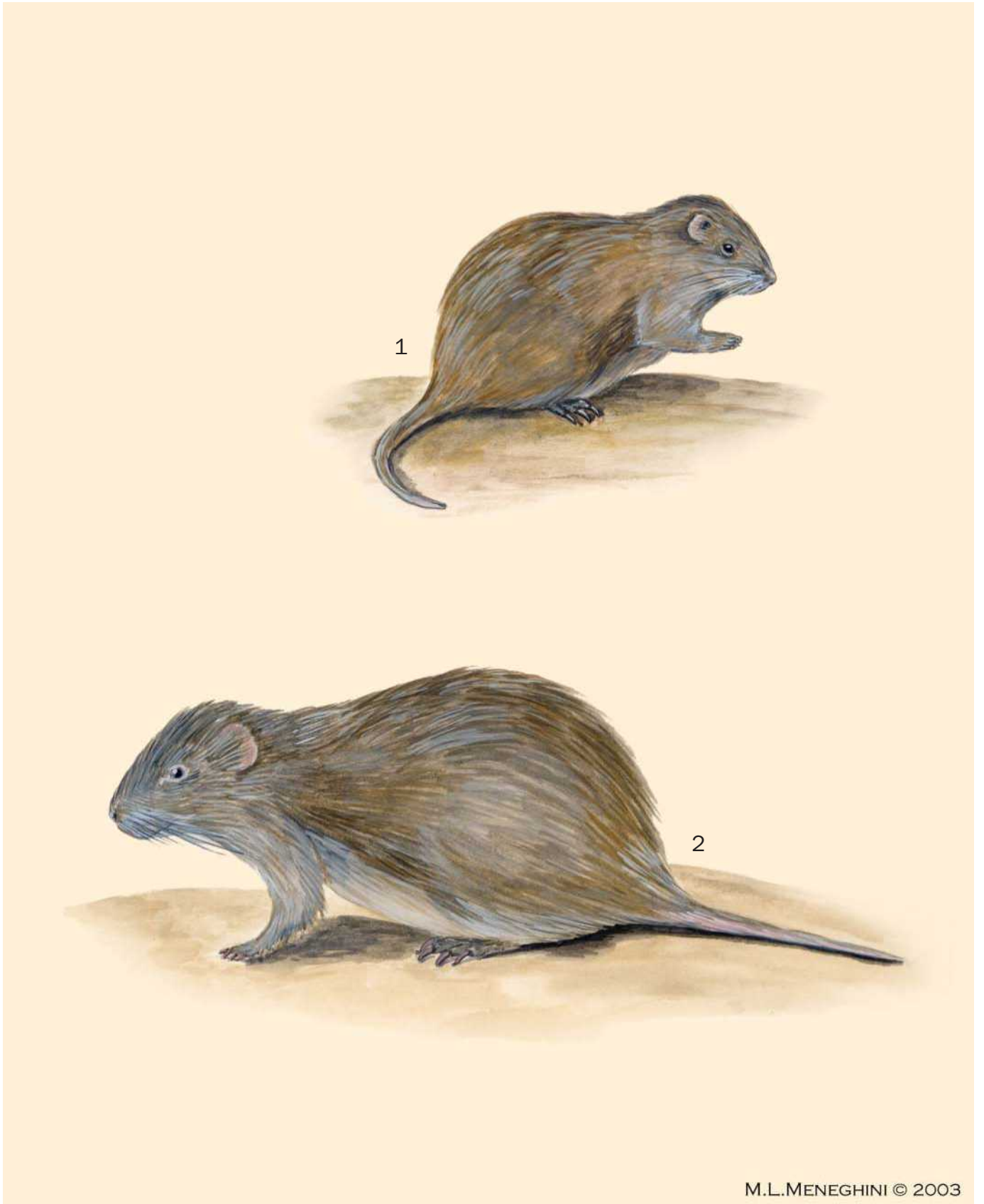
g). Three pairs of teats are situated high on the sides of the abdomen, and females suckle their young while standing or lying on their bellies. The young are weaned at about four weeks. They stay with the parents until about five months when they become sexually mature. At this age, in captivity, the dominant male starts showing aggressive behavior towards the young males. Dominant young males also show aggressive behavior towards their brothers. Young females are not bothered. Cane rats produce throughout the year although birth peaks occur at certain times of the year, presumably during rainy seasons when more food is available. In captivity, birth can occur any time males and females are placed together.

Conservation status

Neither species is threatened.

Significance to humans

Cane rats can be a pest by causing great damage to vegetable gardens and crops. The meat of the cane rat is tasty and is widely utilized in African countries. Cane rat meat is much in demand, and they are often hunted in organized drives with spears, dogs, and firearms. In West Africa, people have traditionally captured cane rats in the wild and raised them at home. As an off-spin of this, some farmers have initiated organized cane rat husbandry. Because the meat is considered excellent and a huge market for the meat exists, some farmers in South Africa are showing an interest in farming these animals as micro-livestock.



1. Lesser cane rat (*Thryonomys gregorianus*); 2. Greater cane rat (*Thryonomys swinderianus*). (Illustration by Michelle Meneghini)

Species accounts

Greater cane rat
Thryonomys swinderianus

TAXONOMY
Thryonomys swinderianus (Temminck, 1827), Sierra Leone.

OTHER COMMON NAMES
French: Le grand aulacode; German: Großen Rohrratte.

PHYSICAL CHARACTERISTICS
Male total length 26.1–30.9 in (670–792 mm); tail length 7.0–7.5 in (180–192 mm); mass 11.0–14.3 lb (5.0–6.5 kg). Females total length 25.5–26.1 in (654–670 mm); tail 6.4–7.6 in (165–195 mm); mass 7.5–8.4 lb (3.4–3.8 kg). They have stocky bodies with strong limbs. The front feet are smaller than the hind ones. The small ears are broader than they are high and almost completely covered by fur.

The skull is powerfully built with enormous orange incisors. Information on the size of these animals in Africa varies greatly with weights of up to 19.8 lb (9 kg) being reported. In the southern African subregion, such large animals have never been reported.

DISTRIBUTION
Almost all African countries west of the Sahara. It does not occur in rainforests, deserts, and dry shrub. Corresponding with their habitat, they either have a wide or restricted distribution in the countries where they occur. They have been documented in West Africa from Gambia to Cameroon, Central African Republic, Sudan, Uganda, Kenya, Tanzania, Malawi, Mozambique, Zambia, Angola, northern border of Namibia and Botswana, Zimbabwe, and South Africa.

HABITAT
They can be found in swampy low-lying areas along river banks and streams where there are reed beds or areas of dense tall grass.

BEHAVIOR
Predominantly nocturnal. Occur solitarily or in small family groups with a dominant male, females, and young. When alarmed, they stamp their hind feet and make a whistling sound. They make grunting noises when relaxed and feeding. When fleeing, they run very fast and will easily take to water.

FEEDING ECOLOGY AND DIET
They are vegetarian and consume various kinds of grass, bark, and shrubs. They can be a severe pest in vegetable gardens and crop plantations.

REPRODUCTIVE BIOLOGY
Assumed to be polygynous. Normal gestation range is 152–156 days. Two to four young at birth; range is one to six. Birth mass 2.8–5.3 oz (80–150 g). Weaning mass 13.1–24.1 oz (374–688 g).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Meat very popular in many African countries. Many families depend on the selling of cane rat meat for income. In South Africa, some farmers are experimenting to farm them on a commercial basis. On the other hand, they can be severe pests in vegetable gardens and crops and can be regarded as a local pest. ◆

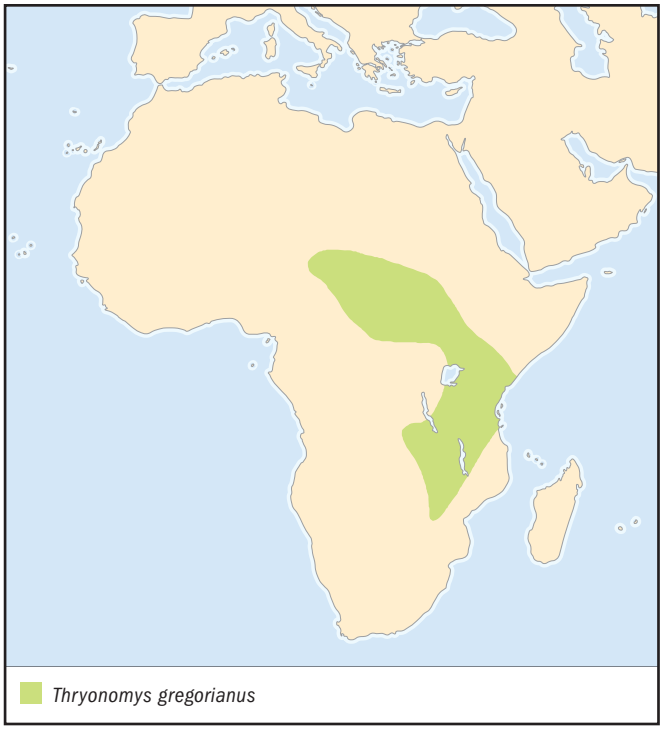
Lesser cane rat
Thryonomys gregorianus

TAXONOMY
Thryonomys gregorianus (Thomas, 1894), Kiroyo, Kenya.

OTHER COMMON NAMES
French: Le petit aulacode; German: Kleine Rohrratte.

PHYSICAL CHARACTERISTICS
Males total length 16.0–22.4 in (410–575 mm); tail 4.3–6.8 in (110–175 mm); mass 3.1–5.3 lb (1.4–2.4 kg). Females total length 19.3–21.1 in (495–540 mm); tail 4.9–5.5 in (125–140 mm); mass 4.0–4.2 lb (1.8–1.9 kg). Except for size they are similar in build to the greater cane rat, with similar features. The skull is powerfully built, with large orange incisors.

DISTRIBUTION
The lesser cane rat can be found in a narrow belt from northern Cameroon to East Africa, where they are common and widespread, and further south as far as Zimbabwe and parts of Mozambique. More thorough investigation may extend their distribution into parts of South Africa.



HABITAT
They prefer higher altitudes on the eastern tropical escarpment where they are able to utilize drier terrain including rocky habitats.

BEHAVIOR
Nocturnal with some diurnal activity. They occur solitarily or in small family groups with a dominant male, females, and young. They prefer good grass cover but will also reside in rock crevices, under rocks, or in abandoned holes of spring-hare.

FEEDING ECOLOGY AND DIET
Vegetarian, feeding on the stems of many plants and grasses.

REPRODUCTIVE BIOLOGY
Information sparse. Assumed to be polygynous. Records from eastern Zimbabwe reveal pregnant females during May (one female, two fetuses) and November (one female, three embryos).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The same as the greater cane rat. They play an equally important role as bushmeat. In cultivated areas, they are regarded as a pest due to the destruction of crops and vegetables. ◆

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Mac van der Merwe, PhD

African mole-rats
(Bathyergidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Bathyergidae

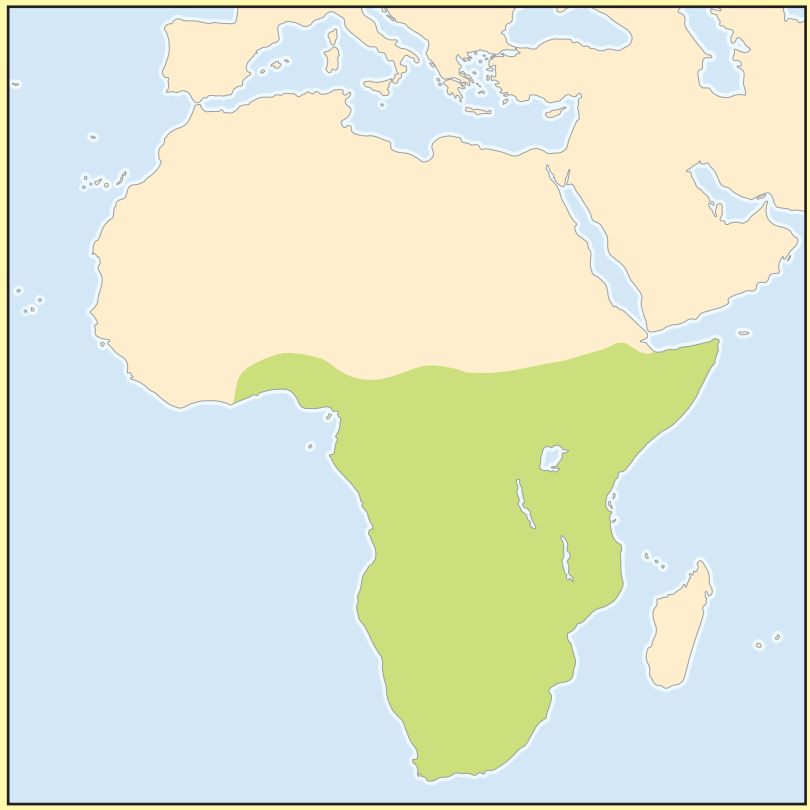
Thumbnail description
Small- to medium-sized rodents that show anatomical adaptations to living underground; bodies are cylindrical in shape and sturdy, limbs and tails (except for naked mole-rats) are short; eyes and external ears are very small, and noses flattened; prominent white incisors lie outside the lips and are used in digging

Size
Head and body length: 1.2–31 oz (34–896 g); mean mass: 3.2–11 in (83–281 mm)

Number of genera, species
5 genera; at least 14 species

Habitat
Arid regions, savanna, grasslands, and open woodlands

Conservation status
Vulnerable: 1 species; Data Deficient: 6 species



Distribution
Sub-Saharan Africa

Evolution and systematics

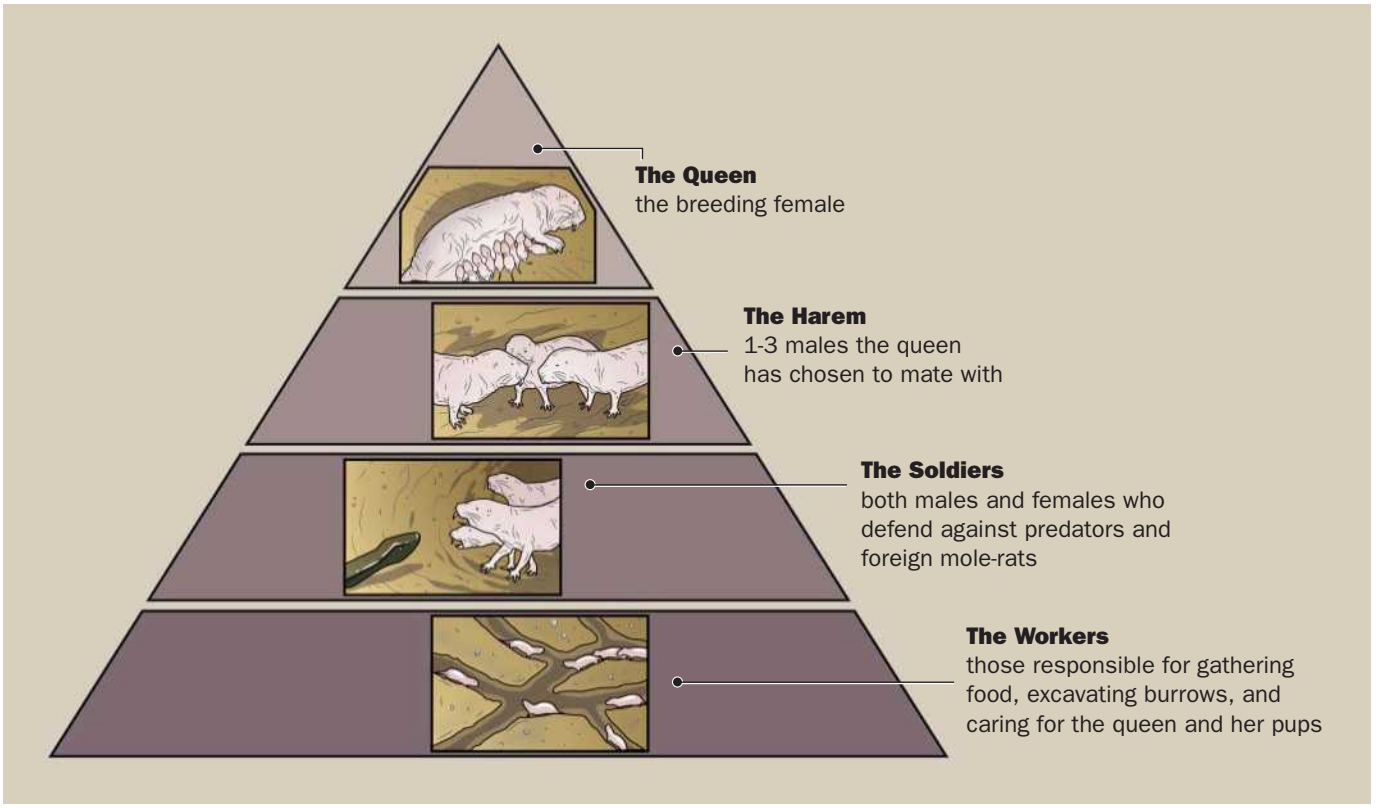
The classification of the Bathyergidae has long been problematic. There is now good support, using morphometric parameters and molecular phylogeny, for grouping them with the phiomorph rodents (the Old World lineage of the suborder Hystricognathi). Their closest relatives are the rock rats (Petromuridae), cane rats (Thyronomyidae), and Old World porcupines (Hystricidae).

The New and Old World Hystricognathi probably separated from their common ancestor during the Eocene, 33–49 million years ago (mya). The Bathyergidae are monophyletic, that is, all taxa can be traced back to a single common ancestor. However, fossil evidence and molecular data indicate an early divergence of *Heterocephalus* from the other genera in the family. Their fossil history is sparse but they most likely had an ancient African origin. The earliest fossil finds, in East Africa and Namibia, are from the early Miocene, around 25 mya.

The five modern genera are grouped into two subfamilies. The Bathyerginae contains one genus, *Bathyergus*, and two species, characterized by having grooved upper incisors and enlarged forefeet with strong digging-claws. The Georychinae contains four genera, *Georychus*, *Heliophobius*, *Cryptomys*, and *Heterocephalus*, all with ungrooved upper incisors and forefeet and claws that are not enlarged. All the Georychinae, except *Cryptomys*, are currently considered to be monospecific. The number of species in the genus *Cryptomys* is uncertain and needs revision; furthermore, the taxa in *Cryptomys* can be placed in two such genetically distinct groups that they may eventually be assigned to separate genera. Three genera are solitary, one animal inhabiting each burrow system; indeed, this is the usual pattern for subterranean mammals. Bathyergidae are exceptional in that *Cryptomys* and *Heterocephalus* are highly social: they live in colonies with a single reproductive female, her consorts, and a number of non-breeding workers (these are closely related to the breeders). Because *Heterocephalus* diverged from the other Bathyergidae early in their history, this unusual type of sociality probably evolved twice in the family.

Physical characteristics

Mole-rats show anatomical adaptations for life underground. Their limbs are short, their bodies are cylindrical in shape, their necks muscular, but indistinct from the head and



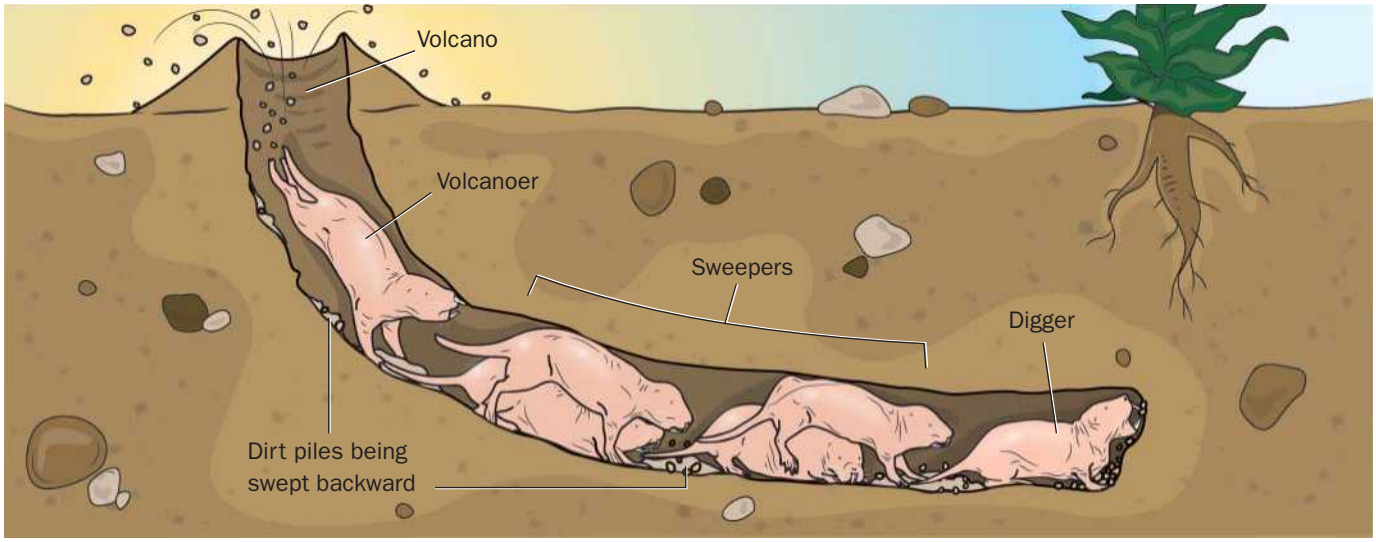
Mole-rats social structure. (Illustration by Katie Nealis)

body. Their heads are robust, ending in flattened pig-like noses. Their streamlined shape and short limbs enable them to move backwards and forwards with equal ease in the narrow confines of their burrows. The outer edges of their hind feet are fringed with stiff hairs and these, together with a brush of stiff hairs on their short tails (in all except in the naked mole-rat), help hold soil when they move it along the burrows. Their eyes are small and, at best, can only detect light and dark. Their ears lack external pinnae, and their range of hearing is more restricted than that of aboveground rodents. Nevertheless, at least two species of social mole-rats (*Heterocephalus* and *Cryptomys mechowi*) have large vocal repertoires, indicating relatively sophisticated levels of communication.

A Cape mole-rat (*Georychus capensis*), South Africa. (Photo by © Michael Dick/Animals Animals. Reproduced by permission.)

Their hair (except in the naked mole-rat) tends to be thick, short, and easily reversible; this is an asset when moving to and fro in the burrow. Strong muscles lying under a very loose skin enable them to vigorously shake their fur free of adhering soil. The loose skin also facilitates turning round in the narrow confines of the burrow. Because mole-rats live in dark burrows, the sense of touch is important to them. Stiff, tactile hairs scattered over much of the body, and projecting above the level of the rest of the hair, act in much the same way as the whiskers of a cat. Long, stiff sensory hairs abound on the front of the face and are also clustered above the eyes. Although otherwise lacking a coat of hair, all these sensory hairs are present in naked mole-rats.

A notable feature of mole-rats is a pair of large, ever-growing, and forwardly-directed incisors; these lie outside the mouth (extra-buccal). All mole-rats, except *Bathyergus*, are chisel-tooth diggers, that is, they excavate their burrows by biting at the soil with their incisors. Strongly haired, muscular lips meet behind the incisors to keep soil out of the mouth



Mole-rats digging system. (Illustration by Katie Nealis)

during digging. In all genera, except *Bathyergus*, the roots of the upper incisors extend back to originate behind the molars. It has been shown that a disproportionate amount of the brain of naked mole-rats is devoted to picking up sensory signals from these incisors; this is probably also true for the other chisel-tooth diggers in this family. The lower jaws of chisel-tooth diggers can move independently so that their incisors can be splayed apart or brought together, thereby making them a very versatile set of tools. Mole-rats groom lower incisors against the upper ones to sharpen their tips. The skull is dorsally flattened and houses strong jaw muscles (masseter and temporal) that are used in feeding and digging.

Physiological adaptations to subterranean life include a tolerance to high carbon dioxide and low oxygen concentrations and, at least in the naked mole-rat (and possibly others), a blood hemoglobin with a high affinity for oxygen. Mole-rats, like many subterranean mammals, have lower body temperatures and resting metabolic rates than do mammals of similar size living aboveground. The humidity in burrows is high and, consequently, evaporative water loss and convective cooling are of little use if the animal overheats when digging. The naked mole-rat has the poorest thermoregulatory ability of the family; indeed, its body temperature varies with ambient temperature in a similar way to reptiles and, in the wild, it usually lies between 82.4 and 86°F (28–32°C), which is close to the burrow temperature. They regulate their body temperature by moving up and down in the burrows and by huddling together. Microorganisms in the cecum aid in the

A common mole-rat (*Cryptomys hottentotus*) tunnels into a dirt burrow. (Photo by © Jeffrey L. Rottman/Corbis. Reproduced by permission.)

A common mole-rat (*Cryptomys hottentotus*) in South Africa. (Photo by Animals Animals ©D. Curl, OSF. Reproduced by permission.)

A close-up view of the incisors on a common mole-rat (*Cryptomys hottentotus*), with the lips closed behind the teeth. (Photo by © Jeffrey L. Rottman/Corbis. Reproduced by permission.)

The naked mole-rat (*Heterocephalus glaber*) is native to East Africa. (Photo by Scott Camazine/Photo Researchers, Inc. Reproduced by permission.)

digestion of fibers in their diet; to fully utilize these digested foods, mole-rats practice coprophagy, a process in which they double up and eat some of the energy-rich feces as they are voided.

Distribution

The family is confined to sub-Saharan Africa. Dune mole-rats (*Bathyergus*) are endemic to South Africa, occurring in coastal sandy soils of the southwestern and northern Cape and southwestern Namibia. The Cape mole-rat (*Georychus*) is also endemic to South Africa, mostly occurring in the Fynbos vegetation of the southwestern and eastern Cape, whereas species of the genus *Cryptomys* occur in western, central, and southern Africa. The silvery mole-rat (*Heliophobius*) occurs in eastern Africa and the naked mole-rat (*Heterocephalus*) in the arid regions of the Horn of Africa, namely Kenya, Somalia, and Ethiopia.

Habitat

They occur in a range of habitats, but not in dense forests. Their distribution is usually associated with the occurrence of geophytes (plants with underground storage organs). The solitary genera (*Bathyergus*, *Georychus*, and *Heliophobius*) tend to be restricted to more mesic areas, whereas the social genera (*Heterocephalus* and some species of *Cryptomys*) can also oc-

A group of naked mole-rats (*Heterocephalus glaber*). (Photo by Gregory G. Dimijian, M.D./Photo Researchers, Inc. Reproduced by permission.)

cur in arid, semidesert habitats. Soil types range from soft sands (*Bathyergus*) to soils that become extremely hard when dry (*Heterocephalus*). Mole-rats live in a burrow system consisting of a network of superficial foraging tunnels, a deeper nest complex with a toilet area, and, often, a food store. Burrows are sealed from the surface, except when disposing of excavated soil on the surface, and, consequently, the mole-rats live in a subterranean micro-habitat that is buffered from the extremes in temperature and humidity. The burrows also offer considerable protection against predators, including snakes, birds of prey, and small carnivores.

Behavior

Mole-rats dig by loosening the soil with strongly developed forefeet (*Bathyergus*) or by biting the soil with their incisors (the other genera). The loosened soil is pushed under their bodies with their forefeet and then collected and kicked behind them with their hind feet. When a pile of soil has accumulated, they reverse with it up a side-branch and use their hind feet to push it onto the surface. After a mound has been completed, the side branch to the surface is sealed. Naked mole-rats dig cooperatively—one animal works at the earth-face, a chain of animals transports the soil, and another animal kicks the soil out of a hole. The solitary species aggressively defend their burrow system against conspecifics and advertise their presence to their neighbors by drumming on the burrow floor with their hind feet. During the breeding season, different drumming patterns of male and female *Georychus* advertise their presence to potential mates. The social species are strongly xenophobic towards foreign animals, and naked mole-rats have a unique colony odor that enables them to differentiate between their own and foreign colony members.

Feeding ecology and diet

African mole-rats favor areas in which energy-rich bulbs, corms, and tubers abound. Although these constitute their main food source, they will also eat roots and the aerial parts of plants. These geophytes often occur in clumps and are encountered by the mole-rats as they dig their foraging tunnels, most of which are dug after rain when the soil is moist and easily worked. In arid regions where rainfall is unpredictable and often widely spaced, the mole-rats have to make the most of each digging opportunity in order to find sufficient food to last them until it next rains (sometimes a year later). Clumps of food in these arid regions also tend to be spaced further apart than in mesic regions, or to occur as large isolated tubers. The limited opportunities in which to dig, and the distribution of food in these arid regions, exclude solitary species from these areas. Social species can mobilize their workforce

The dune mole-rat (*Bathyergus janetta*) primarily uses its claws to dig. (Photo by J. Visser/Mammal Images Library of the American Society of Mammalogists.)

to search a wide area in a short time to locate sufficient food to see them through the dry periods. Colonies of naked and Damaraland mole-rats have been known to dig up to 0.6 mi (1 km) in a single session of digging after a rainfall.

Small-sized geophytes are either immediately consumed or carried to a central store situated near the nest. Large geophytes are left growing and eaten in situ. Sometimes these partly eaten geophytes are abandoned, then they regenerate, and thus provide the mole-rats with a renewable resource. This is important because field studies on the naked mole-rat, Damaraland mole-rat, and the common mole-rat show that colonies remain resident in an area; they do not simply exploit it and then move on. The diet of dune mole-rats includes about 60% aboveground vegetation (forbs, grasses); the mole-rats come up under a plant, loosen its roots, and pull the entire plant into the burrow. They can thus forage with minimal exposure to predators.

Reproductive biology

In solitary species, courtship and mating are brief encounters and the animals then resume their solitary existence. When pups are about two months old, they disperse to establish their own burrow systems. Colonies of all social mole-rats have reproductive division of labor, whereby reproduction is restricted to a single female and a few males. The remaining members are closely related to the breeders, but are reproductively quiescent while in the colony. Colony formation and the mechanisms of suppression differ in the species. Thus, there is strong inhibition to incest in *Cryptomys*, whose colonies are founded by a female and her unrelated consorts. Initially, their offspring remain as non-breeding helpers, only risking dispersing if environmental conditions are favorable. Colonies break up completely when a breeder dies. Mechanisms of reproductive suppression within this genus range from incest avoidance to physiological mechanisms that inhibit ovulation in the females but not sperm production in the males. Colonies of naked mole-rats, on the other hand, are inbred. The aggressive behavior of the breeding female induces neuroendocrine changes in the pituitary that affect the functioning of the gonads of both non-breeding males and females. When the breeding female dies, some of the oldest females in the colony become sexually active (this can occur within a week of the death of the breeder), and they often fight viciously for the vacated position.

Bathyergus, *Georychus*, *C. hottentotus*, and possibly *Heliophobius* breed seasonally, whereas *Heterocephalus*, *C. damarensis*, *C.*

darlingi, and *C. mechowi* breed throughout the year. Gestation lengths range from about 44 days in *Georychus* to 100 days in *C. amatus*. Mean litter sizes are less than four, except *Georychus*, which have up to six, and *Heterocephalus*, which can have up to 13. A breeding female *Heterocephalus* can bear huge litters (up to 28 pups). During her first few pregnancies, her lumbar vertebrae elongate, thereby increasing the size of her abdominal cavity and her capacity to bear these large litters. She thus becomes morphologically distinct from the rest of the colony, a unique feature amongst mammals. This phenomenon, together with having a monopoly of reproduction, large litters, and presiding over colonies of up to 300 animals, makes naked mole-rats the closest mammalian equivalent to social insects such as termites.

Conservation status

The habitat of *Bathyergus janetta* is threatened by diamond mining. Geographically isolated northern populations of *Georychus*, which may be a separate species, are small and possibly threatened. Little is known of the status of some species of *Cryptomys* from central and eastern Africa.

Significance to humans

Mole-rats can be pests in farmlands or in urban developments. The large dune mole-rat (*B. suillus*) causes the most damage because their tunnels undermine roads and runways of airports, and their large mounds and tunnels can cause damage to farm machinery. Mole-rats also chew through underground cables and irrigation pipes.

1. Cape mole-rat (*Georychus capensis*); 2. Damaraland mole-rat (*Cryptomys damarensis*); 3. Common mole-rat (*Cryptomys hottentotus hottentotus*); 4. Cape dune mole-rat (*Bathyergus suillus*); 5. Naked mole-rat (*Heterocephalus glaber*). (Illustration by Joseph E. Trumpey)

Species accounts

Cape dune mole-rat
Bathyergus suillus

SUBFAMILY
Bathyerginae

TAXONOMY
Mus suillus (Schreber, 1782), Cape of Good Hope, South Africa.

OTHER COMMON NAMES
German: Kap-strandgräber.

PHYSICAL CHARACTERISTICS
The largest bathyergid has well-developed forefeet whose digits two, three, and four bear well-developed claws. Upper incisors are grooved. Cinnamon color, base of hairs black, white head spot sometimes present. There is sexual dimorphism: mean mass of males 31 oz (896 g), females 23.5 oz (670 g).

DISTRIBUTION
Endemic to South Africa, predominately in the coastal regions of the southwestern Cape.

HABITAT
Largely restricted to coastal sand dunes; favors grasslands.

BEHAVIOR
Solitary; aggressively defends its burrow from conspecifics. Males have thick skin on underside of neck, presumably as protection during fighting for mates.

FEEDING ECOLOGY AND DIET
About 60% of diet is of aboveground vegetation, the remainder is geophytes.

REPRODUCTIVE BIOLOGY
Breed seasonally (July–October), up to two litters annually. Gestation length about 52 days, mean litter size 2.4 (range one to five); pups weaned and disperse when about two months old.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Important agricultural pests, they also damage roads, runways to airports, and chew through underground cables. ◆

Cape mole-rat
Georychus capensis

SUBFAMILY
Georychinae

TAXONOMY
Mus capensis (Pallas, 1778), Cape of Good Hope, South Africa.

OTHER COMMON NAMES
German: Kap-blessmulle, Kap-mullratte.

PHYSICAL CHARACTERISTICS
Strikingly marked, with a black head, white muzzle, white around eyes and ears, and a white head patch. Body buff-orange, hands, feet, and tail white; 6.3 oz (180 g); no sexual dimorphism.

DISTRIBUTION
Endemic to South Africa, in the southwestern Cape; two small isolated populations occur in KwaZulu-Natal and Gauteng.

HABITAT
In the coastal and mountainous regions in Fynbos vegetation where geophytes abound. Mean rainfall usually exceeds 19.5 in (500 mm).

BEHAVIOR
Solitary, highly territorial.

FEEDING ECOLOGY AND DIET
Geophytes and grass roots, and a small percentage of aboveground material. Geophytes are stored near the nest.

REPRODUCTIVE BIOLOGY
Breeds seasonally (August–December), with a maximum of two litters annually. Males and females signal for mates with drumming of hind feet. Gestation length 44–48 days, mean litter size six, range four to 10; pups weaned and disperse when about two months old.

CONSERVATION STATUS
Not threatened, except for the geographically isolated northern populations.

SIGNIFICANCE TO HUMANS
Pests where root-crops are planted and in urban areas. ◆

Damaraland mole-rat
Cryptomys damarensis

SUBFAMILY
Georychinae

TAXONOMY
Bathyergus damarensis (Ogilby, 1838), Damaraland, Namibia.

OTHER COMMON NAMES
English: Damara mole-rat.

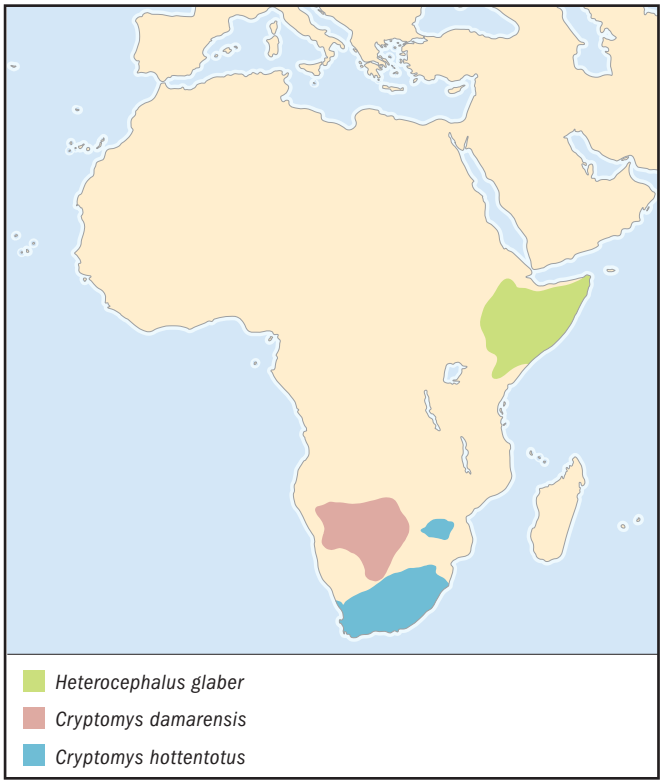
PHYSICAL CHARACTERISTICS
Two coat colors, fawn and dark brown, can occur in one colony; both colors have a large white head patch. Mean body mass is about 4.6 oz (130 g); males tend to be larger than females. However, mass varies with social status.

DISTRIBUTION
Widespread in Kalahari sands of Namibia, much of Botswana, extending into western Zimbabwe and northwestern South Africa.

HABITAT
Arid regions with mean annual rainfall of under 15.6 in (400 mm). Favor red Kalahari arenosols, and loose, unconsolidated alluvial sands.

BEHAVIOR
Social; colonies of up to 40 animals contain a single breeding female, her consorts, and their non-breeding offspring. The reproductives are dominant in the colony.

FEEDING ECOLOGY AND DIET
Geophytes; large geophytes are eaten *in situ*, smaller ones carried to a communal store. Dig cooperatively to find food.



REPRODUCTIVE BIOLOGY
Obligate out-breeders. Breeders are the founding members of the colony, while their pups remain as nonbreeding helpers. Breed throughout the year, gestation length 78–92 days, mean litter size three (range one to five); have up to four litters annually. Breeders can live more than 10 years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common mole-rat
Cryptomys hottentotus hottentotus

SUBFAMILY
Georychinae

TAXONOMY
Bathyergus hottentotus (Lesson, 1826), Paarl, South Africa.

OTHER COMMON NAMES
English: African mole-rat.

PHYSICAL CHARACTERISTICS
Small mole-rats show sexual dimorphism (mean mass 2.7 oz [77 g] for males, 2 oz [57 g] for females). Coat color fawn to gray, head patch missing or very small.

DISTRIBUTION
Widespread over much of South Africa, sometimes in sympatry with other genera.

HABITAT
Occur in a wide diversity of soil types, though not in very loose sand. Occur in very arid to mesic areas.

BEHAVIOR
Social, in small colonies (up to 14) with a breeding female, her consorts, and their nonbreeding offspring, the workers. There is strong inhibition to incest.

FEEDING ECOLOGY AND DIET
Feed almost exclusively on geophytes. Portable geophytes are stored close to the nest. Large ones are eaten *in situ*, and parts may be left to regenerate.

REPRODUCTIVE BIOLOGY
Breed seasonally (October–January), having a maximum of two litters annually. Gestation length 59–66 days, mean litter size three (range one to five); pups do not disperse on weaning but remain as helpers.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A pest where root crops are grown and in urban areas. ◆

Naked mole-rat
Heterocephalus glaber

SUBFAMILY
Georychinae

TAXONOMY
Heterocephalus glaber Rüppell, 1842, Shoa, Ethiopia.

OTHER COMMON NAMES
German: Nacktmull.

PHYSICAL CHARACTERISTICS
Hairless except for scattered sensory hairs. Their skin is pinkish brown and wrinkled, their tails are longer than those of other bathyergids. The smallest of the mole-rats: mean body mass 1.2 oz (34 g). There is no sexual dimorphism but size varies with social status and dominant individuals can weigh up to 2.8 oz (80 g).

DISTRIBUTION
Widespread in arid regions of East Africa (Ethiopia, Somalia, and Kenya).

HABITAT
Arid regions with mean annual rainfall of under 15.6 in (400 mm). Rainfall is unpredictable. Favor fine sandy soils that become very hard in the dry season.

BEHAVIOR
Highly social (eusocial); colonies of up to 300 animals (mean 75), showing marked reproductive division of labor, and a workforce of nonbreeding animals. Socially induced infertility is mediated through aggressive behavior by the breeding female. Most nonbreeders never disperse or breed. Colonies often highly inbred; there is no incest avoidance. Occasional out-breeding occurs: dispersers are fat, highly sexed, attracted to foreign animals, have a strong urge to disperse.

FEEDING ECOLOGY AND DIET
Feed on geophytes located through cooperative searching for food. Colonies occupy the same home range for many years. Coprophagy (eating feces) performed by all colony members. The breeding female and the weaning pups also beg feces from colony members.

REPRODUCTIVE BIOLOGY
Only one female and a few males breed. The breeding female has a distinctive elongated body and up to seven pairs of nipples. She breeds throughout the year. Gestation: 66–74 days; mean litter size: 12 (range one to 28); up to four litters born annually. Multiple paternity of a litter can occur. Naked mole-rats are long-lived (over 28 years in captivity); the reproductive animals remain fertile to old age.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Namaqua dune mole-rat *Bathyergus janetta*	Color variable, blackish head, dark band mid-dorsally from neck to rump, sides silvery. Size varies regionally, animals heavier inland than at coast. Sexually dimorphic: males about 15 oz (425 g), females about 11 oz (315 g).	Prefer slightly consolidated coastal dunes in arid areas with rainfall usually below 13.5 in (350 mm). Solitary; breed seasonally in spring/ early summer. One to seven pups.	Northwestern South Africa, extending into Namibia.	Geophytes, and above-ground vegetation when available.	Lower Risk/Near Threatened; threatened by habitat destruction from diamond mining
Silvery mole-rat *Heliophobius argenteocinereus*	Color light silvery gray or fawn. Have more cheek teeth than other mole-rats (6 upper and 6 lower). No sexual dimorphism, mean weight 5.6 oz (160 g).	Favors grasslands and open forest in mesic areas with annual rainfall about 35 in (900 mm). Solitary lifestyle.	Southern Kenya, Tanzania, southwestern Congo, northern Mozambique.	Little known, does eat geophytes.	Lower Risk/Near Threatened
Mashona mole-rat *Cryptomys darlingi*	Color variable from blackish through seal brown to fawn, white head patch may be present. No sexual dimorphism: mean weight 2.3 oz (64 g).	Scrub and open woodlands, mean annual rainfall exceeds 27.3 in (700 mm). Social, in small colonies with a single breeding pair. Aseasonal breeders, gestation 56–61 days, small litters (maximum of three).	Includes eastern Zimbabwe, west and central Mocambique.	Not known, includes geophytes and roots.	Not threatened
Giant Zambian mole-rat *Cryptomys mechowi*	Color light brown, small head patch occasionally present. Heads are large. Sexual dimorphism apparent: males up to 21 oz (600 g), females 12.3 oz (350 g).	Miombo tropical woodland and savanna with rainfall over 43 in (1,100 mm). Social, at least eight in a colony with a breeding pair. Aseasonal reproduction. Gestation about 100 days, maximum litter size four.	Congo, northern Zambia, and central Angola.	Geophytes, roots, some invertebrates.	Not threatened
Bocages mole-rat *Cryptomys bocagei*	Drab gray to silver gray. Mean head and body length 6 in (152 mm), no data for weight.	Little known of the habitat or behavior of this social mole-rat.	Western Angola and possibly extending into northwestern Namibia.	Not known.	Not threatened

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Nigerian mole-rat *Cryptomys foxi*	Deep sepia color, head patch may be present. Mean head and body length: 5.6 in (145 mm), no data for weight.	Nothing known of habitat. Social with 12 animals caught in one colony. No other details.	Bauchi plateau in Nigeria, Ngaundere in Cameroon.	Not known.	Lower Risk/Near Threatened; threatened by habitat destruction
Togo mole-rat *Cryptomys zechi*	Color variable but generally pale. White head patch sometimes present. Mean head and body length 6.5 in (167 mm), no data for weight.	In Guinea and Doka woodlands. Occur in small colonies but details not known.	Restricted distribution between Oti and Volta rivers.	Not known.	Lower Risk/Near Threatened; threatened by habitat destruction
Ochre mole-rat *Cryptomys ochraceocinereus*	Brown to sepia color with white head patch. Mean head and body length 7.8 in (201 mm), no data for weight.	Savanna with low to moderate rainfall.	Sudan, and possibly includes synonyms *C. lechei* from northern Uganda and northern Democratic Republic of the Congo and *C. kummi* from Central African Republic.	Not known.	Not threatened
Highveld mole-rat *Cryptomys hottentotus pretoriae*	Recent genetic studies suggest that this may be a separate species. Color silvery fawn to seal gray. Head patch rarely present. Body mass 3 oz (90 g). No sexual dimorphism.	Highveld grasslands and savanna woodlands. Social, colonies up to 12 individuals with a breeding pair. Seasonal breeder (May to December), maximum of three pups per litter and two litters annually.	Endemic to highveld of South Africa, in Northwestern, Gauteng, and Mpumalanga provinces.	Grass roots and stolons and geophytes.	Not threatened

Resources

Books

Bennett, Nigel C., and Chris G. Faulkes. *African Mole-rats: Ecology and Eusociality*. Cambridge: Cambridge University Press, 2000.

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Jarvis, Jennifer U. M., M. J. O'Riain, N. C. Bennett, and P. W. Sherman. "Mammalian Eusociality: A Family Affair." *Trends in Ecology and Evolution* 9 (1994): 47–51.

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Jennifer U. M. Jarvis, PhD

Old World porcupines
(Hystricidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Hystricidae

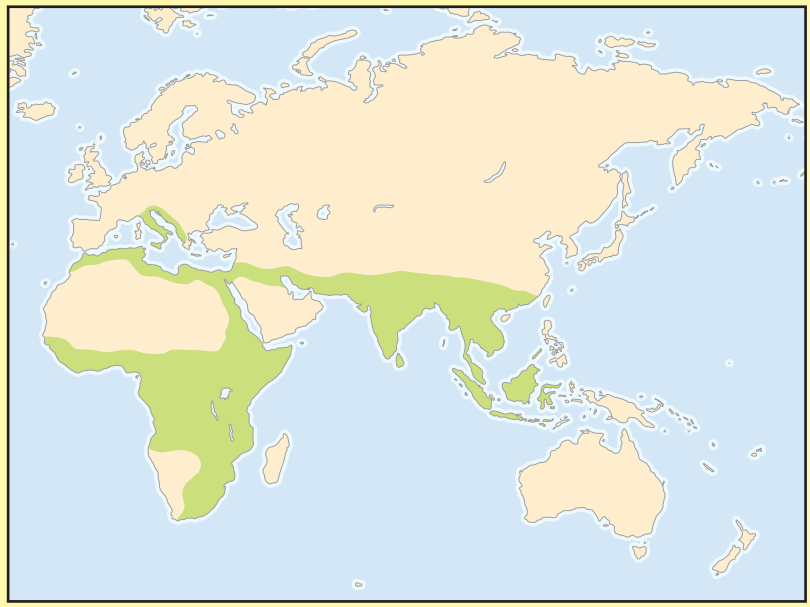
Thumbnail description
Medium-sized to large rodents, with a heavyset body, a tail not more than half as long as the head and body, and short limbs; spines, quills, and bristles cover the back, sides, and parts of the tail

Size
Head and body length 13.8–36.6 in (35–93 cm), tail length 1–10.2 in (2.5–26 cm), weight 3.3–66.1 lb (1.5–30 kg)

Number of genera, species
3 genera; 11 species (extant)

Habitat
Adaptable to a variety of habitats and can be found in such areas as deserts, rocky areas, mountains, savannas, croplands, and forests

Conservation status
Vulnerable: 1 species; Lower Risk/Near Threatened: 2 species.



Distribution
Generally the warmer regions of Asia, Europe, Africa

Evolution and systematics

Old World porcupines evolved from Miocene (24 million to 5 million years ago [mya]) in Asia, from Pliocene (5 to 1.6 mya) in Europe, and from Pleistocene (1.6 mya to 10,000 years ago) in Africa.

Physical characteristics

Bodies range from a rather slender build, in the genus *Trichys*, to a clumsy and stocky build, in the genus *Hystrix*. The tail is very short in some species, but can reach around half the head-body length in others. Eyes and external ears are generally small, with a poor sense of sight but a sharp sense of hearing. Nostrils are usually S-shaped, with a sharp sense of smell. The upper lip is cleft, and the tip of the nose is stubbed and covered with velvety hairs. Large, chisel-shaped lower and upper incisor teeth do not have longitudinal grooves and grow throughout life; molars are rooted and have irregular enamel folds that are rapidly worn down.

The skull is long and sometimes inflated with air chambers over the rostrum and top of head. The infraorbital foramen (lower orbital cavity in upper jawbone) is unusually enlarged, resulting in portions of masseter (chewing) muscle being penetrated through it, thus enabling muscles to adhere to the frontal side surface of the upper jawbone (called hystricomorphous). The lower jaw is hystricognathous. Features (generally called postorbital processes) possibly evolved to enlarge chewing volume and to allow animals to smell underground bulbs.

Both forelimbs and hind limbs are short and heavily built; as a result, Old World porcupines are excellent diggers and sometimes construct their own burrows. On the two forelimbs, each foot has four well-developed clawed digits and one thumb, which is regressed and externally visible only by nail and thumb pad; each of two hind feet has five functional digits. Claws are short and soles of feet are smooth, naked, and fitted with pads. When walking or running, the entire sole of the foot touches the ground. They are able to swim.

The most characteristic physical features are the quills, spines, and bristles. The head, body, and (in some species) tail are covered by barb-less spines, which are thick, stiff, sharp modified hairs, as much as 13.8 in (35 cm) in length. Spine coloration is brownish or blackish, often with conspicuous white bands around them. All spines lack the barbules that characterize spines of New World porcupines. Longest spines tend to be found on rump and shortest on cheeks. In genus *Trichys*, for example, spines are short, flattened, and not especially well developed. In genus *Hystrix*, in contrast, spines develop into hollow quills that reach 7.9 in (20 cm) in length.

Spines vary considerably among species but can be roughly classified into seven groups: (1) stiletto-like quills that are stiff, flattened, with sharp points and longitudinal grooves, which cover most of body; (2) spikes that are thick, inflexible, and

A South African porcupine (*Hystrix africaeaustralis*) eats gemsbok cucumbers. (Photo by Clem Haagner. Bruce Coleman, Inc. Reproduced by permission.)

with sharp points; (3) bristle-like quills (also called tactile bristles) that are flexible toward the ends, with a round cross section and sharp points; (4) rattling cups that are hollow, capsule-like structures fastened on the end of tail by a thin stem; (5) platelet bristles that are hollow, flattened, yellowish-white at tail end, with shafts that enlarge at regular intervals; (6) brush-type bristles that are flattened, smooth bristles at tail end that look like narrow parchment strips; and (7) mane bristles that are tufts of hair on head and neck.

Normally, quills lie flat and point to the rear. When the animal is threatened or showing aggression, quills can be raised instantly. Hind feet are usually then stamped and quills shaken with a rattling sound (except for *Trichys*), which serves as a warning to potential predators. If threat continues, the porcupine may charge backwards or sideways into predator with attempt to strike intruder with quills. Quills are loosely attached but cannot be projected. They penetrate flesh and stick readily. No poison is carried; however, bacteria on quills can infect, and sometimes kill, the victim if the puncture wound is deep enough. The area with detached quills will grow back new quills. Some species possess coarse, flat spines that form an erectable crest on necks and tops of heads.

Distribution

Parts of southern Europe, all across southern Asia, on many islands of the East Indies, and throughout Africa.

Habitat

Old World porcupines are usually terrestrial and normally do not climb trees; need only shelter from the weather and for periodic nesting. They often use abandoned deep burrows of other animals; caves, rock crevices, decaying logs, hollow trees, and holes dug by other animals; or deep burrows that they have excavated themselves. Nests are constructed of plant material within the den. Burrows can be complex systems, where many may live in adjoining burrows and may be used for many years. A single burrow may hold up to 10 individuals.

A South African porcupine (*Hystrix africaeaustralis*) with young in the Kalahari Desert of South Africa. (Photo by Clem Haagner. Bruce Coleman, Inc. Reproduced by permission.)

Behavior

Old World porcupines, which are ground living (terrestrial) and slow moving, are called "Old World" in order to distinguish them from the arboreal (tree climbing) porcupines of the New World. Mainly nocturnal (hiding during the day) and terrestrial. These animals walk heavily on the sole of the foot with the heel touching the ground, and run with a shuffling gait or gallop clumsily when pursued. Except for genus *Trichys*, they rattle their spines when moving and may also stamp their feet when alarmed. Temperament (from obser-

An Indian crested porcupine (*Hystrix indica*) with relaxed quills. (Photo by S. Nagendra/Photo Researchers, Inc. Reproduced by permission.)

A North African porcupine (*Hystrix cristata*) raises the quills along its head, nape, and back in a defensive crest. (Photo by © Joe McDonald/Corbis. Reproduced by permission.)

vations in captivity) ranges from shy and nervous to docile; some species are moderately gregarious. Chief predators are wild cats, birds of prey, hyenas, and pythons.

Feeding ecology and diet

The diet consists of mostly vegetation with many kinds of plant material and crops such as sweet potatoes, bananas, peanuts, pineapple, maize, sugarcane, onions, potatoes, cucumbers, beans, melons, grapes, and mangoes, but carrion feeding and bone gnawing also occurs. Gnawed bones often litter area around dens (may be chewed on for deficient minerals such as calcium). Old World porcupines often gnaw on branches, tree bark, and tree trunks to help teeth wear down properly.

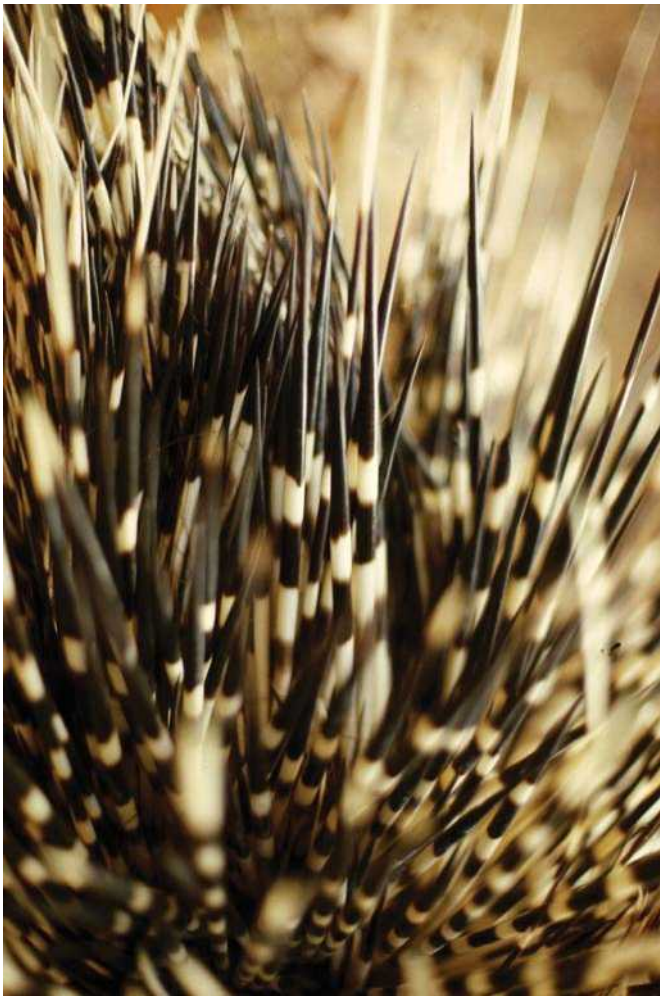
Reproductive biology

An elaborate nighttime dance and courtship involves the male showering the female with urine. If the female is receptive, the male stands motionless in front of the female, then approaches and retreats numerous times while making sounds to her. (If female is not receptive, she will be aggressive toward the courting male.) When ready, the female will raise her rear and tail high with her chest on ground. Male will mount female by clasping her sides with his front paws and balancing on his hind feet. No male weight is transferred to the female. (Males have no external scrotum and the penis normally points backward.) Both males and females loudly whine, grunt, and squeal while mating.

The gestation period is usually 93–110 days, depending on species; breeding occurs usually once a year (sometimes twice), during March to December; usually one to two young, but up to four in a litter is possible. Young are precocial and have fur and the ability to locomote at birth. They weigh about 12 oz (340 g) at birth and nurse for about three to four months, able to feed almost immediately. Eyes are open when born or open within first few hours. Females have two to three pairs of mammae that are located on sides of chest cage, just behind shoulders. After a week or so, soft, short hair-like quills will harden and young may leave nest with mother. Sexual maturity is reached at nine to 18 months. The life span in captivity is at least 10 years, and in the wild, average life span is about 20 years.

Conservation status

The common porcupine (*Hystrix brachyura*) is considered Vulnerable. Both the thick-spined porcupine (*Hystrix cras-*



Close-up of South African porcupine (*Hystrix africaeaustralis*) quills. (Photo by G. D. Dodge and D. R. Thompson. Bruce Coleman, Inc. Reproduced by permission.)

sispinis) and North African porcupine (*Hystrix cristata*) are ranked as Lower Risk/Near Threatened by the IUCN. Predation and human encroachment are the main threats, though many Hystricidae species are quite adaptable to changing habitat.

Significance to humans

Porcupines are hunted for meat (considered a delicacy in some societies) and to acquire quills as ornaments and talismans. The animals carry fleas and ticks and transmit a number of diseases, including rickettsiasis and bubonic plague. Because of their habit of gnawing bark off trees and eating agricultural crops, they are often regarded as pests.

A South African porcupine (*Hystrix africaeaustralis*) watching for predators. (Photo by George Dodge. Bruce Coleman, Inc. Reproduced by permission.)

1. Long-tailed porcupine (*Trichys fasciculata*); 2. Asiatic brush-tailed porcupine (*Atherurus macrourus*); 3. African brush-tailed porcupine (*Atherurus africanus*); 4. South African porcupine (*Hystrix africaeaustralis*); 5. North African porcupine (*Hystrix cristata*). (Illustration by Barbara Duperron)

1. Thick-spined porcupine (*Hystrix crassispinis*); 2. Sumatran porcupine (*Hystrix sumatrae*); 3. Common porcupine (*Hystrix brachyura*); 4. Indian crested porcupine (*Hystrix indica*); 5. Indonesian porcupine (*Hystrix pumila*). (Illustration by Barbara Duperron)

Species accounts

Indonesian porcupine
Hystrix pumila

SUBFAMILY
Hystricinae

TAXONOMY
Hystrix pumila (Günther, 1879), Palawan, Philippines.

OTHER COMMON NAMES
English: Palawan porcupine.

PHYSICAL CHARACTERISTICS
Body length is 1.4–3.0 ft (42–93 cm), tail length is 1.0–7.5 in (2.5–19 cm), and weight is 8.4–11.9 lb (3.8–5.4 kg). Short, rounded head; no head or neck mane; upper side is dark brown to black and partially speckled in light color; underside is brown to gray-white. Body is densely covered with flattened quills, each grooved longitudinally and increasing in rigidity near tip. Quills are smaller along tail and more flexible on underside. Coarse, bristle-like hairs cover feet. Nasal bones are small. Subgenus *Thecurus* resembles subgenus *Hystrix* in having a shorter tail and longer quills. It resembles subgenus *Acanthion* in that it lacks a well-defined crest and its quills have only one black band.

DISTRIBUTION
Palawan, Busuanga, and Balabac Islands (Philippines).

HABITAT
Lowland secondary and primary forests, abandoned and active plantations, and rugged areas.

BEHAVIOR
Takes refuge in ground caves, rock crevasses, and under fallen trees; frequently two, seldom one or three animals per den; poor climber.

FEEDING ECOLOGY AND DIET
An assortment of vegetation (similar to family).

REPRODUCTIVE BIOLOGY
Gestation period is 93–105 days. Mean life span is 9.5 years in captivity.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. Eat farmers' crops. ◆

Sumatran porcupine
Hystrix sumatrae

SUBFAMILY
Hystricinae

TAXONOMY
Thecurus sumatrae (Lyon, 1907), Sumatra, Indonesia.

OTHER COMMON NAMES
English: Sumatran thick-spined porcupine, Sumatran short-tailed porcupine, Indonesian porcupine.

PHYSICAL CHARACTERISTICS
Body length is 1.4–3.0 ft (42–93 cm) with mean of 1.8 ft (54 cm), tail length is 1.0–7.5 in (2.5–19 cm) with mean of 4 in (10 cm), and weight is 8.4–11.9 lb (3.8–5.4 kg). Short, rounded head (described as "cat's head"); no head or neck mane; upper side is dark brown to black and partly speckled in light color; underside is brown to gray-white. Body is covered with flattened spines; each grooved longitudinally and increasing in rigidity near tip; spines are interspersed with short hairs. Quills are smaller along tail and more flexible on underside. Specialized "rattling" quills on tail expand near tips, and are hollow so that quills can rattle when vibrated together to warn potential enemies. Coarse, bristle-like hairs cover feet. Nasal bones are small. Subgenus *Thecurus* resembles subgenus *Hystrix* in having shorter tail and longer quills. Resem bles subgenus *Acanthion* in that it lacks well-developed crest and its quills have only one black band.

DISTRIBUTION
Sumatra.

HABITAT
Takes refuge in ground caves, rock crevasses, and under fallen trees; generally forests, abandoned and active plantations, and in rugged rocky areas.

BEHAVIOR
Frequently two per den (sometimes one or three). Poor climber.

FEEDING ECOLOGY AND DIET
An assortment of vegetation (similar to family).

REPRODUCTIVE BIOLOGY
Gestation period, number of young at birth, weight at birth, weaning period, and sexual maturity are all similar to those of family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. Eat farmers' crops, and are thus perceived as pests. ◆

Thick-spined porcupine
Hystrix crassispinis

SUBFAMILY
Hystricinae

TAXONOMY
Hystrix crassispinis (Günther, 1877), Sabah, Malaysia.

OTHER COMMON NAMES
English: Borneo short-tailed porcupine.

PHYSICAL CHARACTERISTICS
Body length is 1.4–3.0 ft (42–93 cm), tail length is 1.0–7.5 in (2.5–19 cm), and weight is 8.4–11.9 lb (3.8–5.4 kg). Short, rounded head; no head or neck mane; upper side is dark brown to black and partly speckled in light color; underside is brown to gray-white. Body is covered with flattened spines; each grooved longitudinally with increased rigidity near tip. Quills are smaller along tail and more flexible on underside. Coarse, bristle-like hairs cover feet. Nasal bones are small. Subgenus *Thecurus* resembles subgenus *Hystrix* in having shorter tail and longer quills. Resembles subgenus *Acanthion* in that it lacks well-developed crest and its quills have only one black band.

DISTRIBUTION
North Borneo, especially Kalimantan.

HABITAT
Forests and cultivated areas, from sea level to 3,900 ft (1,200 m).

BEHAVIOR
Nocturnal; terrestrial.

FEEDING ECOLOGY AND DIET
Fallen fruits and other vegetable material.

REPRODUCTIVE BIOLOGY
Gestation period, number of young at birth, weight at birth, weaning period, and sexual maturity are all similar to those of family.

CONSERVATION STATUS
Generally, all populations are endangered. Listed by the IUCN as Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. Eat farmers' crops, and are thus perceived as pests. ◆

Common porcupine
Hystrix brachyura

SUBFAMILY
Hystricinae

TAXONOMY
Hystrix brachyura Linnaeus, 1758, Malacca, Malaysia.

OTHER COMMON NAMES
English: Common short-tailed porcupine, Malayan porcupine, Southeast Asian porcupine.

PHYSICAL CHARACTERISTICS
Weight averages 17.6 lb (8 kg), head and body length is 17.9–28.9 in (45.5–73.5 cm), and the tail length is 2.4–5.1 in (6.0–13.0 cm). Spine arrangement and structure resemble subgenus *Thecurus.* Front half of body covered with short, dark brown spines, while hindquarters have long, pointed, whitish spines, usually with one blackish ring. Short, whitish crest found on neck and upper back. Short tail has long, pointed spines and rattle quills. Females and males possess hollow quills on tail, which are shaken to scare predators.

DISTRIBUTION
Nepal to southeastern China and Malay Peninsula, Hainan, Sumatra, Kalimantan (in Borneo).

HABITAT
Forests, lowlands, hills, cultivated areas.

BEHAVIOR
Nocturnal; terrestrial.

FEEDING ECOLOGY AND DIET
Fallen fruits including oil palm, roots, and stems.

REPRODUCTIVE BIOLOGY
Gestation period, number of young at birth, weight at birth, weaning period, and sexual maturity are all similar to those of family.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
Hunted for meat. Eat farmers' crops, and are thus perceived as pests. ◆

Javan short-tailed porcupine
Hystrix javanica

SUBFAMILY
Hystricinae

TAXONOMY
Acanthion javanicum (F. Cuvier, 1823), Java, Indonesia.

OTHER COMMON NAMES
English: Sunda porcupine, Malaysian short-tailed porcupine.

PHYSICAL CHARACTERISTICS
The weight averages about 17.6 lb (8 kg), head and body length is 17.9–28.9 in (45.5–73.5 cm), and the tail length is 2.4–5.1 in (6.0–13.0 cm). Quill arrangement and structure resemble subgenus *Thecurus*.

DISTRIBUTION
Java, Lombok, Madura, Sumbawa, Flores and nearby island of Tanah Djampa, Rintja, and southwestern Sulawesi (presumably only through human introduction).

HABITAT
Forests, lowlands, hills, cultivated areas.

BEHAVIOR
Nocturnal; terrestrial.

FEEDING ECOLOGY AND DIET
Fallen fruits including oil palm, roots, and stems.

REPRODUCTIVE BIOLOGY
Gestation period, number of young at birth, weight at birth, weaning period, and sexual maturity are all similar to those of family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. Eat farmers' crops, and are thus perceived as pests. ◆

Indian crested porcupine
Hystrix indica

SUBFAMILY
Hystricinae

TAXONOMY
Hystrix indica Kerr, 1792, India.

OTHER COMMON NAMES
English: Indian porcupine, long-tailed porcupine.

PHYSICAL CHARACTERISTICS
Subgenus *Hystrix* is distinguished externally from other genera by relatively larger size, shorter tail and presence of rattle quills. Head and body length is 27.6–35.4 in (70–90 cm) in length and tail length 3.2–3.9 in (8–10 cm). Weight is 24.3–39.7 lb (11–18 kg). Short, high head has long, spiny head-neck mane whose length can be up to 16 in (40 cm). Hair is modified to form multiple layers of spines. Beneath longer, thinner spines lies layer of thicker and shorter ones. Each spine is colored black or brown, with alternating white bands. Spines vary in length, with shoulder and neck spines being the longest, measuring 5.9–11.8 in (15–30 cm). Sides and back half of body covered with cylindrical, stout spines up to 13.8 in (35 cm) long and generally marked with alternating dark and light bands. Others may be longer, and more slender and flexible, usually white. Tail is covered with shorter white spines. Among these, are longer, hollow, thin-walled rattling quills that are used to alarm enemies. Many quills vibrate together to produce hiss-like rattle. Rattle quills are better developed than with other subgenera. Hands and feet are broad, with four well-developed digits on fore feet, each with a thick, long claw used for burrowing, and five digits on hind feet. Eyes and external ears are small. Facial region of skull is inflated by pneumatic cavities, and nasal bones are enlarged.

DISTRIBUTION
Throughout southeast and central Asia and in parts of the Middle East, including such countries as India, Bhutan, Nepal, Sri Lanka, Bangladesh, Pakistan, Israel, Saudi Arabia, and Iran.

HABITAT
Highly adaptable to multiple environments. Although favoring rocky hillsides, also found in temperate and tropical scrublands, grasslands, and forests. Also found throughout Himalayan mountains, reaching up to elevations of 7,875 ft (2,400 m). Shelter is usually in caves, rock crevices, or burrows usually dug by themselves or by other animals. Burrows with a long entrance tunnel often have several entrances and a large inner chamber, are sometimes used for many years, and can become extensive.

BEHAVIOR
Generally, nocturnal (but avoids moonlight) and terrestrial. Does not usually climb trees but does swim well. Normal gait is a heavy walk in which it walks on soles of feet with heel touching ground. It often trots or gallops when alarmed. It tends to follow paths and may cover up to 9 mi (15 km) per night in search of food. May remain in dens through winter but does not hibernate. Small groups often share a burrow.

Piping calls and pig-like grunts have been reported. There is considerable grunting and quill rattling as they forage by night. At the first encounter with another animal (such as when irritated or alarmed), they raise, fan, and rattle hollow quills, thereby more than doubling apparent size. If disturbance continues, may launch a backward attack and charge its rear against offending animal. Action can drive spines deep into enemy, often leading to injury or death. Short quills that are hidden beneath longer, thinner spines on tail and back do most damage. Quite often, these quills become dislodged and remain in victim. Injuries and fatalities of tigers, hyenas, leopards, and other animals have been recorded.

FEEDING ECOLOGY AND DIET

Generally herbivores consuming vegetable material of all kinds, including fruits, cultivated and natural grains, roots, tubers, bark, rhizomes, bulbs, and crops. Occasionally eat insects, small vertebrates, and carrion. Known to chew on bones, in search of minerals (such as calcium) that help spines grow and to sharpen incisor teeth. Generally forage alone except when parents accompany young.

REPRODUCTIVE BIOLOGY

Gestation, on average, lasts 112 days. Litter size varies, ranging from one to four offspring per year (usually one to two), normally born in grass-lined chamber within burrow. Well-developed young are born with eyes open and short soft quills covering body. Birth weight is around 12 oz (340 g). Nursing lasts about 3.5 months. Usually monogamous, with both parents found in burrow with offspring throughout year.

CONSERVATION STATUS

Not threatened. Throughout its range, it is common and does not face significant threat. Adaptability to wide range of habitats and food types helps ensure population sustainability.

SIGNIFICANCE TO HUMANS

Throughout its range, hunted as food source. Seeds and pollen are spread with its activities as herbivore. Eats crop plants extensively, thus leading to significant agricultural loss. Burrowing through or consuming plants and vegetation in gardens and landscaping often is destructive. Can cause medical problems as well as injuries to humans and pets from contact with quills. ◆

North African porcupine

Hystrix cristata

SUBFAMILY

Hystricinae

TAXONOMY

Hystrix cristata Linnaeus, 1758, near Rome, Italy.

OTHER COMMON NAMES

English: North African crested porcupine.

PHYSICAL CHARACTERISTICS

Best known of porcupine species, with the longest quills. Stocky body; weight is 22.1–66.1 lb (10–30 kg). Head and body length is 23.6–36.6 in (60–93 cm) and tail length is 3.2–6.7 in (8–17 cm). Head, neck, shoulders, limbs, and underside of body covered with black or dark brown coarse bristles. Characterized by spines along head, nape, and back that can be raised into crest, in addition to sturdier quills about 13.8 in (35 cm) long and 0.4 in (1.0 cm) in diameter along sides and back half of body, which is normally used for protection and defense. Spines are generally marked with alternating dark and light bands. Short tail is apparent, with presence of rattle quills at end of tail. Quills widen at terminal end and are hollow and thin walled, which produce hiss-like rattle when vibrated. Forefeet, which are 2.0 in (5 cm) long, have four well-developed, clawed digits per foot (the thumb is regressed), and the hind feet, which are 3.9–4.3 in (10–11 cm) long, have five digits each. The naked soles of paws contain pads; they walk on soles with heel touching the ground. Eyes and external ears are small, with sensitive hair or whiskers on head. Facial region of skull is inflated by pneumatic cavities, and nasal bones are enlarged.

DISTRIBUTION

Italy, Albania, Sicily, and northern Greece (European populations possibly introduced by humans) and along the Mediterranean coast of Africa to northern Democratic Republic of the Congo and Tanzania.

HABITAT

Highly adaptable, usually found in forests, rocky areas, mountains, croplands, and sand-hill deserts up to 11,480 ft (3,500 m). Shelter often occurs in caves, rock crevices, aardvark holes, or burrows they dig themselves. Burrows are often extensive and used for many years.

BEHAVIOR

Small family groups, consisting of adult pair and various infants and juveniles, share (often) complex burrow system. Females usually establish separate den in order to bear young. Generally terrestrial, rarely climbing trees, but are able to swim. Strictly nocturnal but may avoid moonlight. Individuals may remain in burrows through winter but do not hibernate. Quills serve as an effective defense against predation. When disturbed, quills are raised and fanned in order to create illusion of greater size. If disturbance continues, feet are stamped,

quills whirled, and (if necessary) enemy is charged back end first, attempting to stab with thicker, shorter quills. Such attacks have killed animals such as lions, leopard, and hyenas.

FEEDING ECOLOGY AND DIET
Herbivore that eats bark, roots, tubers, rhizomes, bulbs, nuts, fallen fruits (especially grapes, figs, and dates), and cultivated crops. Occasionally consumes insects, small vertebrates such as frogs, and carrion. Often gnaw on bones for calcium and to sharpen incisors. Significant distances may be traveled in search of food. Possess high-crowned teeth with plane chewing surfaces for grinding plants that are then digested in stomach. Undigested fibers are retained in enlarged appendix and anterior large intestine and broken up by microorganisms.

REPRODUCTIVE BIOLOGY
Monogamous. Most knowledge of breeding behavior comes from captive individuals. Breeding occurs throughout year at London Zoo and South Africa (mainly from August to March with peak in January), from July to December in central Africa, and from March to December in Indian zoos. Females do not show aggression to familiar males, but are aggressive to unknowns. To mate, female raises tail and male stands on his hind legs, supporting himself with his forefeet on female's back. No male weight is transferred to female, no penile lock occurs, and there are multiple thrustings. Mating occurs only at night, both in and out of burrow. Usually females have only one litter per year. After a 35-day estrous cycle and 112-day gestation period, one to two well-developed offspring are born in a grass-lined chamber within burrow system. At birth or shortly afterward, young's eyes are open and incisors are completely broken through; body is covered with short hair; and back spines are still soft with individual sensing bristles projecting far beyond spines. Newborns weigh only 3% of mother's body weight. Leave den after only one week, at which time spines begin to harden. Females have two to three pairs of lateral thoracic mammae. Young begin to feed on solid food between two and three weeks, and five white stripes found on side begin to disappear at four weeks. Usually reach sexual maturity and adult weight (soon thereafter) at one to two years. Life span usually 12–15 years in the wild.

CONSERVATION STATUS
Generally endangered, listed by the IUCN as Lower Risk/Near Threatened. Species is rare and decreasing in number, especially in the Mediterranean region, due to poaching for food and being considered an agricultural pest. Besides humans, other enemies include big cats, large birds of prey, and hyenas.

SIGNIFICANCE TO HUMANS
Porcupine quills are often used as ornaments and talismans. Meat is often considered a delicacy. Animals are considered agricultural pests because they gnaw bark of trees and eat cultivated crops such as corn, pumpkin, sweet potatoes, cassava, and young cotton plants. ◆

South African porcupine
Hystrix africaeaustralis

SUBFAMILY
Hystricinae

TAXONOMY
Africae australis Peters, 1852, Mozambique.

OTHER COMMON NAMES
English: South African crested porcupine, Cape porcupine.

PHYSICAL CHARACTERISTICS
Largest rodent in their region, with weight of 39.7–66.1 lb (18–30 kg). Relatively larger with longer, heavier quills than *Hystrix cristata* (North African porcupine). Tail is shorter compared to other species. Females are, on average, about 2.2 lb (1 kg) heavier than males and both sexes can be of body length 2.3–2.8 ft (71–84 cm) long and tail length up to 1 in (2.5 cm). Sense of hearing and smell is unusually sharp. Body is stout, with sharp quills up to 11.8 in (30 cm) long on its back. Flat, black, bristly hairs cover the body. Difference between quills and spines is largely one of length and thickness, with spines up to 19.7 in (50 cm) long and quills up to 11.8 in (30 cm) long. White and black crest of spines and quills can be voluntarily erected to make animal look enlarged and threatening. Specialized quills on tail are larger and hollow at the tips; used to make rattling (hissing) sound when shaken, often to warn potential enemies. Such sharp, backward-curving quills may be driven into enemy when moving backward toward enemy. Spines and quills come off when touched by predator or shaken off, but grow back quickly. Also have long whiskers. Facial region of skull is inflated by pneumatic cavities, and nasal bones are enlarged.

DISTRIBUTION
Despite its name, only found in sub-Saharan Africa, excluding the coastal desert of the southwest: basically the southern half of Africa up to 11,480 ft (3,500 m).

HABITAT
Found from sea level to 6,560 ft (2,000 m) above sea level in most areas with vegetation such as forests and savannas. Prefer rocky hills and outcrops, and must have shelter during day, often in caves or holes. Builds dens that can be up to 65.6 ft (20 m) long with a 6.6 ft-deep (2 m) living chamber near center.

BEHAVIOR
Primarily nocturnal, although may be seen during day. Generally, either solitary creatures or living in small family groups, clans of up to six family members in which both parents give long-term care to young. Burrows are often dug in order to spend day hours inside, coming out at night to feed. Use an alternating gait when walking slowly and trot when running, able to swim fairly well and can climb if necessary. Very acute hearing and will freeze when approached by predators, such as big cats, large predatory birds, or hyenas. When cornered, can be aggressive, often running sideways or backwards to embed sharp quills in attacker. Cannot throw quills, but may become dislodged when hollow rattling quills are shaken. Defensive behavior is often to hide in their holes facing in and erect their spines so that they cannot be dislodged.

FEEDING ECOLOGY AND DIET
Mostly vegetarian, using strong digging claws to find roots, tubers, and bulbs. Also fond of fallen fruits, thistles, a variety of plants, leaves, and will sometimes gnaw on bark. Cultivated crops such as corn, sweet potatoes, pineapples, sugar cane, young cocoa and oil palms, bamboo, melons, and onions are eaten. Anterior large intestine and enlarged appendix contain microorganisms that break down undigested plant fibers. Also eat carrion in some cases. In areas deficient in phosphorous they gnaw on bones, often accumulating piles of bones in dens.

REPRODUCTIVE BIOLOGY
Males reach sexual maturity between eight and 18 months, while females reach sexual maturity between nine and 16 months. Because of dangerous quills, females initiate copulation by presenting to males. Estrous cycle is about 35 days, and gestation lasts for a little over three months (93–105 days). Young are born in litters of one to four (usually one to two) normally twice a year, usually within grass-lined chamber in parents' den during wet months of August to March. Average newborn weight is 12.4 oz (351 g), but can range from 10.6–14.1 oz (300–400 g). Young are born relatively well developed, with eyes open and teeth present, quills and spines are soft (most likely to ease birthing process) but quickly harden within two weeks. Young can feed on solids from birth and grow rapidly, reaching full size in about one year. Nursing occurs on average of 101 days (but can range from three to four months) at which point young will weigh 8.8–11 lb (4–5 kg). Females have two to three pairs of teats in two rows located behind shoulders, on side of chest. After weaning of young, females cannot conceive for another three to five months. Life span can be 12–15 years in wild.

CONSERVATION STATUS
Not threatened. Generally, throughout its range, it is common and does not face significant threat. Adaptability to wide range of habitats and food types helps protect healthy populations. Its main predators are humans and large cats.

SIGNIFICANCE TO HUMANS
Meat is highly prized by local peoples. Porcupines eat vegetable crops and are destructive feeders. ◆

African brush-tailed porcupine
Atherurus africanus

SUBFAMILY
Atherurinae

TAXONOMY
Atherura africana Gray, 1842, Sierra Leone.

OTHER COMMON NAMES
English: West African brush-tailed porcupine.

PHYSICAL CHARACTERISTICS
Slender, rat-like creature, with distinctive long tail (that is easily broken off), tipped with a tuft of bristles. (Similar features to *Atherurus macrourus*.) Weight is 2.2–8.8 lb (1–4 kg), head and body length is 14.4–23.6 in (36.5–60.0) cm, and tail length is 3.9–10.2 in (10–26 cm). Body is long and slender, but legs are wide and short. Body color varies from black to dark grayish brown on upper side and white to light brown on underside. On each side of jaw, five teeth are present: one incisor, one premolar, and three molars. Body covered with several types of protective spines, with softest ones on head, neck, and stomach. Flattened stiletto-type spines are found on edges of back with more thick, rigid bristle-type spines in middle and lower regions. Also has yellowish brush tail with platelet-type bristles (which can be rattled) and a group of small rattling cups on back. Partially webbed feet (suitable for swimming) are armed with blunt, straight claws. Agile, able to climb trees, and runs well. Postorbital processes are either lacking or very weak in skull.

DISTRIBUTION
Only in Africa in the countries of Gambia, Liberia, Sierra Leone, Ghana, Democratic Republic of the Congo, Uganda, Kenya, and southern Sudan.

HABITAT
Spend days hidden in burrows, caves, crevices, or fallen trees, and generally are most active when it is completely dark outside (avoiding or at least reducing activities during bright moons). Prefer naturally occurring caves, holes in trees, rock crevices, and other natural burrows, and do not usually burrow out their own. Found in tropical forests, river forests, and island forests, at elevations of up to 7,400 ft (2,250 m). Territory is 14–57.5 acres (5.5–23 ha).

BEHAVIOR
Adults usually live in families, generally around six to eight members, which include a mated pair and their offspring from multiple litters. Families share runs, territories, feeding, and latrine areas. Groups of families, up to 20 individuals, often share resources and live close to each other. Mainly terrestrial but are also good at climbing and swimming. Most known predators, such as carnivores (leopards), large owls, snakes, and humans, tend to be scared away by quills. When agitated, quills are raised, giving appearance of a body twice of actual size; also rattle tail and stomp feet in order to further threaten enemies. If predator comes close enough, it aligns itself so its rear faces enemy, then suddenly makes a backward attack, causing quills to become embedded and stuck in enemy.

FEEDING ECOLOGY AND DIET
Mostly herbivorous but occasionally feed on carcasses. Primarily eat bark, roots, tubers, sweet potatoes, leaves, bulbs, fruits such as bananas, and nodules. Tend to be very nervous and quick moving while hunting for food, which is done usually alone.

REPRODUCTIVE BIOLOGY
Form pair bonds before mating, which is necessary because the female acts out in aggression against males with whom she is not familiar (such as raising her quills to halt the mating process). No clearly defined breeding period, up to two litters are possible each year. Females normally give birth to one, sometimes two, young per litter. Gestation period ranges from 100–110 days, after which the mother gives birth to well-developed young. At

birth, eyes are open, teeth are already present, and hair (but not spines) covers the body. Young are born small, only 3% of mother's body weight. Weight at birth averages 5 oz (150 g) with a range of 3.5–6.3 oz (100–175 g, then increases to 18 oz (500 g) after one month, 2 lb (1 kg) after three months, 3 lb (1.5 kg) after five months, and 22 lb (10 kg) after 11 months. Both parents spend much time and effort raising offspring. Mothers nurse nearly constantly for first two months after birth; teats are located laterally on the chest. Sexual maturity is reached at about two years. Documented to live up to 23 years of age.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Possess a keen sense of smell, which is used to locate and uproot buried nodules and bulbs, thereby increasing density of vegetation in areas of forage. Known to feed on cultivated crops; also feed on bark and fleshy tissues of trees, which can damage trees. Also carrier of malaria parasite (*Plasmodium atheruri*). ◆

Asiatic brush-tailed porcupine
Atherurus macrourus

SUBFAMILY
Atherurinae

TAXONOMY
Hystrix macroura (Linnaeus, 1758), Malacca, Malaysia.

OTHER COMMON NAMES
English: Asian brush-tailed porcupine, Indochinese brush-tailed porcupine.

PHYSICAL CHARACTERISTICS
Slender, rat-like creature, with distinctive long tail (that is easily broken off), tipped with a tuft of bristles. (Similar features with *Atherurus africanus*.) Weight is 2.2–8.8 lb (1–4 kg), head and body length is 15.8–21.5 in (40.1–54.6 cm), and tail length is 5.9–9.8 in (15–25 cm). Relatively long body is almost entirely spiny in appearance, though quills are softer on head, legs, and under parts. Longest spines located at mid-upper side region. Most spines are flattened with groove on upper surface; interspersed among them on lower back are a few round, thick bristles, giving appearance of distinct terminal tuft (which is whitish to creamy buff in color). Each bristle consists of chain of flattened discs, allowing tail to be rattled, as warning to predators. Body is blackish brown to grayish brown on its upper parts; individual hairs have whitish tips; underside is dirty white to light brown. On back is located flattened stiletto spikes fluted on outside, with flexible spines in between. Limbs are short and stout, and ears short and rounded. Partially webbed feet (suitable for swimming) possess blunt, straight claws. Agile, able to climb trees, and runs well. Postorbital processes are either lacking or are very weak in the skull.

DISTRIBUTION
Southeastern Asia, generally south-central China (Yunnan, southern Sichuan, Guangxi), Assam, Myanmar, Thailand, Indochina, Malay Peninsula and several small nearby islands, and Hainan.

HABITAT
Forests, river forests, and forest islands at elevations up to 9,850 ft (3,000 m); often near water. Prefer natural caves and dwell in rock caves and crevasses, in underground lodges dug by other mammals, and also in cavities in or under fallen trees. They may dig burrows in soft floors of rainforests. Prefer to stay in burrows during the day to emerge at night to forage.

BEHAVIOR
Social life of clans often include up to four to eight members who often share common runs and trails, excrement depositories, feeding places, territories, and refuges. Running fast, swimming, and climbing are possible, and these animals are able to jump over 3 ft (about 1 m). Enemies include carnivores such as leopards, large owls, snakes, and humans. Normally shelter during the day in a hole among tree roots, rocky crevice, termite mound, cave, or eroded cavity along stream bank.

FEEDING ECOLOGY AND DIET
Usually green vegetation, bark, roots, tubers, leaves, bulbs, and fruits; sometimes also cultivated crops, insects, and carrion. Usually forage alone strictly during the night.

REPRODUCTIVE BIOLOGY
One young, sometimes two, to a litter. Females have two pairs of lateral thoracic mamae. Weaning period is normally two months; sexual maturity reached after two years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. May overfeed on farmers' crops. ◆

Long-tailed porcupine
Trichys fasciculata

SUBFAMILY
Atherurinae

TAXONOMY
Trichys fasciculata (Shaw, 1801), Malacca, Malaysia.

OTHER COMMON NAMES
English: Borean long-tailed porcupine, Malaysian long-tailed porcupine.

PHYSICAL CHARACTERISTICS
Relatively small compared to other species. Overall appearance is of a large, spiny (brown) rat. Weighs 3.3–4.4 lb (1.5–2 kg), with body length of 11.0–18.5 in (27.9–47.0 cm) and (extra long) tail length of 6.7–9.1 in (17.0–23.0 cm). Head and under parts are hairy and the fur underneath is rather woolly. Upper parts of body are black to light brown in color, whereas under parts are whitish. Body is covered with short stiletto-like spines with individual bristle-like hairs in between. Spines are shortest within family and are flattened, grooved, and flexible, with a dark brown color towards the end, and whitish towards base. Tail is brown and scaly, with hollow brush-like quills at the end; it is easily broken off and many adults, especially females, are found without tails. Front legs have four toes while the back feet have five toes, all connected by a continuous membrane. Quills are concentrated on the rear and hindquarters, so a defensive porcupine will often back into an attacker. Unlike other species, quills cannot produce any rattling sounds when shaken. Good climbers with broad paws, along with strong digits and claws for holding onto branches. Skull has well-marked postorbital processes.

DISTRIBUTION
Peninsular Malaysia, Sumatra, and Borneo, especially Kalimantan.

HABITAT
Forests and cultivated areas up to elevations of 3,800 ft (1,290 m).

BEHAVIOR
Although primarily terrestrial creatures that live in burrows, they can be arboreal (climb trees), and are agile climbers. This is considered the most primitive genus within the family. Seem to prefer natural caves and dwell in rock caves and crevasses, in underground lodges dug by other mammals; also in cavities in or under fallen trees. They may also dig their own dens in the soft floor of rainforests. They are active mainly during the night.

FEEDING ECOLOGY AND DIET
Mainly herbivorous (especially fruits, other vegetation such as seeds and bamboo shoots) but diet can include invertebrates. Able to climb into bushes and tops of trees to pick food.

REPRODUCTIVE BIOLOGY
In captivity it may live over 10 years. Reproductive biology is similar to the rest of the family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The tail has apparent value to some native people, who remove it from the rest of the hide. This porcupine destroys crops (such as pineapples) in some areas. ◆

Resources

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William Arthur Atkins

New World porcupines
(Erethizontidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Erethizontidae

Thumbnail description
Stocky animals distinguished by many sharp spines that cover much of their upper bodies and tails

Size
Adults range from about 15.5–51 in (0.4–1.3 m) and about 6.5–22 lb (3–10 kg)

Number of genera, species
5 genera; 19 species

Habitat
Mainly arboreal throughout forests, although one species extends into deserts

Conservation status
Not threatened

Distribution
North, Central, and South America, from Canada and Alaska to Argentina

Evolution and systematics

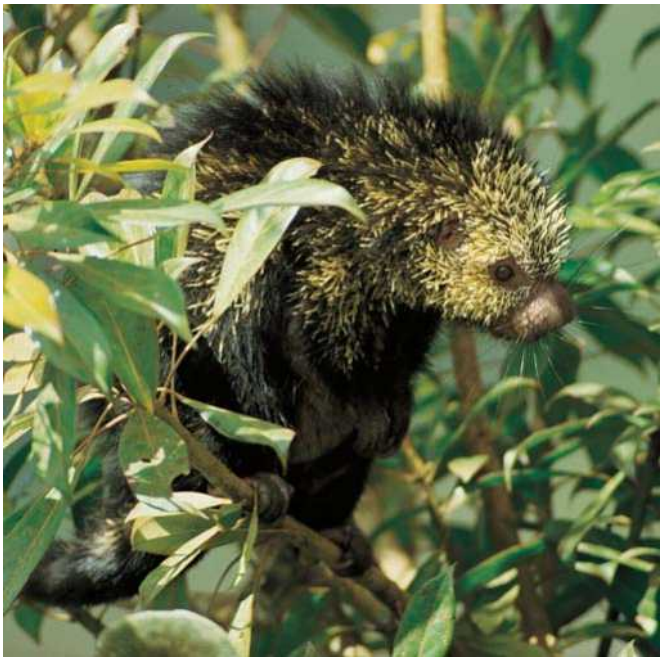
Although both Old World and New World porcupines exist, the New World family Erethizontidae is actually more closely related to pacas, agoutis, and other cavy-like rodents than to the Old World porcupine family Hystricidae.

This family requires additional research before its placement is clear. Until that work is completed, however, this chapter will use the following classification of genera and species:

- *Chaetomys*—*C. subspinosus* (this species was thought to be extinct until it was rediscovered in 1986)
- *Coendou*—*C. bicolor*, *C. ichillus* (described as new species in 2001), *C. koopmani* (described as new species in 1992), *C. melanurus* (sometimes identified as *Sphiggurus insidiosus*), *C. pallidus*, *C. paragayensis* (sometimes identified as *S. spinosus*), *C. prehensilis*, *C. pruinosus* (sometimes classified as *S. vestitus*), *C. roosmalenorum* (described as new species in 2001), *C. rothschildi*, and *C. sneiderni*
- *Echinoprocta*—*E. rufescens*

A North American porcupine (*Erethizon dorsatum*) foraging. (Photo by Animals Animals ©Richard Kolar. Reproduced by permission.)

A North American porcupine (*Erethizon dorsatum*) adult and baby. (Photo by D. Robert Franz. Bruce Coleman, Inc. Reproduced by permission.)



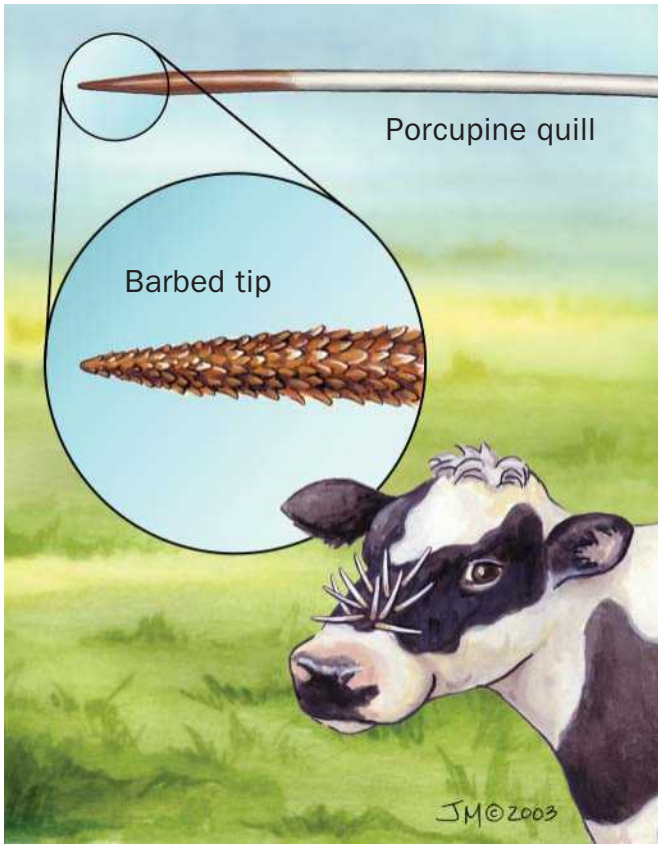
A Mexican hairy porcupine (*Sphiggurus mexicanus*) in the rainforests of Costa Rica. (Photo by Animals Animals ©Michael Fogden. Reproduced by permission.)

- *Erethizon—E. dorsatum*
- *Sphiggurus—S. insidiosus*, *S. mexicanus* (sometimes classified under the genus *Coendou*), *S. spinosus*, *S. vestitus*, and *S. villosus*

Scientists are still grappling with this family's phylogeny and taxonomy, particularly since some of the species listed above are known from only one or a few specimens. Some of the questions involve the genus *Chaetomys*, which has at times been placed in the family Erethizontidae or the family Echimyidae; the genus *Sphiggurus*, which is often grouped as a subgenus of *Coendou*; and *C. rothschildi*, which is considered by some to be a subspecies of *C. bicolor*. Many other questions also remain. Phylogenists tend to agree that the erethizontids likely spread from South America to North America, but they continue to puzzle over whether the *Erethizon* genus branched from the *Coendou* genus or a now-extinct species, known as *Steiromys*.

Physical characteristics

Porcupines are best known for their sharp quills. Spines cover much of a porcupine's dorsal surface from the back of the head to the tail, although a few, such as *C. prehensilis* and *S. mexicanus*, are naked on at least a portion of their tails.



The spines of porcupines are barbed at the tip, making removal difficult. Curious dogs and livestock, like the cow shown here, are occasionally quilled when they cross paths with a porcupine. (Illustration by Jacqueline Mahannah)

Both of these species have prehensile tails, which they use in climbing. The spines are evident on many species, including *E. dorsatum*, but mostly hidden beneath long fur on others, such as *S. mexicanus* and *S. spinosus*, and in most young porcupines of various species. The claws are long and curved.

Porcupines in general are stocky with a blunt muzzle and small eyes. Their short, strong limbs and clawed, four-toed feet make them well-suited for climbing. The ears are small and round, almost concealed by the hair, which also covers the spines. The shoulders are humped, making the back look arched. The short legs are bowed, and the animal stands bear-like with its entire foot planted firmly on the ground. The porcupine is one of the largest rodents in North America, second only to the beaver. Adult porcupines range from about 15.5 to 51 in (0.4–1.3 m), with tails that can stretch about a quarter to more than a half of the total length. *Coendou*, *Chaetomys*, and *Sphiggurus* species have bulbous noses.

Porcupine longevity averages 15 years in the wild and some 21 years in the zoo.

Distribution

The majority of the species occur in South America, from the northern tip of the continent to northern Argentina and Uruguay. A few species reside further north into Central and North America. *E. dorsatum* is the northernmost species with populations existing well into Canada.

Habitat

These are primarily forest animals, dwelling in rainforests, as well as deciduous and coniferous woods. A few, such as *C. prehensilis*, are found in plantations and other cultivated areas. *E. dorsatum* frequently shares its forests with humans, and is often seen dead along roadsides as a traffic victim.

Behavior

Folk stories of porcupines throwing their quills are rampant, but they are untrue. This animal can impale an attacker with its easily detachable spines, but it cannot launch them. Normally, their quills—actually modified guard hairs—lie facing backward on the body. Under duress however, the animal erects the quills, which can reach 4 in (10 cm) long in the North American porcupine (*E. dorsatum*), and becomes a

Prehensile-tailed porcupines (*Coendou prehensilis*) are found in southern Panama, northwest Colombia to northern Argentina, and northwest Brazil. (Photo by Animals Animals ©Jim Tuten. Reproduced by permission.)

The prehensile-tailed porcupine (*Coendou prehensilis*) exhibits a reverse hold on a tree branch while hanging upside down. (Photo by Leonard Lee Rue III/Photo Researchers, Inc. Reproduced by permission.)

formidable pincushion with spines jutting out in various directions. The porcupine may then remain stationary in a defensive pose, or may charge the antagonist. North American porcupines are also known to lash out at predators by quickly batting at them with their quill-laden tails. In all cases, once the quill enters the attacker's body, its barb lodges and the quill lets loose from the porcupine. Although the quills are not poisonous, they are painful and can cause serious damage to internal organs and sometimes death.

Little is known of the habits of many erethizontids, particularly the South American species. However, New World porcupines are presumably all nocturnal and arboreal, spending their days sleeping in trees or in ground-level hideaways. Some, like the thin-spined porcupine (*C. subspinosus*), spend the bulk of their nights resting, too, with most of their activity centered around feeding. Mating behaviors in the wild are best known for *E. dorsatum*, and are described in the separate species account.

Although porcupines are basically solitary, several sometimes share the same winter den. The winter territorial range is small, averaging some 12 acres (5 ha), but in summer it is larger, increasing to up to 35 acres (14 ha). Population densities fluctuate from year to year, and may range from one to 10 animals per 0.4 mi^2 (1 km^2). Although not territorial, porcupines sometimes defend their winter feeding grounds from other species. Porcupine trails on snow are easily identified by the marks made by spines on the edge of the trail. Porcupines do not make a nest or burrow; they den in rock crevices or tree hollows.

Porcupines may seem aloof and unconcerned about danger, but should an enemy start to approach, a porcupine will back down flicking and lashing its tail. During confrontations, a porcupine will also chatter its teeth. Otherwise porcupines are mainly uncommunicative animals. The female may nose her young with gentle grunts and whines. Only in the mating season do porcupines become vociferous and create a variety of moans, screams, grunts, and barks.

Feeding ecology and diet

New World porcupines typically prefer fruits and seeds, but when these are limited, they are known to dine on leaves and bark. *Sphiggurus insidiosus* and *S. spinosus* also eat ant pupae and roots. In all species, feeding occurs at night during the porcupines' nighttime feeding forays.

A juvenile tree porcupine (*Coendou* sp.) in a tree in the Upper Amazon in Peru, South America. (Photo by Animals Animals ©John Pontier. Reproduced by permission.)

The prehensile-tailed porcupine (*Coendou prehensilis*) uses its tail to aid in climbing. (Photo by Dr. Lloyd Glenn Ingles © California Academy of Sciences. Reproduced by permission.)

Reproductive biology

Little is known of the reproductive biology of many erethizontids, particularly the South American species. It appears, however, that female porcupines are generally either pregnant or are lactating for the vast majority of their lives. Gestation commonly lasts about 200 days, after which the female mates almost immediately. She continues lactating for her newborns for approximately eight to 12 weeks.

Each pregnancy commonly results in one precocious offspring, which is born with fur and soft quills that harden quickly. The young generally reach adult size in about a year, and become sexually mature at about 1.5 to 2.5 years old. *Coendou* young have a soft orange color, significantly different from that of the adult species. All are precocious.

Conservation status

Many of the South American species are rarely seen, but that may be due in part to surveying difficulties presented by geographic distribution combined with their nocturnal and arboreal habits. Some, however, appear to have undergone population declines, although none of the New World porcupines is listed by the IUCN as threatened. The thin-spined porcupine, for example, has experienced a severe habitat reduction due to forest clearing, and was thought to have become extinct in the mid 1900s, until an individual was discovered in 1986.

Significance to humans

Some are hunted for meat. The quills of some species are used in artwork.

The prehensile-tailed porcupine (*Coendou prehensilis*) uses its prehensile tail to climb from branch to branch. (Photo by © Martin Harvey; Gallo Images/Corbis. Reproduced by permission.)

1. Prehensile-tailed porcupine (*Coendou prehensilis*); 2. North American porcupine (*Erethizon dorsatum*); 3. Bahía hairy dwarf porcupine (*Sphiggurus insidiosus*); 4. Mexican hairy porcupine (*Sphiggurus mexicanus*). (Illustration by Jacqueline Mahannah)

Species accounts

North American porcupine
Erethizon dorsatum

SUBFAMILY
Erethizontinae

TAXONOMY
Erethizon dorsatum (Linnaeus, 1758), Quebec, Canada. Seven subspecies.

OTHER COMMON NAMES
English: Canadian porcupine, quillpig, pricklepig, quiller; French: Porc-épic; German: Urson, Baumstachelschwein; Spanish: Puercoespín.

PHYSICAL CHARACTERISTICS
Adults can reach nearly 39 in (1 m), with the tail making up a fifth to nearly a third of that total. Body weight is generally less than 26 lb (12 kg), but a particularly large male can top 33 lb (15 kg). Adults have stiff, black or dark-brown dorsal hair, interspersed with mostly white quills at the head, rear of the body, and on the tail. In all, an adult may have more than 30,000 barbed quills covering its dorsal body. The belly is quill-free and woolly. The young are more camouflaged with a nearly all-black head, back, and tail, and short, though still sharp, quills. Females have two pairs of mammae.

DISTRIBUTION
Most of Canada except the far north-central regions, and most of the western half of the United States as well as the north-central and northeastern states. It also extends into the northern edge of central Mexico.

HABITAT
Mainly arboreal animals that are common to forested areas, but occasionally also exist in open areas and even deserts, provided a water source is nearby.

BEHAVIOR
The most temperate member of the family, this nocturnal species will occupy winter dens, which are commonly hollow trees and logs, or gaps beneath rocks. More than one porcupine may share a den, particularly when available denning locations are low in number. Studies conflict over whether severe weather may also prompt den-sharing. Some individuals do not den, instead spending their winters resting in trees.

Other than the group denning behavior, porcupines are generally solitary animals for much of the year. Although they are not normally territorial, an individual may defend a feeding site if resources are limited.

During the breeding season, females produce olfactory and auditory clues that indicate their readiness to mate and attract males. Two or more males may fight with one another over the opportunity to mate with a female. These battles can lead to quill impalements and other injuries. In an unusual courtship ritual, males will sometimes soak females with streams of urine while standing on their hind limbs facing the female. The purpose of the behavior is unknown. When the female is ready to mate, she indulges in a kind of dance with the chosen male, where they both rise on their hind feet to embrace, all the while whining and grunting loudly. Sometimes they place their paws on each others' shoulders and rub their noses together; then they may cuff each other affectionately on the head and finally push one another to the ground.

FEEDING ECOLOGY AND DIET
Porcupines are vegetarians, dining on foliage for much of the year and turning to the inner bark of oaks and pines in the winter months. They are also known to eat seeds, fruits, nuts, berries, and plant stems. Their chisel-like teeth scrape away the tougher, outer bark, then slice off even bits of inner bark for consumption. Cellulose-eating bacteria in the porcupine's gut assist the digestion of plant material. Mothers and young feed together, but they are otherwise solitary feeders. Feeding generally occurs at night, but occasionally they will feed during the day.

Their primary predators include fishers and mountain lions, although lynx, bobcats, coyotes, red foxes, wolves, wolverines, and even great horned owls will occasionally disregard the quills and attack porcupines.

During winter porcupines do not hibernate. However, they do not usually move far and feed within 300 ft (91 m) of their

dens. During snow or rain they remain in the den or, if out feeding, sit hunched in a tree, even during subzero weather, until the weather improves. When the weather is dry in winter, they feed at any time of the day or night, but during the rest of the year they are nocturnal despite the weather. In summer, porcupines range farther from the den, often searching for food up to 1 mi (1.6 km) away. As well as these daily movements within the home range, there may be seasonal movements between winter denning areas and the summer feeding areas. In mountainous country, the porcupines will often descend during the winter along well-defined paths marked by debarked trees. In the spring, they return up the mountainside to summer feeding areas.

REPRODUCTIVE BIOLOGY
Polygynous. Mating typically occurs only once a year in the fall, during a period of eight to 12 hours when the female is receptive. The female has a copulatory plug and if she does not become inseminated, she may mate again a month later. One young per female per pregnancy is the norm, two is rare, and gestation takes about seven months. The young weigh about 1 lb (450–490 g) at birth, and have both spines and fur. They grow quickly, doubling their weight in the first two weeks, but remain with the mother at least until the early fall when lactation ends. Juvenile females then disperse, but juvenile males may move in and out of the mother's range for months and even years. They attain sexual maturity at about 1.5 years and typical longevity is of the order of some 15 years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The quills were once highly regarded among Native American populations, and used both in artwork and as a medium of exchange. These populations also hunted porcupines for meat during lean times. Currently, porcupines are generally seen as pests that gnaw through plywood and nearly anything salty, and damage homeowners' trees. ◆

Prehensile-tailed porcupines
Coendou prehensilis

SUBFAMILY
Erethizontinae

TAXONOMY
Coendou prehensilis (Linnaeus, 1758), Pernambuco, Brazil.

OTHER COMMON NAMES
French: Cuandu; German: Greifstachler, Cuandu; Spanish: Coendú grande, puerco-espín.

PHYSICAL CHARACTERISTICS
An adult can range from about 3 to 4 ft (0.9–1.2 m) in length with half of that total in the tail, and about 9–12 lb (4–5.5 kg) in weight. Grayish to yellowish brown, mainly short-spined porcupine with a typically whitish face and small, black, and long, prehensile tail. The last third of the tail is unspined on its upper surface, providing a smooth contact point for wrapping around even thin branches. The long-clawed toes also aid its arboreal lifestyle. The young are uniquely orangish brown to brown with longer fur that somewhat hides the spines.

DISTRIBUTION
Eastern South America from eastern Venezuela and Trinidad to northeastern Argentina and Uruguay.

HABITAT
Typically found in vine-covered rainforests, but also occurs in farmed areas, gardens drier forests near a water source.

BEHAVIOR
Prehensile-tailed porcupines spend the bulk of their time high in the trees, but since they do not leap from tree to tree, they travel from trunk to trunk on the ground. They normally move rather slowly, but can speed up if necessary. The long, prehensile tail combines with padded, clawed feet to make them excellent climbers. During the day, they sleep in a supportive clump of vegetation in the canopy.

Adults are typically solitary animals, but they do coexist peacefully with conspecifics on occasion. When threatened by a predator, they take on a defensive pose, sometimes rolling into a ball and raising their quills, and will occasionally lunge at an attacker with spines erect. Other displays include foot-stomping, spine-shaking, and threatening snarls and grunts. They also call back and forth with one another via long, moans. During breeding periods, the male commonly sprays urine on the female. He also will occasionally spray newborns.

FEEDING ECOLOGY AND DIET
These nocturnal, sometimes late-day, feeders are vegetarians, commonly dining on fruits and seeds, but also stems, leaves, roots, and bark.

REPRODUCTIVE BIOLOGY
Little is known about mating interactions. Reproduce about every seven months. Although no species-wide seasonal schedule exists, births in some areas spike during the rainy season. Following a gestation period of 195 to 210 days, a female will have one offspring per year, after which she almost immediately mates again. The young are precocial, weaning in about three months, and reaching adult size at about 11 months old and sexual maturity at approximately 19 months.

One female of the species is reported to have produced 10 litters in 8.5 years and still was reproductively active at an estimated age of 11.5 years. A captive *C. prehensilis* lived for 17 years and four months.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Minor use as food. Sometimes regarded as a pest in agricultural areas. ◆

Bahía hairy dwarf porcupine
Sphiggurus insidiosus

SUBFAMILY
Erethizontinae

TAXONOMY
Sphiggurus insidiosus (Lichtenstein, 1818), Bahía, Brazil.

OTHER COMMON NAMES
French: Porc-épic arboricole nain, porc-épic laineux; German: Wollige Greifstachler; Spanish: Coendú, ouriço cacheiro.

PHYSICAL CHARACTERISTICS
Although few specimens exist, they are believed to range from about 24 to 31 in (60–80 cm) in total length with a tail about a third to two-fifths of that length, and to have a body weight of about 2.6–3.3 lb (1.2–1.5 kg). Nearly completely dark-brown porcupine with spines that are concealed beneath thick, soft fur. The spines are whitish at the base, becoming brown distally, sometimes with orangish tips. The prehensile tail is slightly darker than the body, and is without spines or fur for its last third. Reports exist of white forms of this species. Young look similar to adults.

DISTRIBUTION
East-central to northeastern Brazil.

HABITAT
Primarily evergreen forests.

BEHAVIOR
Sightings are limited, but probably nocturnal and arboreal.

FEEDING ECOLOGY AND DIET
A mainly herbivorous animal that eats fruits and roots, but will also eat any pupae.

REPRODUCTIVE BIOLOGY
Little known, but a typical litter likely numbers one. Young are precocial, born with hair and soft quills, which quickly stiffen to provide a level of defense.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Mexican hairy porcupine
Sphiggurus mexicanus

SUBFAMILY
Erethizontinae

TAXONOMY
Sphiggurus mexicanus (Kerr, 1792), Mexico.

OTHER COMMON NAMES
French: Porc-épic arboricole du Mexique, porc-épic préhensile; German: Mexicanische Baumstachler; Spanish: Puerco espín.

PHYSICAL CHARACTERISTICS
Adults range from 21.5 to 31.5 in (55–80 cm) with a tail about a third to two-fifths of that total length, and weigh about 3–5.5 lb (1.5–2.5 kg). Dark brown to black porcupine with fur that covers most of the long spines on the body. The head is marked by yellowish spines that are visible through the fur, and by light-colored fur tufts near each ear. Like *S. insidiosus*, *S. mexicanus* has a prehensile tail that is naked distally. Young look similar to adults.

DISTRIBUTION
Southern Mexico to western Panama.

HABITAT
Favors high-elevation forests, but occasionally found in lowland habitats.

BEHAVIOR
Nocturnal and arboreal animals that spend their days sleeping in vegetation among branches, in tree hollows, or in bamboo undergrowth, although some evidence suggests they might also utilize dens and caves. A usually solitary animal, males will fight with other males, but will tolerate females.

FEEDING ECOLOGY AND DIET
Prefers fruits and seeds, but also eats leaves and buds.

REPRODUCTIVE BIOLOGY
Little known, but a typical litter likely numbers one. Young are precocial, born with hair and soft quills, which quickly stiffen to provide a level of defense.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Meat is used for food. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Bicolor-spined porcupine *Coendou bicolor* Spanish: Puerco-espín	Large, reaching more than 36 in (90 cm), more than half of it tail. Mostly black, except for whitish spine tips.	Found in low- and high-elevation rainforests, this species is nocturnal and arboreal.	Northwestern South America extending south as far as Bolivia.	Unknown, but presumably vegetarian.	Not listed by IUCN
Koopman's porcupine *Coendou koopmani* English: Black dwarf porcupine	This long-tailed, dark-colored porcupine has quills that are particularly long and conspicuous at the rear of the animal. Adults reach about 24–28 in (61–71 cm), about half of which is tail.	Found in the Amazonian lowlands, its behavior is little known.	Amazon, Madeira, and Tocantins River basins in northern South America.	Unknown, but presumably vegetarian.	Not listed by IUCN
Rothschild's porcupine *Coendou rothschildi* Spanish: Puerco-espín, gato de espinas	Obviously spine-covered porcupine with a prehensile tail that is nearly as long as the body.	Found in forested lowlands, its habits are little known.	From Panama south into northwestern South America, possibly as far south as northern Peru.	Vegetative matter, including fruits and probably leaves.	Not listed by IUCN
Short-tailed porcupine *Echinoprocta rufescens* English: Stump-tailed porcupine; Spanish: Puerco-espín	Spiny, brown to black porcupine with a white streak on the nose and measuring at most about 20 in (51 cm). The short tail makes up about a third of the total length.	Unknown.	Andes Mountains, primarily Colombia, at 2,600–6,600 ft (790–2,010 m).	Unknown, but presumably vegetarian.	Not listed by IUCN
Paraguay hairy dwarf porcupine *Sphiggurus spinosus* French: Porc-épic préhensile; Spanish: Coendú chico	Small, grayish brown, short-tailed porcupine with quills hidden by long hair.	Nocturnal and arboreal, it lives in evergreen forests.	Northern and north-central South America.	Vegetative matter, as well as ant pupae.	Not listed by IUCN
Brown hairy dwarf porcupine *Sphiggurus vestitus* Spanish: Puerco espín peludo	Small, brown porcupine with mostly inconspicuous, brown spines. White spines on the head are visible. Reaches only about 17 in (43 cm) total length, with a tail about a half as long as the body.	Lives in both lowland and upper-elevation forests. Behavior is little known.	Northwestern South America, including Colombia.	Unknown, but presumably vegetarian.	Not listed by IUCN
Orange-spined hairy dwarf porcupine *Sphiggurus villosus* Spanish: Ouriç-cacheiro	A mostly black porcupine with orange-tipped spines and fur. Can reach almost 36 in (91 cm) in length, about two-thirds or more of it tail.	Live in forests along the coast. Behavior is little known.	Northeastern South America, primarily eastern Brazil.	Unknown, but presumably vegetarian.	Not listed by IUCN
Black-tailed hairy dwarf porcupine *Coendou melanurus* Spanish: Ouriço cacheiro, puerco-espín	Spines are mostly visible on the hind portion of the body. A fairly large porcupine, reaching up to 29 in (74 in), including a tail that is almost as long as the body.	Prefer rainforests. Behavior is little known.	Northern South America.	Unknown, but presumably vegetarian.	Not listed by IUCN
Frosted hairy dwarf porcupine *Coendou pruinosus* Spanish: Puerco espín peludo	Reaching at most only 24 in (61 cm), this small porcupine is distinguished by gray to black fur and white bristles that hide the short spines.	Little known, but at least somewhat social, as a group of four individuals were discovered in a single nest.	Western Venezuela.	Unknown, but presumably vegetarian.	Not listed by IUCN
White-fronted hairy dwarf porcupine *Coendou sneiderni*	Similar in size to *C. pruinosus,* but with visible spines and a prominent white stripe down the center of the head. Prehensile, but short, tail.	Little known.	Columbia.	Unknown, but presumably vegetarian.	Not listed by IUCN
Thin-spined porcupine *Chaetomys subspinosus* English: Bristle-spined porcupine; Spanish: Ouriço preto	Light brown (sometimes dark brown) animal with a bristly back and short, but prominent spines only at the shoulder and head. Prehensile tail makes up about two-thirds of the total 29 in (73 cm) length.	Found in coastal forests and cultivated or disturbed areas. Excellent climbers that that travel slowly, and spend considerable time sleeping even during their nocturnal "active" period. Solitary.	Brazil.	Mainly fruit.	Not listed by IUCN

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Leslie Ann Mertz, PhD

Viscachas and chinchillas

(Chinchillidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Chinchillidae

Thumbnail description
Rabbit-sized, stout bodied, large hind limbs for leaping, dense and soft fur, large head, dorsal pelage ranging from gray to black

Size
Head and body 11.8–23.6 in (300–600 mm); tail 2.9–10.5 in (75–267 mm); weight 1.1–19.8 lb (0.5–9 kg)

Number of genera, species
3 genera; 6 species

Habitat
Andean, barren, steppe, pampas, rocky outcrops, scrub, and grasslands

Conservation status
Critically Endangered: 1 species; Vulnerable: 1 species; Lower Risk/Near Threatened: 1 species; Data Deficient: 1 species

Distribution
Southern cone of South America, primarily in southern Peru, Bolivia, Argentina, extending from northern Chile to the Andean foothills in Patagonia

Evolution and systematics

Representative lineages of the family Chinchillidae extend from the Oligocene to the Recent in South America. Members of this family are placed in the superfamily Chinchilloidea. Determination of the closest relative of chinchilloids has been difficult. Based on postcranial features and musculature, it has been suggested that chinchilloids shared a common ancestry with the New World porcupine superfamily Erethizontoidea. On the other hand, recent molecular phylogenetic studies are indicative of a strong relationship between the families Chinchillidae and Dinomyidae. Within the family, the Andean genera *Lagidium* and *Chinchilla* appear most closely related with *Lagostomus* being the most divergent lineage. Some taxonomic controversy persists over the recognition of *Chinchilla lanigera* as a distinct species from *C. brevicaudata*.

Physical characteristics

All species are large-bodied rodents with large, broad heads, thick fur, and rabbit-like in appearance. Chinchillas have extremely large auditory bullae relative to the other genera. The plains viscacha, *Lagostomus maximus*, is the largest species, weighing up to 20 lb (9 kg). Compared to the mountain viscacha, *Lagidium viscacia*, which weighs up to 6.6 lb (3 kg), chinchillas are much smaller, weighing less than 2.2 lb (1 kg). All species have strong hind legs and feet. Mountain viscachas and chinchillas are adapted for leaping, whereas the plains viscacha is more adapted to burrowing. Except for the plains viscacha, most species have minimal digit reduction. Chinchillas and mountain viscachas have longer tails relative to the head and body length. All species have soft underfur, and pelage color is generally darker on top and lighter on the ventral side. The plains viscacha varies in dorsal pelage color in response to differences in substrate coloration, and chinchillas have bluish dorsal coloration with lighter underside.

Distribution

Both mountain viscachas and chinchillas occur in Andean regions, distributed from Peru to Patagonia, while the plains viscacha occurs at lower elevations in portions of southern Paraguay and northern Argentina.

A long-tailed chinchilla (*Chinchilla lanigera*) in the mountains of Chile. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

A baby long-tailed chinchilla (*Chinchilla lanigera*) greeting its mother in the Peruvian Andes. (Photo by Jane Burton. Bruce Coleman, Inc. Reproduced by permission.)

Habitat

All species live in burrows or rocky crevices. Elevations of preferred habitats vary from below 1,640 ft (500 m) for the plains viscacha to 13,120–16,400 ft (4,000–5,000 m) for chinchillas and mountain viscachas. The plains viscacha occurs in steppe or grassland regions characterized by barren vegetation near the burrow system. Species of the other genera reside in rocky areas with sparsely distributed vegetation.

Behavior

Plains viscachas excavate complex burrow systems with their front feet that can be occupied for up to 70 years. Burrow systems of the plains viscacha are colloquially known as a "viscacheras," a term used to describe the characteristic piles of debris collected and placed at the burrow's entrance. Both the mountain viscacha and chinchilla are equipped for leaping and generally live in crevices under rocky outcrops. Like chinchillas, plains viscachas are nocturnal, whereas the mountain viscacha is active during the day. All species of chinchillids are colonial, yet vary in the

In the wild, the long-tailed chinchilla (*Chinchilla lanigera*) can be found in groups of 100 or more. (Photo by H. Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

A southern viscacha (*Lagidium viscacia*) basking at Atliplano Lauca National Park and Biosphere Reserve, Chile. (Photo by François Gohier/ Photo Researchers, Inc.Reproduced by permission.)

A moutain viscacha (*Lagidium peruanum*) in the wetlands at Altliplano Lauca National Park and Biosphere Reserve, Chile. (Photo by Fletcher & Baylis/Photo Researchers, Inc. Reproduced by permission.)

degree of social structure. According to some accounts, colonies of the plains viscacha are restricted to a communal burrow system and consist of a dominant male and other member of the family group. Colony size range is 15–30 individuals. Both chinchillas and mountain viscachas live in smaller family groups, with a more dispersed colonial structure of individual groups within an area. These large, more sparsely distributed colonies range in size from as few as four up to 100 individuals. Plains viscachas have a broad repertoire of vocalizations consisting of high-pitched whines, alarm calls, and the characteristic "uh-huh" sound. The mountain viscacha's warning call consists of a tweeter or high-pitched whistle.

Feeding ecology and diet

All species are herbivorous, feeding on grass and seeds. Both the mountain viscacha and the chinchilla eat while sitting erect. The plains viscacha forages at dusk and during the night. The intensity of grazing by the plains viscacha has been observed to result in open patches where forbs become the

A long-tailed chinchilla (*Chinchilla lanigera*) sunning on a log. (Photo by Hans Reinhard. Bruce Coleman, Inc. Reproduced by permission.)

A plains viscacha (*Lagostomus maximus*) foraging in South America. (Photo by Loenard Lee Rue III. Bruce Coleman, Inc. Reproduced by permission.)

dominant vegetation. If colonies are removed from these regions, grasses displace forbs as the dominant vegetative cover. Mountain viscachas feed on vegetation such as lichens, mosses, and grasses that occur at high altitudes.

Reproductive biology

All chinchillids have long gestation periods ranging from 90 to 154 days. Average at sexual maturity for females is eight to 15 months. Young are born precocial, and one to three litters are produced each year with size of litters ranging from one to six.

Conservation status

Overharvesting by humans has impacted all species of chinchillids. *Chinchilla lanigera* is listed as Vulnerable by the IUCN, and *C. brevicaudata* as Critically Endangered. *Lagidium wolffsohni* is considered common in southwest Argentina and Chile, data on *L. viscacia* are deficient, and the status of *L. peruanum* is unknown. According to 1999 reports, the plains viscacha is considered a pest and has declined throughout its range as a result of eradication programs.

Significance to humans

Both species of chinchilla were commercially harvested in Chile, with over 500,000 pelts exported between 1900 and 1909. The plains viscachas compete with domestic livestock, and this species has also been intensely harvested, with over 370,000 skins exported over a three year period in the 1970s. Mountain viscachas also are prized for their meat and fur.

1. Long-tailed chinchilla (*Chinchilla lanigera*); 2. Mountain viscacha (*Lagidium peruanum*); 3. Plains viscacha (*Lagostomus maximus*). (Illustration by Patricia Ferrer)

Species accounts

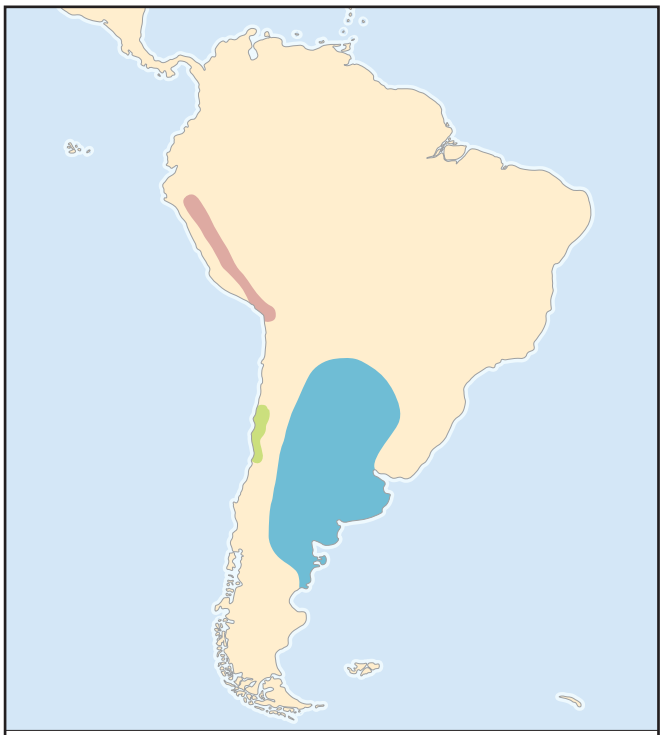
Plains viscacha
Lagostomus maximus

TAXONOMY
Lagostomus maximus (Desmarest, 1817), type locality unknown; possibly from pampas of Buenos Aires, Argentina.

OTHER COMMON NAMES
English: Vizcacha; French: Viscache, lièvre des pampas.

PHYSICAL CHARACTERISTICS
Large rodents with head and body length averaging over 19.7 in (500 mm). Tail length averages 6.9 in (175 mm) and total weight up to 19.8 lb (9 kg). Males tend to be larger than females by approximately 15% in body length and 30% in body weight. Individuals have large, broad heads, and males have a distinctive black mustache and stiff whiskers. Broad black and white stripes on face. Underparts are white and dorsal pelage ranges from gray to brown, depending upon soil color. The tail has stiff hairs, is bare ventrally, and provides support for sitting upright. Digits reduced to three on the hind foot.

DISTRIBUTION
Occurs in southern Paraguay, southeastern Bolivia, and Argentina.



HABITAT
Prefers grassland and steppe habitats at elevations below 9,840 ft (3,000 m). Areas around burrow systems are sparsely vegetated with piles of debris around openings located under bushes.

BEHAVIOR
Construct elaborate burrows that house successive colonies for decades. Single males defend burrow systems and are the dominant breeders. Variety of vocalizations and gestures are used during aggressive interactions among individuals. Members of colonies produce alarm calls and perform allogrooming.

FEEDING ECOLOGY AND DIET
Feed at night on grasses and seeds. Heavy grazing alters the abundance and diversity of grass species. They are ecologically similar to North American prairie dogs. Almost 94% of diet is grass, resulting in severe grass cover depletion. Cattle and plains viscachas share the same diet.

REPRODUCTIVE BIOLOGY
Polygamous. Gestation 152 days, seasonal breeder with one litter per year in southern portion of range, no more than two litters per year in other ranges. Litter size is two.

CONSERVATION STATUS
Not listed by the IUNC though extinction of local colonies as a result of eradication programs is common.

SIGNIFICANCE TO HUMANS
Considered a competitor with domestic species of livestock. Burrow system presents a potential threat to horses and cattle. Harvested for food and fur. In the past, pelts were exported. ◆

Mountain viscacha
Lagidium peruanum

TAXONOMY
Lagidium peruanum (Meyen, 1833) Pisacoma, Puno Department, Peru.

OTHER COMMON NAMES
English: Peruvian mountain viscacha, common mountain viscacha; French: Viscache du Pérou.

PHYSICAL CHARACTERISTICS
Weight averages 2.9 lb (1.3 kg), head and body length 14.8 in (375 mm), and tail 10.5 in (267 mm). Rabbit-sized with powerful legs and long tail. Fur is thick and soft, dorsal pelage is gray to orange with lighter ventral region. Tip of tail is dark, ears long, and four digits on front and hind feet.

DISTRIBUTION
Andes mountains in Peru at elevations ranging between 9,840 and 16,400 ft (3,000–5,000 m).

HABITAT
Prefers dry, rocky, habitats between the timber line and snow line of the Andes mountains with sparse vegetation and coarse grasses. Often found near water that offers better vegetation

than the drier regions within their habitat. Seeks shelter in rocky crevices.

BEHAVIOR
Diurnal species that is active throughout the year. Leaps among rocks and performs a series of whistles and trills associated with warning. Colonial structure composed of small family units of two to five individuals in a subdivided colony that can be as large as 75 animals.

FEEDING ECOLOGY AND DIET
Herbivorous, feeds on grasses, lichens, and mosses occurring at high elevations.

REPRODUCTIVE BIOLOGY
Males tend to be promiscuous. Gestation is 140 days, litter size of one precocial offspring.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Harvested by humans for food and pelts. ◆

Long-tailed chinchilla
Chinchilla lanigera

TAXONOMY
Chinchilla lanigera (Molina, 1782), Coquimbo, Coquimbo Province, Chile.

OTHER COMMON NAMES
French: Chinchilla laniger.

PHYSICAL CHARACTERISTICS
Average total length of 14.4 in (365 mm), tail length 5.6 in (141 mm), and weight 0.9 lb (0.4 kg). Appearance is rabbit-like with larger ears than *C. brevicaudata* and a longer brushy tail. Dorsal fur is gray and black. Tympanic bullae are inflated.

DISTRIBUTION
Mountainous regions of Chile.

HABITAT
Arid to semi-arid, montane regions between 9,840–16,400 ft (3,000–5,000 m). Prefers rocky habitats with sparse vegetation.

BEHAVIOR
Either nocturnal or crepuscular, excellent leapers, and colonial. Colony size can be several hundred individuals organized into smaller subgroups. Highly vocal with females apparently dominant sex displaying higher levels of aggression.

FEEDING ECOLOGY AND DIET
Female chinchillas are mostly monogamous. Predominantly herbivorous feeding on grasses and seeds, yet will eat insects. Eats while sitting on hind legs and holding food with front paws.

REPRODUCTIVE BIOLOGY
Produces two litters per year, and females experience postpartum estrus. Gestation averages 111 days, and litter size is two on average.

CONSERVATION STATUS
Listed as Vulnerable with a high risk of extinction by IUCN. Chilean government lists both species as Endangered. According to a 1996 account, *C. lanigera* is almost extinct in the wild, with the last official citing in 1953. Commercial hunting resulted in the decimation of populations, with almost seven million pelts exported from Chile prior to protection.

SIGNIFICANCE TO HUMANS
Prized for pelts. Captive stocks are maintained for the fur industry, and these stocks are the result of cross breeding. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Short-tailed chinchilla *Chinchilla brevicaudata* French: Chinchilla á queue courte; Spanish: Chinchilla de cola corta	Upper coat bluish, pearl, or gray with black-tipped hairs, underside yellowish white. Soft, dense fur. Head and body length 12–13 in (30–33 cm) , tail length 5–6 in (12–15 cm), weight 17.6–28.2 oz (500–800 g).	Mountain shrub and grassland at elevations of 9,800–4,775 ft (3,000–4,500 m). Nocturnal and vocal animals. Live in colonies from a few individuals to over 100.	Andes of southern Bolivia, southern Peru, northwestern Argentina, and northern Chile.	Primarily herbivorous, but occasionally eat insects.	Critically Endangered
Southern viscacha *Lagidium viscacia* English: Mountain viscacha; Spanish: Viscacha montesa de Cuvier	Upperparts gray to brown; underparts white, yellow, or pale gray; black tail tip. Soft, dense fur; coarse hair on tail. Long ears. Head and body length 12–18 in (30–45 cm), tail length 7.8–15.7 in (20–40 cm), weight up to 6.6 lb (3 kg).	Dry, rocky, mountainous areas with sparse vegetation. Diurnal; most active at dusk and dawn.	Western Argentina, southern and western Bolivia, northern Chile, and southern Peru.	Herbivorous, primarily eating grass, mosses, and lichens.	Data Deficient
Wolffsohn's viscacha *Lagidium wolffsohni* Spanish: Viscacha montesa del sur	Upperparts gray to brown; underparts white, yellow, or pale gray; black to reddish brown tail tip. Soft, dense fur; coarse hair on tail. Long ears. Head and body length 12–8 in (30–45 cm), tail length 7.8–15.7 in (20–40 cm), weight up to 6.6 lb (3 kg).	Dry, rocky, mountainous areas with sparse vegetation. Diurnal.	Southwestern Argentina and southern Chile.	Herbivorous.	Lower Risk/Near Threatened

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Rodney L. Honeycutt, PhD

Pacaranas
(Dinomyidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Dinomyidae

Thumbnail description
Like a solidly-built, medium-dog-sized rodent with a large head

Size
Weight 22 to 33 lb (10 to 15 kg), head and body length range from 28 to 31 in (730 to 790 mm), plus a tail length of about 7.5 in (190 mm)

Number of genera, species
1 genus; 1 species

Habitat
Lowland and montane tropical rainforest

Conservation status
Endangered

Distribution
Western South America, from Venezuela into Bolivia

Evolution and systematics

Dinomys branickii is the only surviving species of the family Dinomyidae, genus *Dynomys*, an ancient and once varied group of South American rodents whose rat-like ancestors probably rafted on vegetation from Africa to South America between 45 and 36 million years ago (mya). The dinomyids were far more diverse in the Oligocene-Pliocene (34 to 1.8 mya). At least eight species of Dinomyidae are known from fossils, and some were the largest rodents ever to exist. The unusually large size of pacaranas recalls but merely echoes creatures like its extinct relative, *Telicomys gigantissimus*, as big as a rhinoceros, and, rivaling it in size, *Artigasia magna*. The great size of these and a few other related species gave rise to the family name, Dinomyidae, meaning "terrible mouse."

Pacaranas are hystricognath rodents, within the suborder Hystricognathi, that classification based on peculiarities of their skulls, lower jaws, and jaw muscles, shared among all member species. Hystricognath rodent species live mainly in South America and Africa, plus some species in southern Europe and Asia, and one species of New World porcupine (*Erethizon dorsatum*) in North America. The suborder is vast, made up of 18 families, which include the African mole rats, dassie rats, grasscutter rats, Old and New World porcupines, capybaras, chinchillas, agoutis, and many others. With few exceptions, hystricognath rodents produce small litters of one or two young; infants are precocial, i.e., born furred, with eyes open, and able to move about. Suborder Hystricognathi can

Pacarana (*Dinomys branickii*). (Illustration by Jaqueline Mahannah)

be separated into two infraorders, Caviomorpha, the New World hystricognaths, and Phiomorpha, the Old World hystricognaths.

Some taxonomists have tentatively explained the similarities of the American and African hystricognaths as resulting from convergence. Some of the latest studies in genetic and molecular evolution involve the "molecular clock" method, whereby genes from related species are sequenced and the number of mutations in neutral genes are noted, providing an estimation of the time a new species diverged from the ancestral line. As of 2001, molecular clock studies among hystricognath species on both sides of the Atlantic strongly support their sharing a common ancestor, and strongly suggest a single colonizing event of African hystricognaths to South America, in the interval of 45–36 mya, that eventually gave rise to the great diversity of New World hystricognaths, including *Dinomys branickii* (Honeycutt; Huchon & Douzery; Honeycutt, Nedbal & Schlitter). During the interval of 45–36 mya, the Atlantic ocean was about half as wide as it is today, and had ocean currents between the two continents that would have been favorable for a rafting and colonization event from Africa to South America. There is, however, far from universal agreement on this scenario.

The taxonomy for this species is *Dinomys branickii* Peters, 1873, Montana de Vitoc, Department of Junin, Peru. The pacarana was first described in Western science in 1873 by a Polish count named Branicki, who did field research on South American wildlife for the Warsaw Museum of Natural History. Other common names include false paca, Branick's giant rat, machetero ("cutter" or "chopper"), rukupi, piro, teconi, tecon, lapa rabuda, lapo, lapa cacique, guagua lanuda, and guagua loba.

Physical characteristics

An adult pacarana weighs from 22 to 33 lb (10–15 kg), with head and body length from 28 to 31 in (730–790 mm), plus a tail length of about 7.5 in (190 mm). The body is compact and heavily built, and the broad head is large in comparison to the body. The limbs are moderately short, and powerfully muscled. A fairly thick coat of coarse hair covers the body. The upperparts of the pelage are dark brown or blackish, with rows of whitish spots running the length of the body. A bushy set of long, grayish whiskers arises from the snout. The paws bear four digits apiece and as many claws.

The name of the species is derived from a Tupi Indian word meaning "false paca" referring to its overall resemblance to the paca, *Agouti paca*. The pacarana is the third largest living rodent, after capybaras (Family Hydrochoeridae) and beavers (Family Castoridae), its weight ranging from 22 to 33 lb (10 to 15 kg), head and body length from 29 to 31 in (730 to 790 mm), and an additional tail length of about 7.5 in (190 mm). The body is compact and heavily built, and the broad head is large in comparison to the body. The second and third vertebrae of the neck are fused. Those who have seen living pacaranas have compared them to small bears, huge guinea pigs, and porcupines robbed of their quills.

A pacarana bears a fairly thick coat of coarse hair over nearly its entire body, including the bushy tail, but excepting the nostrils and the soles of all four feet. The dorsal/upper parts of the pelage are dark brown or blackish, with four rows of whitish spots forming broken white stripes along its upper body length. Two or three rows of more randomly arranged spots decorate both flanks. The underparts are a lighter shade. Adding the final touch to the rough coat is a bushy set of long, grayish whiskers situated about midway on the upper snout. The individual whiskers can be as long as the head or longer. The ears are relatively short and round, the eyes are large, and the upper lip is deeply cleft.

All four feet are plantigrade, i.e., the entire heel rests on the ground as the animal walks or stands, and it walks with a waddling gait. Each of the four paws bears four digits, each digit fitted with a long, curved, heavy claw. The limbs are powerfully muscled and only moderately short, but the thick, hanging pelage may obscure the lengths of the limbs. All the features of the legs and feet would seem to indicate that pacaranas are diggers, but no one has ever seen a wild or a captive pacarana dig, although they may widen the entrances to their shelters with clawstrokes. They sometimes climb, and they can and will walk bipedally.

The cheek teeth of a pacarana grow continuously. The gnawing incisors are designed according to the basic rodent pattern, and they are broad and powerful.

Distribution

Pacaranas are thinly scattered in a band running through mountainous territory from western Venezuela through western Colombia, central Ecuador, Peru, a small section of western Brazil, and into northwestern Bolivia. In Peru, pacaranas live from 800 to 6,600 ft (240 to 2,000 m) above sea level, and up to 7,870 ft (2,400 m) above sea level in Venezuela.

Habitat

Pacaranas inhabit forested mountain slopes and valleys of rainforests in the Andes mountains, from 800 to 6,600 ft (240 to 2,000 m) above sea level. According to the classification of

A pacarana (*Dinomys brenickii*) basking in the sun on the lower slopes of the Andes Mountains. (Photo by Francisco Erize. Bruce Coleman, Inc. Reproduced by permission.)

Little is known about pacaranas (*Dinomys branickii*) in the wild. (Photo by Zoological Society of San Diego. Reproduced by permission.)

World Wildlife Fund Global 200 Terrestrial Ecoregions, pacaranas are found in Bolivian Yungas, Southwest Amazon moist forests, Venezuelan Andes montane forests, and Magdalena Valley montane forests.

Behavior

Pacaranas are nocturnally active. Captive pacaranas are unagressive, peaceful creatures, but they are well adapted for defense and can be disconcertingly vicious. Adults are solitary or live in pairs or in family groups. Pacaranas communicate with a varied and complex array of sounds and postures.

Pacaranas have been but little studied in the wild, and much information about their behavior and biology has been learned from observing captive animals.

Captive pacaranas, most of the time, are unaggressive, peaceful creatures. Pacaranas are often the butt of jokes comparing their peaceful, pokey nature to their genus name, *Dinomys*, which adds up to an irony. Nevertheless, pacaranas are not only well-equipped for self-defense, but have a well-earned reputation for occasional but effective viciousness. In a Brazilian zoo, several pacaranas in an enclosure ganged up on and killed a paca introduced into the compound, the keepers probably assuming that the normally phlegmatic pacaranas would prove no threat to the new tenant. Domestic dogs living in areas inhabited by pacaranas have learned to fear and avoid them, because of the large rodents' spirited defense. This may partly explain their continued survival, despite their low numbers and density. The pacarana is a strong, fairly large animal with formidable claws and powerful limbs, and can apparently give a good account of itself in a tight spot. Nevertheless, pacaranas are vulnerable to humans, who can kill them from a distance.

In the wild, pacaranas live in cracks between rocks or in natural caves. Adults live alone, in pairs, or in family groups of a parent pair with one or more litters of their young.

Pacaranas communicate with a varied repertoire of sounds, stamping with their forepaws, tooth chattering, whining, melodious songs, and hissings. Researchers have found seven distinct pacarana vocalizations used in social situations.

Life spans of wild pacaranas are unknown, but a captive pacarana reached the impressive age, for a rodent, of nine years and five months.

Feeding ecology and diet

Pacaranas are nocturnal foragers, feeding on palm and other kinds of fruits, leaves, and young, tender stems of plants. They will sometimes climb trees in quest of edibles, aided by their strong, curved claws, but spend most of their active time on the ground. When feeding, they sit on their hind legs and hold their food with both forepaws.

Reproductive biology

Pacaranas make crying vocalizations during the breeding season to attract sexual partners. Individuals in first-time male-female encounters most often communicate with hisses,

Pacaranas (*Dinomys branickii*) are the third largest living rodent. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

growls, and staccato whimpering sounds. If courtship ensues, the male vocalizes with a string of whimpering notes that he may segue into singing lasting up to two minutes. As the two approach each other more closely, they touch noses, sniff genitals, and begin an elaborate contact ritual that looks like a combination of dancing and wrestling. The two stand bipedally, grappling, and interlocking their incisors. Courtship moves may include ritual head-tosses and dancing, ending at last with mounting. The male's forelegs tremble as he approaches the female, a common courtship ritual in rodents. Males may also approach bipedally, with an erect penis.

Pregnant females have been seen in February and May, while births have been observed in January and February. A pregnant female will show a sudden weight gain at about 90 days of gestation, and she can become irritable. No nest building by pregnant or postpartum females has been observed.

The gestation period of captive animals ranges from 222 to 283 days, and the common litter size is one or two. A newborn pacarana weighs about 32 oz (900 g). The infant is precocial, i.e., fully furred and able to see and move about, groom itself, and actively investigate its new world within a few days of birth. Weaning period and age of sexual maturity for pacaranas are as yet unknown.

Conservation status

As of 2002, pacaranas are classified as Endangered in the IUCN Red List of Threatened Species. Not common to begin with, their low population levels are vulnerable to hunting by humans and to habitat loss, and has several times been feared extinct.

Significance to humans

Indigenous people in South America hunt pacaranas for food.

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Organizations

IUCN—The World Conservation Union. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41 (22) 999 0000. Fax: +41 (22) 999 0002. E-mail: mail@hq.iucn.org Web site: <http://www.iucn.org>

Other

2002 IUCN Red List of Threatened Species. <http://www.redlist.org>

Animal Diversity Web. *Dinomyidae*. <http://animaldiversity.ummz.umich.edu/chordata/mammalia/rodentia/dinomyidae.html>.

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Kevin F. Fitzgerald, BS

Cavies and maras
(Caviidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Caviidae

Thumbnail description
Range from short, stocky body form to rabbit-like with long slender legs and nails that are hoof-like; either clawed digits or nails; scampering or cursorial locomotion; pelage relatively short and gray to agouti dorsally and paler on ventral surface

Size
Head and body length 5.9–29.5 in (150–750 mm); tailless or tail length 0.9–1.3 in (24–35 mm); weight 7 oz to 35.2 lb (200 g to 16 kg)

Number of genera, species
6 genera; 16 species

Habitat
Low elevations up to elevations of 16,400 ft (5,000 m), semiarid thorn shrub, grassland and savanna, riparian forest and forest edge, rocky outcrops, steppe vegetation with sparse shrubs, and cultivated areas

Conservation status
No species listed by the IUCN

Distribution
Broadly distributed throughout South America

Evolution and systematics

The family Caviidae first appears in the fossil record during the middle Miocene of South America. The family is a member of the monophyletic Cavioidea, a superfamily containing three additional families, Agoutidae, Dasyproctidae, and Hydrochaeridae. Traditionally, the Caviidae has been subdivided into two subfamilies, with *Galea*, *Cavia*, *Microcavia*, and *Kerodon* placed in the subfamily Caviinae and *Dolichotis* and *Pediolagus* in the subfamily Dolichotinae. Based on morphological studies, capybaras of the family Hydrochaeridae are considered to be the closest relative to the Caviidae. A molecular phylogenetic study by Rowe and Honeycutt in 2002 suggests considerable modification of the current phylogenetic arrangements of both genera in the Caviidae and relationships among families in the superfamily Cavioidea. Cavids appear most closely related to the family Agoutidae, and rather than being a separate family, these molecular data suggest that the Hydrochaeridae is related to *Kerodon*, and these two lineages are most closely aligned with *Dolichotis* and *Pediolagus*, members of the subfamily Dolichotinae. Therefore, the Caviinae is confined to three genera, *Cavia*, *Microcavia*, and *Galea*, with the first two genera being more closely related. Assuming that *Kerodon* was a member of the Caviinae, Lacher in 1981 suggested that similarities in the social system seen in *Kerodon* and members of the Dolichotinae provided evidence of convergence in response to similar habitat constraints and the distribution of resources. The molecular phylogenetic arrangement has implications for understanding the evolution of life history traits, especially those related to mating systems and resource availability. The placement of the rock cavy, *Kerodon* and *Hydrochaeris*, as members of the Dolichotinae suggests that shared ancestry, rather than similarities in ecological constraints, best explains the evolution of social behavior in these rodents. In this regard, both the rock cavy and the capybara have a harem-based polygynous breeding system and are habitat specialists. If the molecular data are correct, then the ancestor to capybaras, rock cavies, maras, and salt-desert cavies may have been highly social. This complex social system may very well be associated with patchily distributed resources.

The genus *Cavia* is the most diverse in terms of species and overall geographic distribution. Although as many as eight species have been recognized, Wilson and Reeder in 1993 listed five species. The other Caviinae genera, *Microcavia* and *Galea*, each contain three species, whereas *Kerodon*

A rock cavy (*Kerodon rupestris*) resting its front paws on a branch. (Photo by © Frank W. Lane; Frank Lane Picture Agency/Corbis. Reproduced by permission.)

is represented by one species with a restricted distribution. Although *Pediolagus salinicola* was considered a species within the genus *Dolichotis*, recent treatments based on morphology and nucleotide sequences suggest that it represents a genus separate from the currently recognized *Dolichotis patagonum*.

Physical characteristics

Members of the family are stout bodied with large heads and short pelage. Like many mammals that feed on plant materials, cavids have high-crowned jaw teeth that are continuously growing. Dorsal coloration varies from yellow, gray, olive, and agouti, with ventral pelage color being white or lighter than upper parts. Size and basic body plan ranges from small, tailless, short-legged cavies (*Cavia*, *Microcavia*, and *Galea*) with body lengths 5.9–15.7 in (150–400 mm) and weights of 7.0–21.1 oz (200–600 g) to large-bodied, rabbit-like salt-desert cavies and maras (*Dolichotis* and *Pediolagus*) with short tails 0.9–1.3 in (24–35 mm) and long, slender limbs, and larger body sizes 17.7–29.5 in (450–750 mm) and weights of 2.2–35.2 lb (1–16 kg). *Dolichotis* is considerably larger than *Pediolagus*. Unlike the small, scampering cavies, salt-desert cavies and maras are highly specialized for cursorial or fast-running locomotion displaying digit reduction and hoof-like nails. Cavies have clawed digits with less reduction in number (four on front and three on rear). The rock cavy, *Kerodon rupestris*, is the ecological-equivalent of rock hyraxes in Africa. Its padded feet and nail-like digits make it highly adapted for climbing rocks and trees.

Distribution

Cavia is the most broadly distributed genus, occurring throughout most of South America from Colombia to Argentina, whereas rock cavies are confined to rocky outcrops in restricted areas of Brazil. Other genera and species are common in parts of southern Peru, Bolivia, Paraguay, Chile, and Argentina.

Habitat

Habitat utilization varies with species that are generalists occurring in areas containing an even distribution of resources and more specialized species adapted to arid conditions and sparsely distributed resources. Maras and salt-desert cavies are more common in temperate steppe habitats characterized by

Patagonian maras (*Dolichotis patagonum*) mate for life. (Photo by Karen McGougan. Bruce Coleman, Inc. Reproduced by permission.)

A brown domestic guinea pig (*Cavia porcellus*). (Photo by Carolyn A. McKeone/Photo Researchers, Inc. Reproduced by permission.)

A female Patagonian mara (*Dolichotis patagonum*) with her young. (Photo by Rod Williams. Bruce Coleman, Inc. Reproduced by permission.)

scattered shrubs and grasslands. Habitat preferences of cavies are more varied, represented by thorn bush, forested areas near water, grasslands, and cultivated lands. Compared to guinea pigs, the cuis lives in more arid habitats, and the rock cavy is specialized for patchily distributed rocky outcrops. Most species prefer lower elevations and none occur above 16,400 ft (5,000 m).

Behavior

The cuis, mountain cavy, and mara excavate burrows. All species have diverse repertoires of vocalizations related to alarm calls, aggressive interactions (especially among males), courtship, and play. Most species exhibit scent-marking behaviors, especially rubbing of the ano-genital region. Males may urinate on females during courtship (enurination). All species are diurnal, with highest activity peaks in mornings and afternoons. Species within the family are colonial and vary in mating system. According to Rood's classic study in 1972, which detailed the behavior of cavies, species within these three genera are colonial, and males have a linear dominance hierarchy that maintained by aggressive interactions. In 1995 Kunkele and Hoeck observed communal suckling in the cuis,

Guinea pigs (*Cavia porcellus*) in grass. (Photo by Hans Reinhard/ OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

The rock cavy (*Kerodon rupestris*) does not hibernate and can be found in dry rocky areas in Brazil. (Photo by © Ken Lucas/Visuals Unlimited, Inc. Reproduced by permission.)

The Brazilian guinea pig (*Cavia aperea*) is the ancestor of the domestic guinea pig. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Galea musteloides. During courtship, cuis males perform hops, and individuals within a colony socially groom. Vocalizations are varied squeaks, "churrs," screeches, whistles, and chattering of teeth. Male cavies have very distinctive courtship, with a "rhumba" display, best described for guinea pigs. The mating system of guinea pigs (genus *Cavia*) and mountain cavies (genus *Microcavia*) is polygynous with a dominant male breeding several females. The cui is promiscuous, and there is evidence of multiple paternities for single litters of the cuis. Sachser and others in 1999 indicated that these contrasting mating systems in the cuis and guinea pig are related to testes size in males, with male cuis having larger testes sizes than male guinea pigs.

A Patagonian mara (*Dolichotis patagonum*) foraging. (Photo by Norman Owen Tomalin. Bruce Coleman, Inc. Reproduced by permission.)

A Patagonian mara (*Dolichotis patagonum*) mother with her young. (Photo by Ernest A. James. Bruce Coleman, Inc. Reproduced by permission.)

Rock cavies display resource defense polygyny, whereby males protect rock piles and attract groups of females. Both males and females have linear dominance hierarchies. Maras have a male-dominant hierarchy and display monogamy. The studies of Taber and Macdonald revealed the formation of pair bonds lasting several breeding seasons with the female representing a mobile "territory" defended by the male. During the breeding season, the offspring of multiple pairs occupy a communal den, unlike the cuis, whose mothers nurse only their offspring.

Feeding ecology and diet

Many species like the rock cavy are generalist herbivores, feeding on a variety of leaves, seeds, fruits, and flowers. Others feed more on grasses, leaves, and cacti. Some species, like rock cavies and mountain cavies, climb while foraging. Most non-climbers feed more on grasses and low growing vegetation.

Reproductive biology

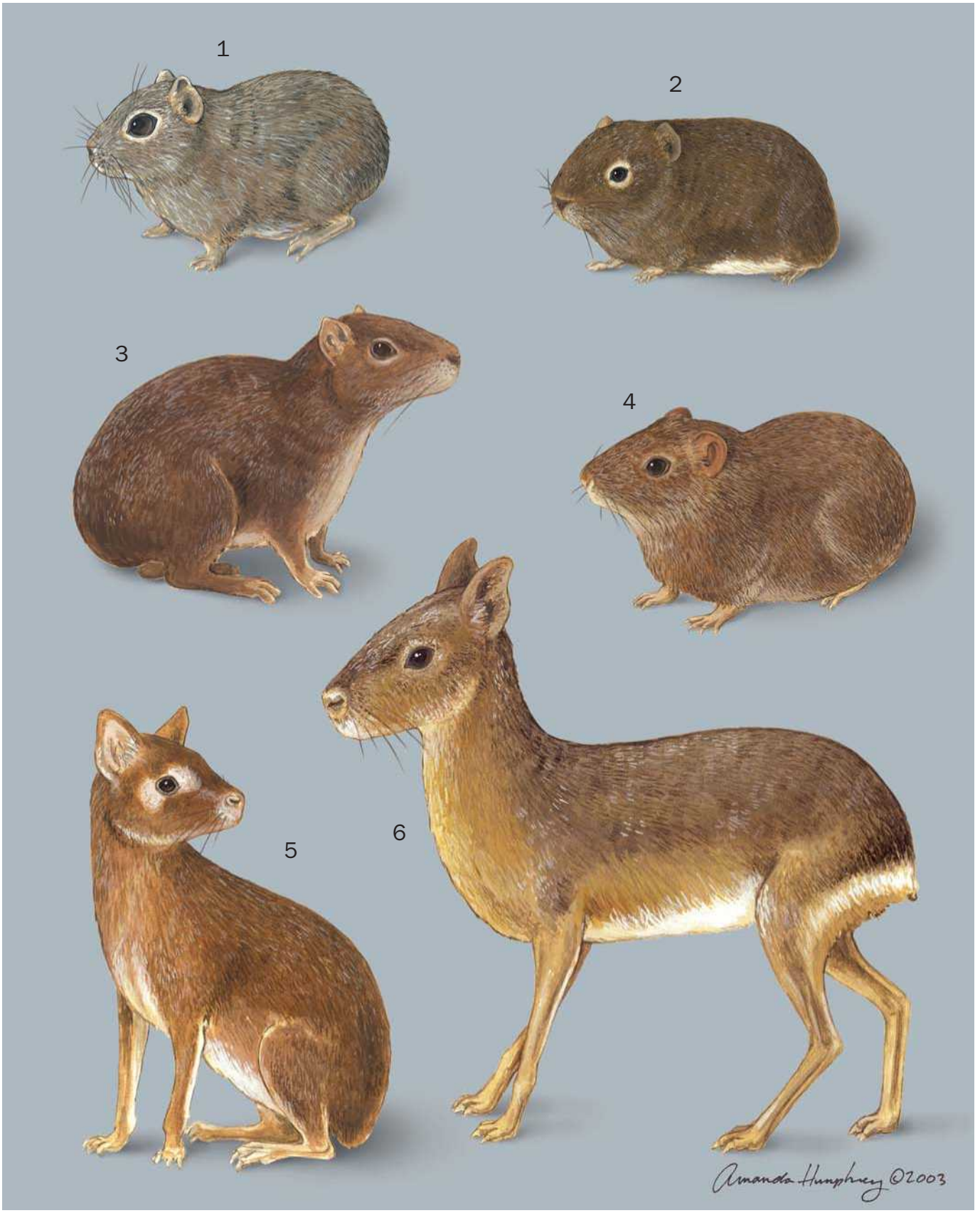
Cavids display a range of mating systems including hierarchical promiscuity, polygyny, and monogamy. Young are born precocial and mature sexually at an early age. Smaller cavies, including the rock cavy, range in gestation period from 50–70 days, are polyestrous (producing multiple litters per year), and are capable of postpartum estrus. Litter size can be as high as seven, but in most small species litter size is one to three. Maras and salt-desert cavies are more seasonal in breeding patterns and produce small litters of one to two offspring, which are extremely precocial, due to convergence with small antelopes. In general, the smaller species have larger reproductive outputs.

Conservation status

No species are currently listed by IUCN.

Significance to humans

The guinea pig has been domesticated since 1000 B.C. and, in some areas of Ecuador, Peru, and Bolivia, is raised for food. Ancient Incas apparently used the guinea pig in religious sacrifices. Smaller cavies are considered agricultural pests in some regions, and other species can impact grazing areas. Larger cavies are hunted for food and skins.



1. Mountain cavy (*Microcavia australis*); 2. Cui (*Galea musteloides*); 3. Rock cavy (*Kerodon rupestris*); 4. Guinea pig (*Cavia aperea*); 5. Salt-desert cavy (*Pediolagus salinicola*); 6. Mara (*Dolichotis patagonum*). (Illustration by Amanda Humphrey)

Species accounts

Mountain cavy
Microcavia australis

SUBFAMILY
Caviinae

TAXONOMY
Microcavia australis (I. Geoffroy and d'Orbigny, 1833), Patagonia, near lower part of Rio Negro, Argentina.

OTHER COMMON NAMES
English: Desert cavy; Spanish: Cuis chico.

PHYSICAL CHARACTERISTICS
Head and body length averages 8.2 in (210 mm), weight 12.3 oz (350 g). Males are somewhat larger than females. Dorsal pelage is agouti mixed with yellow and brown, and ventral side paler. Hair around the eye appears as a ring. Individuals are tailless, have clawed digits.

DISTRIBUTION
Occurs primarily in Argentina and portions of southern Chile.

HABITAT
Occurs at lower elevations than related species in arid and semiarid habitats; a desert specialist. In portions of its range, it occurs in more mesic, forested habitats. Groups live in burrow systems.

BEHAVIOR
Diurnal, live in burrows, and form colonies. Colonies sizes of up to 38 individuals in one burrow system have been observed. Social structure is based on a linear male dominance hierarchy, with aggressive interactions among males. Colony stability is habitat dependent. Three types of vocalizations include a low pitched "tsit" for alarm, series of squeaks during mating and social grooming, and a high-pitched shriek emitted when afraid. During breeding and play, hops and other body postures are observed.

FEEDING ECOLOGY AND DIET
Varied herbivorous diet consisting of leaves, seeds, grass, and other types of vegetation; browse and climb.

REPRODUCTIVE BIOLOGY
Males are promiscuous and breed with multiple females. Multiple litters averaging three offspring per litter are produced each year, and the average gestation period is 54 days. Young are precocial.

CONSERVATION STATUS
Common, and not threatened or endangered throughout its range.

SIGNIFICANCE TO HUMANS
Adapts well to humans and is considered an agricultural pest in some areas. Sometimes used as food by humans. ◆

Guinea pig
Cavia aperea

SUBFAMILY
Caviinae

TAXONOMY
Cavia aperea Erxleben, 1777, Pernambuco, Brazil.

OTHER COMMON NAMES
English: Cavy; Spanish: Quiso, cui, cori, cobaye.

PHYSICAL CHARACTERISTICS
Head and body length average 13.7 oz (350 mm), tailless, and weight 17.6–52.9 oz (500–1,500 g). Legs are short, large head, digits clawed and slightly reduced (three on hind foot and four on front). Color of dorsal pelage is olive brown with paler coloration underneath. The domestic species, *Cavia porcellus*, is larger, more robust, and varied in color. Some have short hair, while others have long, straight, or curly hair. Considerable research on genetics of coat color and characteristics of the fur has been performed on domestic varieties of guinea pigs.

DISTRIBUTION
Occurs broadly in South America from Colombia through Brazil and Argentina. Most widely distributed genus in South America.

HABITAT
Takes shelter in brush and piles of rocks. Habitat varied, consisting of savanna in both subtropical and tropical regions,

grasslands, and edges of forests. Have a preference for grassy habitat.

BEHAVIOR
Displays both diurnal and nocturnal activity. Guinea pigs form colonies with a linear dominance hierarchy for both males and females. Males are less tolerant of each other in the wild species relative to the domestic species. The species is highly vocal and has calls for warning, courtship, and aggressive interactions; these calls range from "clucks" to "whets."

FEEDING ECOLOGY AND DIET
Generally feed throughout the day on grasses, and have been observed feeding in groups. Feeding areas normally close to cover.

REPRODUCTIVE BIOLOGY
The mating system is polygynous and involves males mating with more than one female. Gestation averages 62 days for wild species and is shorter in the domestic guinea pig. Guinea pigs breed continuously and experience postpartum estrus. Minimum age for first reproduction in females is 30 days. Young are precocial and weaned at an early age. Offspring have been observed eating solid food two to three days after birth. The social organization of guinea pig populations changes with increases in number of individuals. There is a stronger linear dominance hierarchy when populations are low, and when populations are larger, individuals form subgroups of a few males and females. In the small subgroups dominant males appear to be highly successful at monopolizing breeding of females in estrus.

CONSERVATION STATUS
Common, not threatened.

SIGNIFICANCE TO HUMANS
Still used for food today; presumably, the Incas used guinea pigs for food and in religious ceremonies. The domestic species has been used as an animal model for studying human diseases and toxins harmful to man. Other medical uses have involved the development of serums and vaccines as well as psychological experiments. Early studies of animal population genetics focused on variation of the guinea pig's coat color. Guinea pigs are kept as pets and become very interactive. ◆

Cui
Galea musteloides

SUBFAMILY
Caviinae

TAXONOMY
Galea musteloides Meyen, 1832, Paso de Tacna, Peru.

OTHER COMMON NAMES
English: Yellow-toothed cavy.

PHYSICAL CHARACTERISTICS
Short legs and large head. Head and body length average 6.8 in (175 mm), tailless, and weighs 10.5–21 oz (300–600 g). Females tend to be heavier than males. Upper parts are agouti and ventral surface is a pale white. Digits show little reduction and are clawed.

DISTRIBUTION
Found in southern Peru, Bolivia, Argentina, and the northern portion of Chile.

HABITAT
Habitat is varied and includes savanna and thorn shrubs, grasslands, and scrub forests. Populations can be found at several elevations up to 16,404 ft (5,000 m).

BEHAVIOR
The cui is diurnal, colonial, and forms a male linear dominance hierarchy that is established and maintained by aggression in the form of threats and attacks; the level of aggression is dependent upon both age and sex, and females are generally dominant over males of the same age. In captivity, females have been observed to communally nurse young. Display a variety of vocalizations associated with sexual encounters, aggression, and warning.

FEEDING ECOLOGY AND DIET
Herbivorous and feeds on grasses, forbs, and other vegetation. Individuals observed feeding throughout the day.

REPRODUCTIVE BIOLOGY
Breeding is promiscuous, and females may breed with more than one male. Evidence of multiple paternity has been confirmed. Presumably, low success of single male mating is the result of promiscuity on the part of the female. Breeding appears to be continuous with females capable of producing up to seven litters per year. Apparently, males can induce ovulation in females by copulation. Gestation is 53–54 days. In comparison to other cavids, testes size of males is large.

CONSERVATION STATUS
Common, not threatened.

SIGNIFICANCE TO HUMANS
Potential agricultural pest. ◆

Rock cavy
Kerodon rupestris

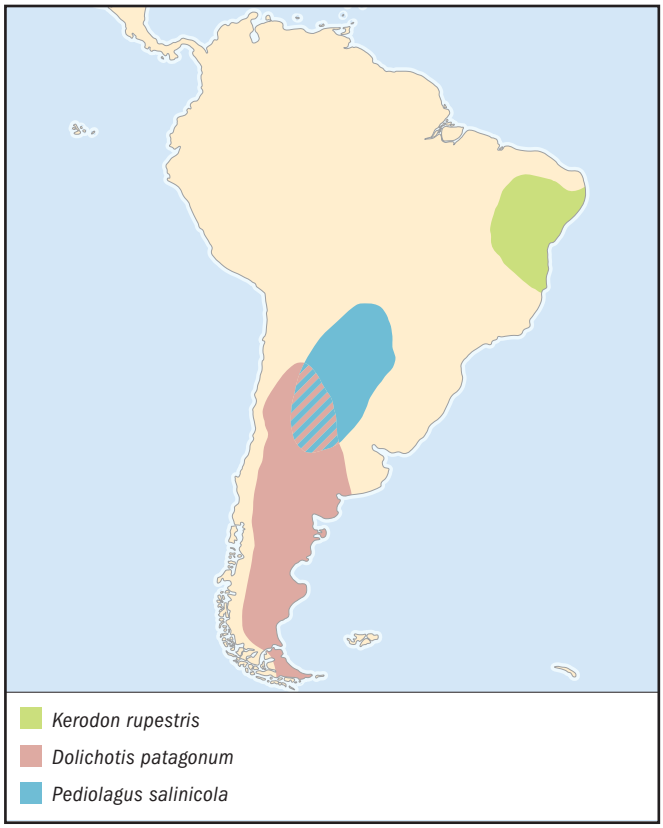
SUBFAMILY
Caviinae

TAXONOMY
Kerodon rupestris (Wied-Neuwied, 1820), Rio Belmonte, Bahia, Brazil.

OTHER COMMON NAMES
Spanish: Moco.

PHYSICAL CHARACTERISTICS
Little information exists on measurements of head and body lengths for either males or females. Individuals weigh 31.7–35.2 oz (900–1,000 g). Dorsal coloration is gray with some black, ventral surface is brown with yellow, and the throat is white. Relative to other small cavies, the overall body is longer, and the face has a muzzle similar to that of a dog. Rather than clawed, the digits have nails, except for one grooming claw, and the feet are padded for movement on rocky surfaces. Rock cavies have long, slender legs.

DISTRIBUTION
Occurs only in eastern Brazil from the state of Piaui to the northern part of Minas Gerais.



HABITAT
The species is considered a habitat specialist, preferring arid areas with rocky outcrops.

BEHAVIOR
Excellent rock climbers. Individuals are active later in the day, colonial with males defending optimal piles of rocks. Alarm calls consist of a whistle, and during estrus, males and females perform elaborate courtship behavior. They frequently exhibit scent marking, and social grooming is common.

FEEDING ECOLOGY AND DIET
Herbivorous and prefers leaves of plants. Spend considerable time foraging in trees and have been observed sitting upright during feeding.

REPRODUCTIVE BIOLOGY
A harem-based mating system; both males and females form linear dominance hierarchies. Females undergo postpartum estrus, gestation averages 75 days, and several litters are produced each year, with the size between one to two young per litter. Young are born precocial and capable of foraging for solid food.

CONSERVATION STATUS
Although not listed by IUCN, habitat specialization and limited distribution make this species potentially vulnerable. Two reserves have been established in Brazil.

SIGNIFICANCE TO HUMANS
Sometimes used for food. ◆

Mara
Dolichotis patagonum

SUBFAMILY
Dolichotinae

TAXONOMY
Dolichotis patagonum (Zimmermann, 1780), Puerto Deseado, Santa Cruz Province, Argentina.

OTHER COMMON NAMES
English: Patagonian hare, Patagonian cavy.

PHYSICAL CHARACTERISTICS
Largest of the cavids with head and body length average 28.3 in (720 mm), tail short averaging 1.4 in (35 mm), and weight averages 26.4 lb (12 kg). Males tend to be larger than females. Highly adapted for fast running, appearing rabbit-like. Large body and head, hind legs are long and claws appear hoof-like; the foot posture is digitigrade. The muzzle is broad and rostrum short. Dorsal pelage is agouti in color, the rump black, and the under parts are cream colored. Rump area with a distinctive patch and chin appears orange colored.

DISTRIBUTION
Resides in central and southern Argentina, and is subdivided into two subspecies, one occurring in the more northern provinces of Catamarca, La Rioja, and Cordoba, and the other found in the provinces of Buenos Aires, southern Cordoba, San Luis, and Mendoza.

HABITAT
Preference for temperate steppe habitats in more arid area characterized by coarser grasses and sparsely distributed shrubs, flats containing creosote bush of the genus *Larrea*; also occurs in forested gullies and more open grassland and steppe regions of Patagonia.

BEHAVIOR
Diurnal, active throughout most of the day, and lives in burrows. Monogamous and establish pair bonds that span several breeding seasons. The mated pair stays in close proximity, and the male tends the female, keeping his guard against other males and predators. Males enurinate over females. Contact between the male and female is maintained by vocalizations consisting of "grumbles." Form colonial groups consisting of communal den sites that house offspring from several different pairs; however, mara mothers attend to only their offspring and visit the den one pair at a time.

FEEDING ECOLOGY AND DIET
Herbivorous and eats a variety of vegetation including *Acacia* seeds, cactus, fruits, grasses, herbs, and leaves. Captive animals in zoos subsist on hay, green vegetation, vegetables, and crushed oats. A considerable amount of required water is obtained directly from their diet without the need for drinking standing water.

REPRODUCTIVE BIOLOGY
Monogamous over several breeding seasons. Gestation is generally 93–100 days, and females tend to reproduce for the first time around eight months of age. Multiple litters are produced, and the litter size is one to two offspring. Females have postpartum estrus. Reproduction in Patagonia tends to be more seasonal.

CONSERVATION STATUS
In portions of its range, the mara appears to be declining. While some consider the mara to be vulnerable, the species is

not officially listed. Habitat destruction and over-hunting are threatening populations in some areas, especially in the Buenos Aires Province.

SIGNIFICANCE TO HUMANS
Humans have hunted maras for their skins. ◆

Salt-desert cavy
Pediolagus salinicola

SUBFAMILY
Dolichotinae

TAXONOMY
Pediolagus salinicola (Burmeister, 1876), southwest Catamarca Province, Argentina.

OTHER COMMON NAMES
Spanish: Mara chico.

PHYSICAL CHARACTERISTICS
Head and body length averages 17.1–17.7 in (435–450 mm), tail averages 0.9 in (24 mm), and the weight is 4.6–5.9 lb (2.1–2.7 kg). Basic body form is similar to the mara. The pelage is thick, with the dorsal region being agouti, sides lighter, and the under parts white. Has a distinct band of either white or yellow extending around the flank region to the stomach. Sides of the face are tan colored, and white patches appear behind the eyes. Highly adapted for cursorial locomotion.

DISTRIBUTION
Overlaps with the larger mara, occurring in the southern portion of Bolivia, northern Argentina, and the Chaco of Paraguay.

HABITAT
Prefers low, arid or semiarid flats characterized by thorn scrub and woody vegetation. Also occurs in temperate steppe regions.

BEHAVIOR
Diurnal and digs burrows. Forms social groups consisting of an adult pair and young. Animals scent mark and reveal play activity characterized by frisky hops and rolling in sand where scent marking has occurred. Females tend to nurse their young while sitting in open areas, and males tend to show little evidence of extended parental care. Vocalizations are warning calls consisting of a whine. Relationship among individuals is a linear male dominance hierarchy, and alpha males dominate subordinates with aggressive encounters. Females are less aggressive toward each other.

FEEDING ECOLOGY AND DIET
Herbivorous, with dietary preferences that vary seasonally. In the Chaco region, the diet consists of over 28 species of forbs, 26 species of shrubs, and eight species of grasses. The most popular food items were plant species not preferred by livestock. Grasses preferred during the rainy season, and succulent vegetation during the dry season. Generally forage on lower leaves of bushes, but also stand upright and feed on higher vegetation by grasping with front paws. They have been observed to climb during foraging.

REPRODUCTIVE BIOLOGY
Gestation period averages 77 days in the wild and approximately 75 days in captive populations. Two offspring are born per litter, and young are weaned around four weeks of age.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Shiny guinea pig *Cavia fulgida*	Coarse, long pelage, crest of hair on neck. Color is grayish or brownish. Short legs, and short, unfurred ears. Head and body length 7.8–15.7 in (20–40 cm), weight 17.6–52.9 oz (500–1,500 g).	Open grasslands, forest edge, swamps, and rocky areas, sometimes at elevations up to 13,800 ft (4,200 m). Live in small groups, usually five to 10 individuals.	Southeastern Brazil.	Many of kinds of vegetation.	Not threatened
Domestic guinea pig *Cavia porcellus*	Stocky body with short legs. Color varies from white, black, red, cream, lilac, to brown or a combination of these colors. Length, texture depends on breed. Head and body length 7.8–19.7 in (20–50 cm).	In the wild, they can be found in temperate forest and rainforest, temperate grassland. Very social, live in groups of five to 10 individuals. Breed continuously throughout the year.	Northwestern Venezuela to central Chile.	Commercial pellets, fruits, and vegetables.	Not threatened
Yellow-toothed cavy *Galea flavidens*	Upperparts are agouti-colored, underparts are grayish white. No external tail. Head and body length 6–10 in (15–25 cm), weight 10.6–21.2 oz (300–600 g).	Grasslands at high or low elevations, as well as rocky and brushy areas. Live in groups, female hierarchy weaker than male hierarchy. Breed throughout the year.	Brazil.	Grasses, forbs, and other kinds of vegetation.	Not threatened
Rock cavy *Kerodon rupestris*	Tail is absent. Upperparts are grayish with white and black mottling, throat is white, underparts are yellowish brown. Nails are blunt and sharp. Adult weight 31.7–35.3 oz (900–1,000 grams).	Near stony mountains or hills, seeking shelter under rocks or in the fissures between stones, sometimes making a burrow under the stones. Births occur throughout the year.	Eastern Brazil.	Mainly tender leaves.	Not threatened
Andean mountain cavy *Microcavia niata*	No external tail, upperparts are olive gray agouti, underparts are pale gray. Prominent white ring around eyes. Head and body length 7.9–8.6 in (20–22 cm), weight 7.1–52.9 oz (200–500 g).	In high mountains. Population size varies. Considered a pest.	Southwestern Bolivia in the high Andes.	Leaves and fruits.	Not threatened
Greater guinea pig *Cavia magna*	Coarse, long pelage, crest of hair on neck. Color is grayish or brownish. Short legs, and short, unfurred ears. Head and body length 7.9–15.7 in (20–40 cm), weight 17.6–52.9 oz (500–1,500 g).	Open grasslands, forest edge, swamps, and rocky areas, sometimes at elevations up to 13,800 ft (4,200 m). Live in small groups, usually five to 10 individuals.	Dept. of Rocha, Uruguay, to Estados Rio Grande del Sur and Santa Catarina, Brazil.	Many kinds of vegetation.	Not threatened
Montane guinea pig *Cavia tschudii*	Coarse, long pelage, crest of hair on neck. Color is grayish or brownish. Short legs, and short, unfurred ears. Head and body length 7.9–15.7 in (20–40 cm), weight 17.6–52.9 oz (500–1,500 g).	Open grasslands, forest edge, swamps, and rocky areas, sometimes at elevations up to 13,800 ft (4,200 m). Live in small groups, usually five to 10 individuals.	Peru, southern Bolivia, northwestern Argentina, and northern Chile.	Many kinds of vegetation.	Not threatened

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Rodney L. Honeycutt, PhD

Capybaras
(Hydrochaeridae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Hydrochaeridae

Thumbnail description
Large terrestrial and semi-aquatic herbivore rodent; the body is covered with coarse, reddish brown to grayish hair; underparts are lighter yellow-brown

Size
Head and body length 39.4–51.2 in (100–130 cm); shoulder height up to 19.7 in (50 cm); average weight 138.9 lb (63 kg)

Number of genera, species
1 genus; 1 species

Habitat
Lowland wetlands of forest, woodland, savanna, and open areas

Conservation status
Not threatened

Distribution
Range spans in lowlands from Panama throughout South America to Northern Argentina and Uruguay

Evolution and systematics

Capybaras of today do not differ essentially from those forms of the past. Many Pleistocene rodents, such as capybaras, have probably undergone little change in the past million years. Cenozoic fossils recovered from the Antilles island of Grenada differ from the existing capybara.

There is only one single living genus and species, *Hydrochaeris hydrochaeris*; some authors consider the smaller form of capybara living in Panama, western Colombia, and northwestern Venezuela (*H. isthmius*) as a separate species; other consider this form a subspecies, *H. h. isthmius*.

The taxonomy for this species is *Hydrochaeris hydrochaeris* (Linnaeus, 1766), Suriname. Other common names include "capivara" in Portuguese and "carpincho" and "chigüire" in Spanish.

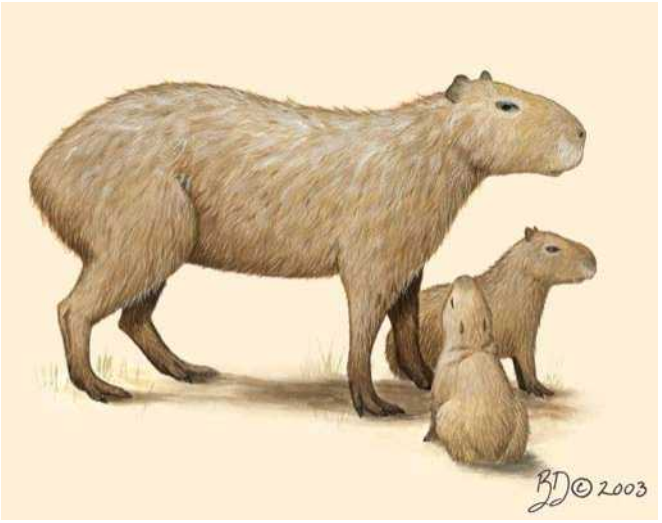
Physical characteristics

Capybaras resemble agoutis but are much larger. The head is large and broad, the ears are small and rounded, the eyes located dorsally, the neck is robust and short, not differentiating in diameter from the head. The body is covered with coarse hair that is reddish brown to grayish, and lighter yellow-brown in the underparts. The capybara is the largest living rodent, with a pig-sized pregnant female reaching 176.4 lb (80 kg) in weight; head and body length is 39.4–51.2 in (100–130 cm); shoulder height is up to 19.7 in (50 cm); and average weight is 139 lb (63 kg).

The muzzle is truncate with an enlarged upper lip and large nostrils. The forefeet have each four toes and the hind feet three, all armed with short but strong claws. Feet are partially webbed to allow swimming. The coarse pelage is so sparse that it allows one to see the animal's skin. Females have four pairs of ventral mammae.

Adult males can be identified by their black sebaceous gland, a scent gland, located on the top of the muzzle, which is used to mark with essence plants and other substrates in their territory. The tail is very short and vestigial.

As an herbivorous rodent, the teeth are distinctive; the incisor teeth are white and shallowly grooved. The third molar



Capybara (*Hydrochaeris hydrochaeris*) adult and young. (Illustration by Barbara Duperron.)

is longer than the other three molar teeth. The cheek teeth are modified and ever-growing.

Distribution

Capybaras occur in Panama, close to the Canal Zone, and on the east side of the Andes from Colombia, Venezuela, and the Guianas, throughout Brazil, Bolivia, and Paraguay, to Uruguay and northeastern Argentina. The original distribution range is wide but some local populations have been eliminated by hunting or by drastic habitat modification.

Habitat

Capybaras inhabit areas along rivers and streams, lakes, ponds, marshes, and swamps. There are at least three habitat components important for capybaras: water, grass vegetation, and a patch of forest or woodland. At least three regions are well known to harbor conspicuous concentrations of capybara populations: the llanos in Venezuela, the pantanal, mostly in western Brazil, and the Taim lowlands, in southern Brazil.

Capybaras are also abundant in the Amazonian floodplain, comprising all the countries forming the biome, but particularly Marajó Island, located at the mouth of the Amazon river.

In the pantanal of western Brazil there exist vigorous populations of capybaras. Flooding is the most important element to characterize the habitats of the pantanal. When the land dries out, grasslands and scattered pools appear. The capybara densities in these grassland fields during the dry season reach spectacular numbers due to the provision of feeding and reproductive habitats. During the floods, the capybara groups subdivide and are largely confined to the woodland and forest patches.

Capybaras are able to take advantage of modified habitats to increase their populations. They rapidly colonize areas surrounding artificial lakes formed by dams. They also explore habitats that may offer food, even with some degree of pollution, such as the Tietê River in the city of São Paulo. Sometimes they cause damage to plantations of corn, rice, manioc, and legumes, and may be hunted for that reason.

Behavior

Capybaras are social animals, usually living in family groups composed adult males, adult females, and young. Mean group size is six animals, but they exhibit variation in size during the year. In the pantanal, for example, the group size increases from the beginning of the year (rainy season) to the middle of the year (dry season). Groups of eight to 12 animals are relatively common.

The group composition is usually formed by a dominant full adult male, one or two full adult submissive males, two to four or more adult females, and the others are subadults and young. The dominant male in the group exhibits aggressive and hostile behavior to keep the other males submissive. Females in the group also display a hierarchy. The social behavior reflects group sizes. They are docile, quiet, crepuscular animals but may show activities during the day, except for some rest periods in their shelters in the forest, during the hotter hours of the day.

Ranging behavior is variable. The home range occupied by a given social group averages 200 acres (80 ha), but may be much larger in some cases, depending on the season of the year. This home range contains foraging area, patch of woodland or forest where the group rests and reproduces, and water where the animals swim. Neighboring groups may share parts of their home ranges, but maintain some core areas within these home ranges that are for the exclusive use of the group. In flooded areas, groups have larger ranges and core areas during the dry season than during the rainy and flooding season, a change that is associated with the reduction of

A capybara (*Hydrochaeris hydrochaeris*) with a bird sitting on its back in Pantanal, Brazil. (Photo by Animals Animals ©Fabio Colombini. Reproduced by permission.)

A capybara (*Hydrochaeris hydrochaeris*) mother, followed by her young. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

the feeding grassland habitat. During the dry season, larger groups are seeing feeding on the grassland seasonal fields. During the flooding season, the groups split into smaller groups, and disperse among the patches of the forest or woodland, using more of the water habitats of ponds or inundated areas.

Capybara groups in the wild have been observed displaying three different activities: foraging on grasses, sleeping or resting, and exhibiting social interactions. They display distinctive postures, movements, sounds, and activity patterns:

- Alert. The capybara remains immobile on its four feet or sitting, staying in whatever position it happens to be in at the time of the stimulus. The animal keeps its head raised, looking in one direction, with the ears erect. If an intruder continues to approach, the capybara barks like a dog, jumping into the water or running away.
- Grazing. The capybara grazes, moving slowly while foraging, sometimes raising its head to check its surroundings.
- Lying. Usually the animal lies down with its head erect while resting.
- Sleeping. The animal sleeps intermittently during the daylight hours and evening in wooded areas.
- Sitting. This is also a resting posture, common on the river banks.
- Swimming. Capybaras are good swimmers and divers.
- Intimidating. One dominant male or female circles an intruder or submissive capybara in order to impose its dominance or to ward off an approach.
- Fighting. Two animals in an upright position embrace each other and engage in a fight or a male and female exhibit courtship.
- Contacting. During the encounter between two animals one may actively initiate contact, either sexual or antagonistic. The male may inspect the sexual receptivity of a female by nasal-genital contact.
- Mounting. The female swims back and forth in the water, pursued by the male, and when she displays a receptive position, the male mounts.
- Maternal care. Involves nursing with a mother and her young.

A capybara (*Hydrochaeris hydrochaeris*) with young in the floodplain of Brazil. (Photo by Harald Schütz. Reproduced by permission.)

Capybaras (*Hydrochaeris hydrochaeris*) live in large groups. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

- Marking. The male rubs his snout gland up and down a stalk, or the animal straddles a stalk in order to rub it with its anal scent gland.

Male to male aggressive interaction is the most common display seen in the field. Subadults of either sex are always subordinate to adults of either sex. The dominant male of the group initiates the attack. Some subadults suffering attacks are excluded from the group and become satellite animals. These animals suffer stress and are subject to being weak, sick, and killed by predators.

The males compete more strongly for access to breeding partners than do females; a female's reproductive success depends on her ability to acquire food. The females spend a great deal of their time caring for young of different ages, who move from one female to another. The females suckle young in a crèche-behavior fashion.

Feeding ecology and diet

Capybaras invest a great deal of their time in feeding behavior. In Brazil, the states of Minas Gerais and Goiás are separated by a river. People living in two small villages, of the river, are rivals. The villagers on the Minas Gerais border, where there are grassland fields, say that Goiás is so bad that capybaras prefer to feed on their side. The villagers in Goiás claim that Minas Gerais may have some good food but Goiás is a nicer place to live, since the capybaras cross the river to sleep there.

A capybara (*Hydrochaeris hydrochaeris*) mother nursing her young. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

Apart from the beliefs of human rivals, capybara ranging behavior is based on a daily need for food and shelter. The Portuguese priest José de Anchieta, traveling through Brazil in 1560, wrote about the animals named by indigenous people as "capivaras," which means "herb feeders." Another Portuguese explorer, Fernão Cardim, wrote in 1584, about the "water pigs" known as capivaras that eat herbs and fruits found along the rivers.

Capybaras are very selective in food items they prefer. The diet composition varies from the dry season, when more pasture is available, to the flooding season, when they can feed upon floating plants. Preferred food items, such as protein rich grasses, tend to be more seasonal than poorer food items. During the dry season, natural pasture in lower areas is abundant and is preferred by capybaras. Capybaras may re-ingest their own fresh feces (coprophagy) in order to maximize the absorption of nutrients.

Young are precocious, travel on the back of their parents when they swim, forage on grasses with few days of age, and suckle their mother or other lactating female in their social group.

Reproductive biology

Depending on the quality of the habitat, capybaras breed throughout the year, presenting a peak of reproduction when more feeding grounds are available. Copulation usually occurs in the water. The forest and woodland provide shelter from midday heat and a resting place, as well as a birth place. The gestation period is about 147 days and it is possible that this length may be influenced by environmental and social variables. Litter size is one to seven, averaging 3.5 neonates,

Capybaras (*Hydrochaeris hydrochaeris*) grazing on aquatic vegetation. (Photo by Erwin and Peggy Bauer. Bruce Coleman, Inc. Reproduced by permission.)

The capybara (*Hydrochaeris hydrochaeris*) forages using its incisors to cut the grass above the root. (Photo by Christian Grzimek/OKAPIA/ Photo Researchers, Inc. Reproduced by permission.)

each weighing about 3 lb (1,400 g). Lactation period is about 10 weeks. However, at certain times of year, it is possible to observe a female with 10 or more young of different ages and sizes. It is believed that the group of young are relatives, and one lactating female takes turns caring her own young and those of her sister or relative. The sex ratio for the population in the field averages one male to three females. At birth, the sex ratio averages one male to one female, but due to the social structure, this relation changes. As soon as the subadults begin to attain sexual maturity, some are excluded from the group, mainly males, by the dominant males. These excluded subadults become satellite or solitary individuals. Under stress, these animals are susceptible to diseases.

Before capybaras die, their bodily appearance declines visibly. A sick individual is often isolated from the group. In addition, capybaras are preferred prey for jaguars and young are captured by anacondas and other predators.

The capybara (*Hydrochaeris hydrochaeris*) is the largest rodent. (Photo by M. Wendler/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)

Conservation status

Capybaras are common animals distributed over a wide range. Thus, they are not considered threatened, although in many places they, have been extirpated due to human influence, mainly hunting. They are very tolerant of habitat modification and, when that change benefits the offering of food and reproduction niches, the population increases, if they are not otherwise disturbed.

Significance to humans

The first Portuguese explorers traveling through Brazil in the sixteenth century reported that they learned from the local indigenous people that capybara meat was consumed and considered beef or sometimes fish. In fact, in the llanos of Venezuela, people eat capybara meat during Lent, in place of fish, as a religious and cultural tradition. Throughout the Amazon basin, capybara is consumed by local people as a real meat, since people living along the rivers consume fish daily and sometimes appreciate a different kind of meat.

There is a growing interest in the management of capybaras to commercially exploit their meat and skin (the leather is valuable). In some countries such as Venezuela and Brazil two options for exploitation were identified: management in natural areas and raising or farming in enclosures.

In wild populations of higher densities in good habitats, such as the llanos of Venezuela, it is possible to establish a harvest quota, based on the fact that part of the population would disappear due to disease and predation. Harvest quotas could be increased through the implementation of programs to control mortality caused by diseases. The predation in ranches is low and the capybara population can increase in number. The construction of ponds and the offer of food

can also increase population levels for management and sustainable use.

There are some authorized farming structures to raise capybaras in Brazil. However, the final cost of the meat is still higher than the traditional beef.

Some health researchers, working with free ranging capybaras that reached the plazas in the city of Campinas, Brazil, by traveling through small creeks, discovered that the animals can pose a potential threat to humans. The ectoparasites they carry with them into the city, mainly ticks, could potentially transmit bacterial or viral diseases to humans.

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Cleber J. R. Alho, PhD

Agoutis
(Dasyproctidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Dasyproctidae

Thumbnail description
Rabbit-sized, large-headed, short-eared, long-legged forest rodent with glossy fur and hind legs conspicuously longer than front legs, giving a "dragster-like" appearance when moving

Size
Dasyprocta: Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg); *Myoprocta*: Head and body length, 12.6–14.9 in (32–38 cm); tail, 1.8–2.75 in (4.5–7 cm); weight, 1.3–2.8 lb (0.6–1.3 kg)

Number of genera, species
2 genera; 13 species

Habitat
Rainforest, secondary forest, scrub, cultivated areas and parks; to 6,560 ft (2,000 m)

Conservation status
Endangered: 2 species; Lower Risk/Near Threatened: 1 species; Vulnerable: 1 species; Data Deficient: 3 species

Distribution
Central and South America

Evolution and systematics

Fossils are known that date from the Oligocene of South America. The family Dasyproctidae belongs to the superfamily Caviomorph of the suborder Hystricognathi. Caviomorphs probably evolved in Africa, and (along with cebid primates) crossed a then much-narrower Atlantic to South America in the late Eocene, where they diversified greatly. Many attained great size and occupied a number of ecological roles. Modern caviomorph diversity is but an echo of this. Of the two genera in the Dasyproctidae, the acouchis are considered to be the more primitive; they are smaller, have a longer tail, and exhibit simpler foraging patterns and social structure. The genus *Dasyprocta* has speciated widely in South America. In addition to the forest species, there are species in the open savanna-like habitat of the cerrado (*D. azarae*) and scrubby dry caatinga (*D. prymnolopha*).

Physical characteristics

These are glossy-furred, big-headed, rabbit-sized rodents with chunky bodies on long delicate legs. A prominent nose and whiskers, large eyes, and small ears perch high on the head. The tail is either a tiny nub and barely visible (*Dasyprocta*) or it is longer and readily visible (*Myoprocta*). Color is highly variable over the extensive ranges of the two genera; even within species, color variation can also be quite extensive. They are best distinguished from the larger and closely related pacas (Agoutidae) by the absence of prominent patterns of spots and stripes on the flanks. The scientific name is derived from the Greek *dasus*, meaning "hairy," and *proktos*, meaning "rump." Agoutis not only have hair on their rumps, but it is especially long hair.

Distribution

Agoutis range from southern Mexico to northern Argentina and Paraguay.

Habitat

Agoutis are associated with primary and secondary forest and scrub. They require some dense vegetation for cover, but often prefer open areas for foraging. Highly adaptable, agoutis are often associated with water, and they frequently display a distinct preference for using stream banks to make burrows.

The brown agouti (*Dasyprocta variegata*) mates for life. (Photo by © Steve Kaufman/Corbis. Reproduced by permission.)

A green acouchi (*Myoprocta acouchy*) nursing its young in Costa Rica. (Photo by Mark Newman. Bruce Coleman, Inc. Reproduced by permission.)

Behavior

Agoutis are ground living and day active, unless heavily hunted. Their home range will often include several sleeping spots, often inside fallen hollow logs or under tree roots. These spots are so well used that well-beaten paths will radiate out from them into the forest, linking favored foraging and resting sites. A favorite food of jaguar and other large forest carnivores, agoutis and acouchis have many behaviors aimed at predator avoidance. They will freeze in mid-stride if threatened. If threats continue, they will run quickly through the forest, their passage assisted by their cone-shaped body form. When resting, they will sit in an erect body posture with feet and ankles flat on the ground, ready to dart away if danger is sensed. From a standing position, they are able to leap over 6.5 ft (2 m) into the air.

Feeding ecology and diet

Agoutis eat primarily fallen fruit, but their diet also includes insects and shoots. They collect and store seeds and fruit, rarely eating those that have freshly fallen, preferring those in their various scattered and perpetually replenished larders. Some of their stores are forgotten, so agoutis and

An agouti (*Dasyprocta* sp.) female, foraging. (Photo by Animals Animals ©Nigel J. H. Smith. Reproduced by permission.)

A central American agouti (*Dasyprocta punctata*) near its burrow in Costa Rica. (Photo by Animals Animals ©J. & C. Sohns. Reproduced by permission.)

A female red-rumped agouti (*Dasyprocta leporina*) with her young. (Photo by Rod Williams/WILLO. Bruce Coleman, Inc. Reproduced by permission.)

achouchis are important dispersers of rainforest seeds. Burying the seeds not only reduces insect predation, but also provides the seeds with a better chance of establishing a good root system while germinating, thus reducing vulnerability to the stress of drought. Species such as *Hymenaea courbaril* originally evolved to be dispersed by large mammals (such as gompotheres) that went extinct in the Pleistocene. Agoutis are now the major disperser and *Hymenaea* germination rates are very low in areas in which agoutis have been hunted out. Some agouti seed larders are raided by other animals, including peccaries, coatis, and spiny rats. Food is generally eaten while the animal sits on its haunches and holds the food in its hands. This dexterity allows the rodent to manipulate the seed or fruit until the weakest spot is discovered; manipulation then ensures that this area remains under dental attack until the defensive walls are breached. In this way the agouti (and acouchi to a lesser extent) can break open and eat the contents of such hard fruits as the Brazil nut (*Bertholecia excelsa*).

Reproductive biology

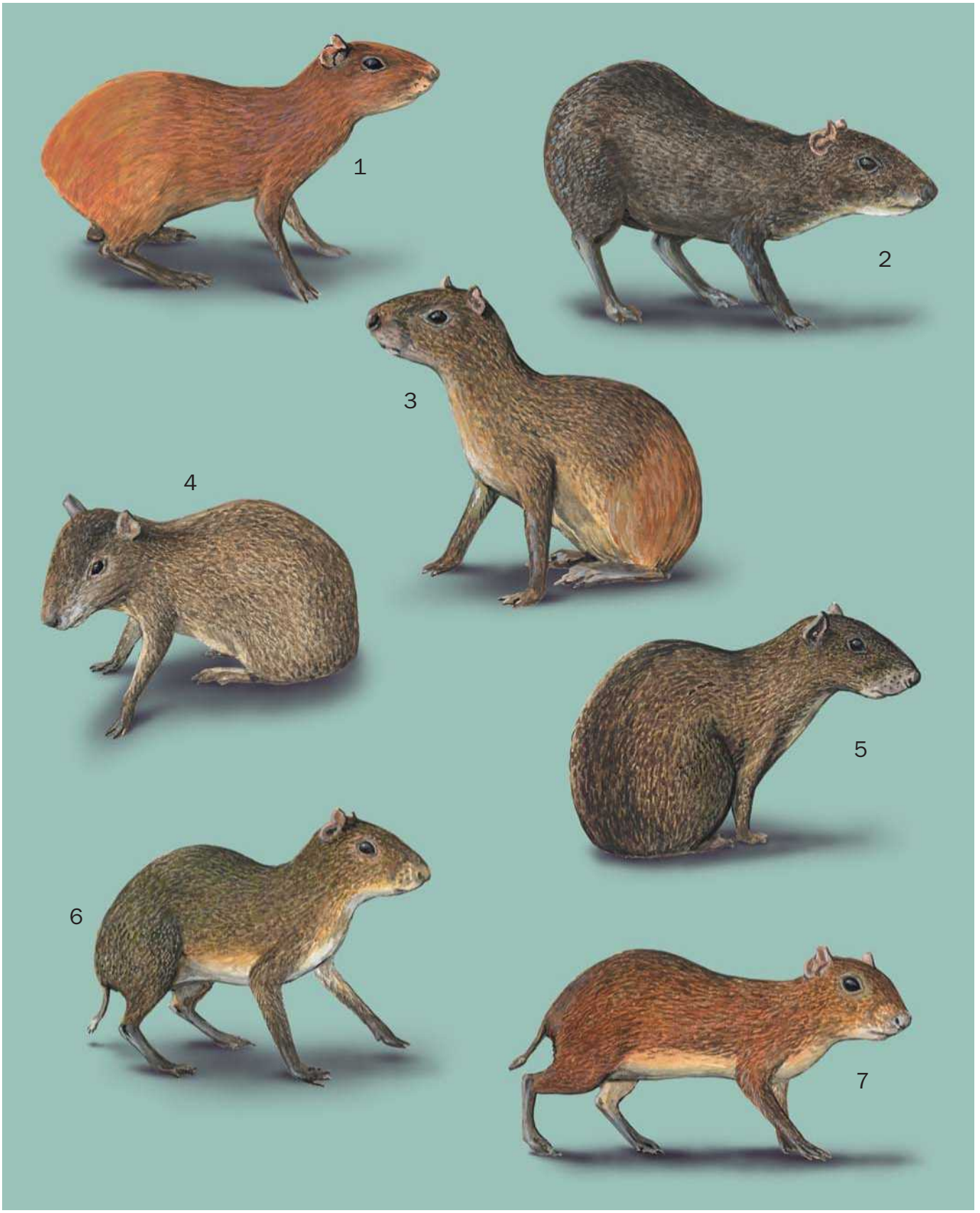
Agoutis are capable of breeding throughout the year, whenever conditions (especially availability of fallen fruit) are favorable. The basic social unit is the mated pair; the pair bond lasts for life. Reproduction may occur twice a year, if food supplies permit. Unlike the familiar rats, mice, and hamsters, these rodents have small litters of large young in which they invest a great deal of time and parental care. The litter size is generally one or two, with occasional records of three and (very rarely) four. Lactation lasts for around 20 weeks. However, because of the high risk of predation, the young are precocial, being born fully furred, with open and functioning eyes and ears. They are well coordinated and able to run within an hour of birth. Gestation varies between 104 and 120 days. The estrous cycle is around 34 days.

Conservation status

The IUCN lists *D. ruatanica* and *D. coibae* as Endangered, *D. azarae* as Vulnerable, *D. mexicana* as Lower Risk/Near Threatened, and *D. cristata*, *D. kalinowskii*, and *M. exilis* as Data Deficient. The remaining species are not currently threatened.

Significance to humans

Agoutis are often heavily hunted and may constitute a regional mainstay for local hunters. They are a very important disperser of the seeds of rainforest trees.



1. Roatán Island agouti (*Dasyprocta ruatanica*); 2. Mexican black agouti (*Dasyprocta mexicana*); 3. Red-rumped agouti (*Dasyprocta leporina*); 4. Coiba Island agouti (*Dasyprocta coibae*); 5. Central American agouti (*Dasyprocta punctata*); 6. Green acouchi (*Myoprocta acouchy*); 7. Red acouchi (*Myoprocta exilis*). (Illustration by Brian Cressman)

Species accounts

Central American agouti
Dasyprocta punctata

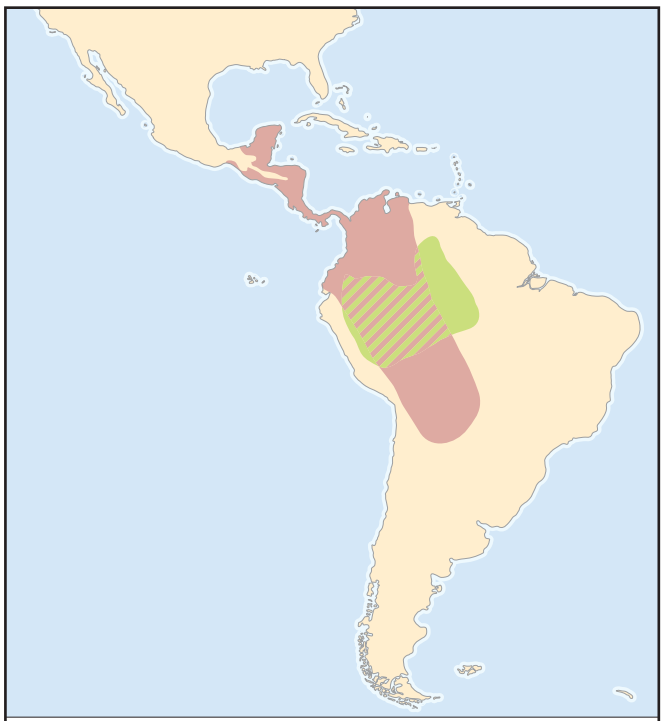
TAXONOMY
Dasyprocta punctata Gray, 1842, Realajo, Nicaragua.

OTHER COMMON NAMES
English: Indian rabbit; Spanish: Guatusa, guaqueque alazan, neque.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg). Body color variable, leading to a plethora of subspecific names (11 in Central America alone). Body color varies from yellowish or orange, finely grizzled with black, to that of populations on the Atlantic slope of Costa Rica and Panama that have dark brown foreparts, orange mid-back, and a cream rump.

DISTRIBUTION
From Chiapas and Tabasco States, Mexico, south through Central America to southern Bolivia and northern Argentina.

HABITAT
Primary and secondary rainforest, at densities varying from one per 2.5 acres (1 ha) to one every 25 acres (10 ha). Also occurs in parks and gardens wherever there is sufficient food and cover.



BEHAVIOR
Each mated pair holds a territory of 2.5–5 acres (1–2 ha). They stay together for life, but rarely forage together. Tolerant of other pairs if there is abundant food, the male will (in the dry season) aggressively defend the area against incursion, especially by other agoutis. During aggressive interactions, rival males may erect the long hairs covering the rump to form a fan-shaped crest, and thump the ground with their hind feet. There are a number of vocalizations, including a doglike bark, made when fleeing from danger. They make burrows in riverbanks and link them, along with temporary sleeping spots in hollow logs, with a series of paths.

FEEDING ECOLOGY AND DIET
Fruits are the main dietary staple, but they also eat freshwater crabs, fungi, and insects. They have been shown to be important dispersers for *Virola nobilis* (Myrisicaceae), a rainforest-canopy giant that is primarily dispersed by birds and monkeys. The agoutis act as secondary dispersers, foraging seeds from dung piles of the primary dispersers and dispersing them a second time when they deposit them in their food stashes.

REPRODUCTIVE BIOLOGY
The social unit consists of a life-mated pair. Reproduction may occur once or twice a year. Courtship is initiated when the male sprays the female with urine, causing her to go into a "frenzy dance." After several interactions of spraying and dancing, the female permits the male to advance and mate. The young are raised in small nest holes, the entrance to which is too small to permit the ingress of most predators. The mother calls the young out twice a day to suckle. Young grow quickly and move through a succession of larger resting chambers. Weaning occurs at around five months. Soon afterwards, the newly aggressive parents drive off the current offspring. This may either announce the impending arrival of a new litter or of unfavorable conditions. Post-weaning mortality can reach 70%, with deaths being mainly due to starvation and predation by male coatis (*Nasua*).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Heavily hunted. Important source of meat in rural areas. ◆

Red-rumped agouti
Dasyprocta leporina

TAXONOMY
Dasyprocta leporina (Linnaeus, 1758), Peninka, Suriname. Also known as *Dasyprocta aguti*.

OTHER COMMON NAMES
English: Brazilian agouti, orange-rumped agouti; Spanish: Acure, picure.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg). Head, shoulders,

forelegs, and mid-back are a greenish brown; the rump is a dark red to bright fire orange (this may not be visible unless the rump hairs are erect). There is sometimes a crest of longer black hairs between the shoulders and up to the top of the head. The belly varies from shades of muddy to pure orange, sometimes with a white midline. Populations on Caribbean islands tend to be smaller than those on the mainland and are less colorful, being dark brown with long chocolate-colored hairs forming a "cape" over the shoulders.

DISTRIBUTION
Found in northeastern South America, ranging from northeastern Venezuela and the Guianas, south to south-central Brazil. They are also in the eastern Amazon basin. They also occur on the Lesser Antilles (Bermuda, Grenada, and Barbados), and in Trinidad and Tobago. They have been introduced onto the Virgin Islands.

HABITAT
Occur in primary and secondary forest growth. This species has a preference for areas with dense undergrowth and so is frequently found in natural clearings like tree falls and along riverbanks.

BEHAVIOR
Monogamous pairs travel together and are most active in the early morning and later afternoon. They may also be active on bright moonlit nights.

FEEDING ECOLOGY AND DIET
Nuts are buried in seasons of plenty against times of scarcity. Although the agouti's spatial memory is good, some seeds get overlooked. These, buried in the ground, grow to replenish the forest; the agouti is an important disperser of forest tree seeds.

REPRODUCTIVE BIOLOGY
One individual lived nearly 18 years in captivity.

CONSERVATION STATUS
Not threateed.

SIGNIFICANCE TO HUMANS
Heavily hunted. An important source of meat in rural areas. ◆

Roatán Island agouti
Dasyprocta ruatanica

TAXONOMY
Dasyprocta ruatanica Thomas, 1901, Roatán Island, 40 mi (64 km) off the coast of northern Honduras.

OTHER COMMON NAMES
French: Agouti de l'Ile de Ruatan.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg). A classic case of island dwarfism. This species is like a small *Dasyprocta punctata*, the ancestral mainland species from which it is thought to be descended. The body appears brown with each hair having alternating black and yellow rings. Undersurface is a lighter brown, with a white spot on the chin and a yellow patch in the middle of the belly.

DISTRIBUTION
Only on Roatán Island, Honduras.

HABITAT
Occurs mainly in forest and vegetation heavily disturbed by humans.

BEHAVIOR
Agoutis are diurnal and wary of humans. They have been observed to use bamboo patches for sleeping. They are attracted to bat roosts, under which they feed on dropped fruits. Recorded as spending 23% of time sitting and 22% feeding; walking, sniffing, and digging (unearthing or burying nuts or excavating burrows) occupied 29% of their time. Socially interactive muzzling reported as a frequent interaction in the island's dense agouti population. Scent marking with anal glands also observed. In aggressive interactions one animal will flee with rump hairs erect. No territorial behavior was observed, but food was abundant and supplemented by local people.

FEEDING ECOLOGY AND DIET
They are known to eat coconuts, hibiscus flowers (both introduced), and pods of indigenous leguminaceous trees. They also eat rice, oranges, and corn.

REPRODUCTIVE BIOLOGY
This has not been studied in detail. Mothers have been observed being followed by single young in March. All females rebutted attempts of young to nurse, suggesting some breeding synchronicity. Young were seen experimentally sampling foodstuffs.

CONSERVATION STATUS
Endangered. They are thought to have declined by 50% between 1985 and 1995.

SIGNIFICANCE TO HUMANS
They are hunted by local people. Their habitat is threatened by resort and hotel development. Resort management wishes to protect the agouti as an ecotourism attraction, but the habitat fragmentation the hotels have caused may destabilize the populations. The Honduran government is making strong efforts to protect the area. ◆

Coiba Island agouti
Dasyprocta coibae

TAXONOMY
Dasyprocta coibae Thomas, 1902, Coiba Island, off southwestern Panama.

OTHER COMMON NAMES
French: Agouti de l'Ile de Coiba.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg). The fur is a coarsely grizzled brown. Rump hairs are orange tipped, but not as conspicuously elongated as in mainland populations of *D. punctata*, from which it is presumably descendant. The body size is like that of *D. punctata*, but the tail is much longer than usual (to 1.18 in [3 cm]). The belly and throat are yellowish.

DISTRIBUTION
Coiba Island, Panama.

HABITAT
Occurs in deciduous seasonally dry forest.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Endangered. It is restricted to a very small area of declining habitat.

SIGNIFICANCE TO HUMANS
Not known. ◆

Mexican black agouti
Dasyprocta mexicana

TAXONOMY
Dasyprocta mexicana Saussure, 1860, Veracruz, Mexico.

OTHER COMMON NAMES
Spanish: Serete, guaqueque negro.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–25.2 in (32–64 cm); tail, 0.4–2.75 in (1–7 cm); weight, 1.3–8.8 lb (0.6–4 kg). This species is characterized by black body fur. Under parts are grayish or olive; there are long black hairs on the rump, and the eyes are ringed with conspicuous patches of naked pink skin. Pink skin also shows up at the base of the ears, contrast with the black fur and black pigmented ears.

DISTRIBUTION
Occurs only in a small area of southeast Mexico in Veracruz, north Oaxaca, northwest Chiapas, and west Tabasco states.

HABITAT
Lives in evergreen forests and secondary growth, from lowlands to 1,970 ft (600 m).

BEHAVIOR
Mostly diurnal. Mated pairs occupy territories of 2.5–5 acres (1–2 ha) in extent.

FEEDING ECOLOGY AND DIET
Known to eat fruit.

REPRODUCTIVE BIOLOGY
Two precocial young are born during the dry season.

CONSERVATION STATUS
Lower Risk/Near Threatened; was probably never common in its restricted range.

SIGNIFICANCE TO HUMANS
Hunted for food; it is also considered an agricultural pest. ◆

Red acouchi
Myoprocta exilis

TAXONOMY
Myoprocta exilis (Erxleben, 1777).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Weight is 2.2–3 lb (1–1.4 kg); shoulder height is 6.7–7.9 in (17–20 cm). Smaller than adult agoutis, but has a significantly longer tail. The eyes and ears are large compared to those of agoutis. They are often beautifully marked. The fur is coarse, stiff, and shiny. The upper parts are reddish, and the belly and throat are brownish or orange. The cheeks and muzzle are often yellow or orange. The tail is white underneath.

DISTRIBUTION
Found in northern South America, in two isolated populations: one in the east of the Amazon basin and the second in the foothills of the Colombian Andes. It is also found east to the Uaupes river basin.

HABITAT
Found in primary forest and avoids disturbed areas. It favors areas of dense vegetation such as natural tree-falls and areas dense with vines. It avoids swampy ground.

BEHAVIOR
Diurnal, its activity starting at sunrise and tailing off until a second peak in the declining hours of daylight. Lactating females have four periods of activity, each separated by resting periods of three to four hours. Nocturnal activity is rare and normally due to disturbance by a perceived threat. It uses hollow logs as refuges during the day. It holds its tail erect to show white underside. When frightened, it will skip away, giving birdlike whistles. It does not use established paths through its territory, preferring to push through dense vegetation. Up to seven acouchis will share a territory, with females using dense vegetation more often than males. Individuals rarely travel together unless it is a female with dependant young. Group territories are not continuous.

FEEDING ECOLOGY AND DIET
An important agent of seed predation and dispersal in primary rainforests; it is known to cache seeds under leaf litter. Utilizes the seeds of the palm *Astrocaryum paramaca*. Such seeds are large and are cached individually. Other smaller seeds may be cached in groups. It is highly dependant on caches in the dry season.

REPRODUCTIVE BIOLOGY
The litter size is usually two. In juveniles, males are more numerous than females. By adulthood, this has dropped to 1:1, reflecting the greater predation rates on young males who disperse farther than females. Mating system is not known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for its meat in rural areas. ◆

Green acouchi
Myoprocta acouchy

TAXONOMY
Myoprocta acouchy (Erxleben, 1777), French Cayenne, Guiana.

OTHER COMMON NAMES
Spanish: Chachure, oatiara, curi, tintin, guatusa, papali, punchana.

PHYSICAL CHARACTERISTICS
Head and body length, 12.6–14.9 in (32–38 cm); tail, 1.8–2.75 in (4.5–7 cm); weight, 1.3–2.8 lb (0.6–1.3 kg). The back and flanks are greenish or blackish, with reddish or orange on the throat, cheeks, and muzzle, and the belly and inner surface of the legs are generally yellow or white. The rump hairs have distinct bands of contrasting colors. The underside of the tail is prominently covered in short white hairs that contrast with the body colors.

DISTRIBUTION
Found in northern South America, east of the Andes, and in the western part of the Amazon basin.

HABITAT
Lives in primary lowland forest, proximity to water preferred. It is not found in disturbed and open areas.

BEHAVIOR
Similar to red acouchi.

FEEDING ECOLOGY AND DIET
Similar to red acouchi.

REPRODUCTIVE BIOLOGY
The estrous cycle is 42 days and the gestation period is around 99 days. The litter size is two (exceptionally three), each of which weighs approximately 3.5 oz (100 g) at birth and is fully furred and is born with open eyes. The female has four pairs of mammae. Time to wean can be as short as 14 days. In both sexes puberty is reached in eight to12 months. Has lived more than 10 years in captivity. Mating system is not known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for meat. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Black agouti *Dasyprocta fuliginosa*	Fur is coarse, glossy, longest, and thickest on posterior of back. Color ranges from pale orange to brown to almost black. Underparts are white, yellow, or buff. Body is slender, ears are short. Head and body length 16–24 in (41.5–62 cm), tail length 0.39–1.4 in (1–3.5 cm), weight 2.2–8.8 lb (1–4 kg).	Forests, thick brush, savannas, and cultivated areas. Diurnal, terrestrial, breeds throughout the year.	Colombia, southern Venezuela, Suriname, northern Brazil, and Peru.	Fruits, vegetables, and various succulent plants.	Not listed by IUCN
Kalinowski's agouti *Dasyprocta kalinowskii*	Upperparts range from pale orange to brown to black. Underparts are white, yellow, or buff. Slight stripes may be present. Slender body, short ears. Head and body length 16–24 in (41.5–62 cm), tail length 0.39–1.4 in (13–3.5 cm).	Forests, thick brush, savannas, and cultivated areas. Constructs burrows among limestone boulders, along riverbanks, or under the roots of trees. Diurnal.	Southeastern Peru.	Mainly fruits.	Data Deficient
Crested agouti *Dasyprocta cristata*	Upperparts range from pale orange to brown to black. Underparts are white, yellow, or buff. Slight stripes may be present. Slender body, short ears. Head and body length 16–24 in (41.5–62 cm), tail length 0.39–1.4 in (1–3.5 cm).	Forests, thick brush, savannas, and cultivated areas. Constructs burrows among limestone boulders, along riverbanks, or under the roots of trees. Diurnal.	Guianas.	Mainly fruits.	Data Deficient
Orinoco agouti *Dasyprocta guamara*	Upperparts range from pale orange to brown to black. Underparts are white, yellow, or buff. Slight stripes may be present. Slender body, short ears. Head and body length 16–24 in (41.5–62 cm), tail length 0.39–1.4 in (1–3.5 cm).	Forests, thick brush, savannas, and cultivated areas. Constructs burrows among limestone boulders, along riverbanks, or under the roots of trees. Diurnal.	Orinoco Delta, Venezuela.	Mainly fruits.	Not threatened
Black-rumped agouti *Dasyprocta prymnolopha*	Upperparts are dark red to shining orange Ears are pale yellow, bases are orange. Crown, neck, and parts of back are blackish. Eyes are large. Head and body length 19.3–26 in (49.2–65.2 cm).	By streams, rivers, or marshy areas. Diurnal, terrestrial, lives in pairs.	Northeastern Brazil.	Fruits, nuts, and seeds.	Not threatened
Azara's agouti *Dasyprocta azarae*	Upperparts range from pale orange to brown to black. Underparts are white, yellow, or buff. Slight stripes may be present. Slender body, short ears. Head and body length 16–24 in (41.5–62 cm), tail length 0.39–1.4 in (1–3.5 cm).	Rainforests and chaco habitats. Constructs burrows among limestone boulders, along riverbanks, or under the roots of trees. Diurnal.	East-central and southern Brazil, Paraguay, and north-eastern Argentina.	Fruits, nuts, and seeds.	Vulnerable

Resources

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Adrian A. Barnett, PhD

Pacas
(Agoutidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Agoutidae

Thumbnail description
Like a giant guinea pig, it is a large square-headed rodent, with small ears, almost no visible tail, and a pattern of white spots and stripes on its flanks

Size
Head and body length, 20–30.5 in (50–77.4 cm); tail, 5–9 in (13–23 cm); weight, 13.2–31 lb (6–14 kg)

Number of genera, species
1 genus; 2 species

Habitat
Forests and semi-open areas

Conservation status
Lower Risk/Near Threatened: 1 species

Distribution
Central and South America

Evolution and systematics

Fossils exist from the Pleistocene of Brazil. The two species are well defined and occur at different altitudes (though they do overlap in altitudinal range and are not always easy to distinguish under field conditions). Part of an ancient rodent family with its origins in South America, pacas are one of the few mammal species that successfully moved north after North and South America became connected by the central American isthmus. Possessing a cone-shaped body, hind limbs longer than the forelimbs, and a diet devoted largely to fruit, pacas show a remarkable convergence with the chevrotain (*Hyemoschus aquaticus*), a deer-like ungulate of the West African rainforests. Like the paca, the chevrotains also have a pattern of strong horizontal bars and blotches along its flanks. Pacas were formerly grouped with the agoutis in the family Dasyproctidae, under the subfamily Agoutinae, but were eventually given full family status because they differed from agoutis in the number of toes on the feet, the shape of the skull, and the patterning of the fur. The family name Cuniculidae was formerly used instead of Agoutidae.

The name paca comes directly from the Tupi indigenous language, as does the word agouti. The fact that the genus name for this animal is the common English name for another, quite similar-looking animal shows why it is a good idea to have the Linnean naming system as a final arbiter for whichever animal is being talking about.

Physical characteristics

The third and fourth largest living rodents, both paca species have a heavy and robust appearance. The flanks are characteristically patterned with four to seven horizontal lines of pale blotches and stripes. The ears are small and set high on the square-looking head. The legs are long and, though sturdy, appear almost too dainty for such a chunky animal. There are four toes on the forefoot and five on the hind (two of which are short and rarely touch the ground). Both are adapted to swift movement with toes that are broad, down-pointing, and powerful, and stout nails that resemble small hooves. In body form, the paca closely resembles a small forest deer. The streamlined cone-shaped body form allows swift passage through dense vegetation. The skin of young pacas is covered with horny scales about 0.08 in (2 mm) in diameter. These disappear in adults. They are thought to have a protective function against some of the smaller paca predators.

Seeing pacas in the field is difficult; there is little size difference between adults, no color differences, and all genitalia is hidden in an anal pouch.

Distribution

Pacas are found in southern and eastern Mexico to southern Brazil, but not Uruguay. Pacas are not found west of the Andes in Ecuador and Peru.

Habitat

Pacas live in rainforest, cloud forest, and some slightly more open habitats. They prefer to be near water.

Behavior

Pacas are active in the morning and late afternoon in remote areas, but strictly nocturnal in areas of high hunting pressure. They lessen their activity on moonlit nights. Good swimmers, they will try to reach water when threatened, where they may remain submerged for up to 15 minutes. Other escape mechanisms include the ability to leap up to 3.28 ft (1 m) into the air; they can also rush away from the source of disturbance and then freeze for as long as 45 minutes. Normal travel is by a series of established paths. A new route will be made if a path shows any sign of disturbance. Pacas sleep in burrows up to 9.8 ft (3 m) deep. Burrows are either a hole in the soil (often adapted from a hole originally dug by an armadillo), in hollow logs, or among rocks. They are often near water, but above the seasonal flood line. There are generally at least two entrances, which will be plugged by the paca with wads of leaves (to hinder the dispersion of their body smell and so avoid alerting their many predators, and to provide an early warning system if a predator should try to enter while the paca is asleep). Pacas make a low growling noise that is surprisingly loud for the size of the animal. The call is amplified by bony expansions on the side of the skull and by the fleshy sacs contained within them. Modified in duration and pulse pattern, this is used to indicate territorial ownership, aggression, threat, or, by the female, to call to her young. At around 1 kHz, this call is audible to humans. When threatened, pacas may grind their teeth, a noise that is also amplified by the cheek-side resonating chambers. A pair of pacas marks their mutual territory with urine. Paca densities may reach 70 adults per 0.4 mi^2 (per 0.2 km^2). Because of this high density, pacas often constitute nearly 20% of the biomass of terrestrial mammals in a forest. The number of pacas in an area is often determined by the availability of territories, the size of which is ultimately determined by the productivity of the region's soil. If they escape their numerous predators, pacas can live up to 13 years in the wild.

Feeding ecology and diet

Pacas eat fruits of understory trees and shrubs and fallen fruits of taller trees. They have also been recorded as eating leaves, buds, flowers, and fungi. Studies in Costa Rica iden-

A paca (*Agouti paca*) eating fallen fruit. (Photo by Nick Gordon/Naturepl.com. Reproduced by permission.)

The paca (*Agouti paca*) is a very good swimmer. (Photo by Frans Lanting/Minden Pictures. Reproduced by permission.)

Pacas (*Agouti paca*) will sometimes take to the water when threatened. (Photo by © Partridge/OSF/Animals Animals. Reproduced by permission.)

tified 33 plant species consumed by pacas. Pacas play a major role in seed predation and in seed dispersal. Home ranges may have an activity core that centers on a cluster of fruiting trees. This center shifts as fruit availability changes. Pacas rarely use their forepaws to manipulate fruits. Accordingly, they are unable to exploit some types of fruits that the smaller agoutis manage to penetrate through the ability to keep gnawing at a chosen spot while dexterously manipulating the fruit in their forepaws. However, pacas do have powerfully muscled jaws and strong teeth; they are even able to break open the species of the very woody hard-shelled fruits of *Shelia* palms. In addition, pacas browse on seedlings and nibble flowers. The remains of ants and caterpillars have been found in their feces and stomach contents. It is not known if these were ingested intentionally or accidentally.

The loss of pacas in Los Tuxtlas, Mexico is believed to be one of the key reasons for a two-thirds drop in plant diversity in this rainforest remnant. Unlike agoutis, pacas can store fat to see them through seasonal slumps in fruit availability. Consequently, they have less of a need to cache seeds against hard times. Ever alert for predators, pacas like to eat seeds in the darkest possible place (such as a burrow or a hollow log). Pacas disperse seeds by active transportation in their stomachs and then voiding them in their feces, and (more rarely) by forgotten caches and accidental dropping of fruits held in cheek pouches. However, they are less efficient dispersers than agoutis. Competition with agoutis is avoided by different cycles of activity and slightly different food preferences. Pacas supplement their diet with mineral-rich soil from salt licks. Like rabbits, pacas practice caecotrophy, the ingestion of specially produced fecal pellets from which they absorb protein and carbohydrates synthesized by microorganisms living in the caecum, with a second passage through the digestive system. These moist soft pellets are different from the hard dry pellets that are fully excreted, and are a way by which the animal gets an additional bonus of nutrients from their food. Caecotrophy occurs in the burrow when the paca is asleep in its characteristic posture of mouth close to the base of its tail.

Reproductive biology

Litter size is usually one (exceptionally two). Young are precocial, born furred, and with open eyes. They are able to

A paca (*Agouti paca*) stands amid fallen leaves. (Photo by © Terry Whittaker; Frank Lane Picture Agency/Corbis. Reproduced by permission.)

A paca (*Agouti paca*) in Belize. (Photo by © Partridge-Foster/Animals Animals. Reproduced by permission.)

run with the mother from an early age, and they are weaned at around six weeks but may stay with the mother for up to a year afterwards. Gestation lasts between 114–119 days. Interbirth interval is around 190 days. Females generally breed seasonally, but will bear up to three litters if conditions allow. Sexual maturity occurs at between six and 12 months, whenever the weight of females reaches 14.3 lb (6.5 kg) and males reach 16.5 lb (7.5 kg). Where two litters a year occur, the lactation period of the existing young overlaps the female's second pregnancy. Females in breeding condition will exhibit a "frisky hopping" behavior at the approach of the male. This will become more developed if he sprays her with urine. Copulation frequently takes place in water.

Pacas go to considerable effort to reduce the possibility of predation of their offspring. The young is born away from the burrow, in one of the mother's habitual sleeping spots. The morning after its birth, female leads the 22.9–25 oz (650–710 g) young to various holes in the territory. It will choose one with an entrance hole too small for such predators as coatis (*Nasua nasua*) and tayras (*Eira barbara*) to enter. The female will bring it leaves and twigs for its nest. Morning and evening, the mother, who is likewise unable to enter this natal burrow, uses a low rolling vocalization to call the young to suckle. Suckling lasts some 90 days, by which time the young paca weighs about 8.8 lb (4 kg). Before it is allowed to suckle, it must defecate and urinate, stimulated to do this when the female licks it. She ingests the resulting products to reduce the possibility of odors around the natal burrow that might attract predators. Thus, pacas have modified the familiar rodent strategy of high numbers, low individual investment into one very much like deer and most other large mammals, which use a strategy of low fecundity but high survivorship. Apart from human hunters, pacas have a large number of other predators, including jaguar, puma, ocelot, margay, jagarundi, bush dog, boa constrictor, and caiman.

Conservation status

Pacas are being exterminated as they sometimes destroy several different crops such as yams, cassava, sugar cane, and corn. They are also hunted intensively throughout their range for their meat. Their numbers are dwindling over large areas of their distribution due to the hunting and habitat destruction.

Significance to humans

Occasionally, pacas may become pests of agricultural crops. Often a mainstay for rural populations who hunt for meat, it is also a favorite in specialist restaurants. In Amazonas, paca constitutes some 8% of the meat eaten by indigenous people, and is the third most-consumed meat after tapir and peccary.

Some 70% of an adult paca's 22–31 lb (10–14 kg) is usable meat, so it is frequently an important source of meat for rural populations. Because of the fat stored in the flesh, the meat has a very high caloric value (1,620 calories per 2.2 lb [1 kg]). It often sells for a higher price than beef. Habitat fragmentation makes things worse, concentrating populations and increasing ease of access for hunters. This is true even in supposedly protected areas. Sometimes an agricultural pest, pacas eat maize, manioc, and on plantations, cocoa pods. In Costa Rica, its flesh is served on special occasions such as baptisms and weddings. Populations are locally threatened by over hunting. Pacas are important dispersers of many tree species used by humans, including *Virola surinamensis*, an important commercial timber tree. Attempts have been made to domesticate the paca for use in rural populations, as a means of increasing rural health, conserving wild paca populations, and protecting the ecosystem services they provide.

1. Mountain paca (*Agouti taczanowskii*); 2. Paca (*Agouti paca*). (Illustration by Brian Cressman)

Species accounts

Paca
Agouti paca

TAXONOMY
Agouti paca (Linnaeus, 1766), Cayenne, French Guiana. Currently, five subspecies are recognized.

OTHER COMMON NAMES
English: Gibnut; German: Tieflandpaka; Spanish: Jochi pintado, sari, borugo, guartinaja, guagua, tinaja, tepezcuintle, guanta, guardatinajas, tuza real, conejo pintado, picuru, lapa.

PHYSICAL CHARACTERISTICS
Head and body length 20–30.5 in (50–77.4 cm); tail 5–9 in (13–23 cm); weight 13–31 lb (6–14 kg). Head, back, and flanks either gray, brown, or reddish, depending on the subspecies. The fur is slick and shiny and there is no underfur. Underparts and cheeks are always pure white. Marks on the flanks may be either cream, pale grayish, or white. Whiskers prominent. The head of an adult paca is some 7–87.7 in (18–223 cm) long. Each incisor is nearly 0.2 in (5 mm) wide; no other forest-dwelling Neotropical rodent has incisors this big. To aid in escape from predators, the skin of the back of a paca is very loose and slips and tears easily over an under layer of thickened connective tissue. Wounds to such areas are reported to heal within days. Distinctively, their eyes shine a brilliant yellow when spotlit.

DISTRIBUTION
From southern Mexico to northern Argentina.

HABITAT
Primarily rainforest near streams, but also recorded from scrubby and seasonally dry habitats, mangrove swamps, gallery forests bordering streams, and tree thickets in public parks. Recorded up to 8,000 ft (2,500 m) where it overlaps with the mountain paca.

BEHAVIOR
Occurring in monogamous pairs that share a territory, but generally forage alone (although they may be seen together under an especially heavily fruiting tree). Animals may have up to four burrows within their home range. In places where food is abundant, home range size is around 8.6 acres (3.5 ha), with an activity core of some 1.5 acres (0.6 ha). Despite the use of urine and anal gland secretions as scent markers, home ranges are not exclusive and may overlap by up to 74%. Each animal may have several burrows. Males are most active in territory defense, first engaging in a contest of rumbling vocalizations and teeth chitterings. If this fails, they stand head to head and slash at each other with their large incisors. As part of their predator avoidance strategy, pacas habitually defecate in streams. Their sense of hearing and smell are acute.

FEEDING ECOLOGY AND DIET
Eat fruits of understory trees and shrubs and fallen fruits of taller trees. They have also been recorded as eating leaves, buds, flowers, and fungi.

REPRODUCTIVE BIOLOGY
Litter size is usually one (exceptionally two). Young are precocial, born furred, and with open eyes. They are able to run with the mother from an early age, and they are weaned at around six weeks, but may stay with the mother for up to a year afterwards. Gestation lasts 114–119 days. Inter-birth interval is around 190 days. Females generally breed seasonally, but will bear up to three litters if conditions allow.

CONSERVATION STATUS
Listed on CITES III (Honduras). Not threatened according to the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally, they may become pests of agricultural crops. Often a mainstay for rural populations that hunt for meat, they are kept under the house in rural areas of Belize and Mexico and fed on kitchen scraps. Gibnut meat was served to Queen Elizabeth II during her visit to Belize in 1985. ◆

Mountain paca
Agouti taczanowskii

TAXONOMY
Agouti taczanowskii (Stolzmann, 1865), Andean Ecuador.

OTHER COMMON NAMES
French: Pace de Montagne; German: Berkpaka; Spanish: Guagua negra, tinajo, sachacuy, picure de montana, lapa andina.

PHYSICAL CHARACTERISTICS
Smaller than the lowland *A. paca*, with reddish brown fur that is shorter, denser, and softer. There is a dense undercoat for insulation. Combined this gives the impression of a thicker, woollier animal with fluffier fur. The face is less broad, with a longer snout, smaller eyes and thinner claws. There is some spotting on the back as well as on the flanks. The throat and belly are generally cream colored.

DISTRIBUTION
Andean cordilleras of Venezuela, Colombia, Ecuador, and northern Peru.

HABITAT
High cloud forest and into the tree less paramo grasslands. In Venezuela, the maximum abundance occurs between 6,560 and 10,000 ft (2,000–3,050 m).

BEHAVIOR
This species is much less well known than its lowland relative. Prefers to den in forest with a dense cover of *Blechnum* ferns. Males recorded as making loud aggressive noises out of all apparent proportion to their size.

FEEDING ECOLOGY AND DIET
Known to eat 48 different species of plants. Eats more leaves and fungi than does *A. paca*.

REPRODUCTIVE BIOLOGY
Gestation time 165 days. Sexual maturity reached in 12–15 months. Litter size is one.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
Not as extensively exploited for food as the lowland paca, but hunting does occur. The species is also threatened by habitat destruction and forest fragmentation. Considered nationally At risk in Venezuela where its hunting is prohibited, though this still continues even in national parks such as Guaramacal. Hunting only with permit in Colombia, where it is considered to be a species of Lower Risk. ◆

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Adrian A. Barnett, PhD

Tuco-tucos
(Ctenomyidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Ctenomyidae

Thumbnail description
Small- to medium-sized herbivores, big head, strong and big incisors, reduced ears, heavily built body, medium tail, powerful nails with supraungual comb-like hairs

Size
Body length 8.6–16.9 in (22–43 cm); weight 3.5–38.8 oz (100–1,100 g)

Number of genera, species
1 genus; 58 species

Habitat
Subterranean

Conservation status
Vulnerable: 1 species; Lower Risk/Near Threatened: 3 species

Distribution
South America, in southern Peru, Bolivia, Chile, Paraguay, Argentina, Uruguay, and southern Brazil

Evolution and systematics

Today, Ctenomyidae has one living genus with 58 species and eight fossil genera. These numbers are highly variable, because description of new species and reconsideration of old ones continues. Genus *Ctenomys* exists from the lower Pleistocene, and Ctenomyidae is found from the upper Miocene. Among the Hystricognathi, Ctenomyidae is closely related to: Octodontidae (octodonts), Abrocomidae (chinchilla rat), and Myocastoridae (coypu). *Ctenomys* is the most specious group of living rodents.

Physical characteristics

The head is big and there is no evident neck. Incisors are big, strong, easily visible, and generally have an orange coloration on their frontal side. Limbs are powerful and short, and the ears are reduced. Their forepaws sport strong nails with characteristic supraungual hair combs. The tail is medium in length, stiff, and almost hairless.

Size ranges approximately from 8.6 in (22 cm) in *C. pundti* to 16.9 in (43 cm) in *C. conoveri* (total length), and their weights vary 3.5–38.8 oz (100–1,100 g).

The coat color is also variable, from pale to black. The majority of the species have brown reddish pelage.

Distribution

Ctenomys lives exclusively in South America, from 12° to 54°S latitude and from Pacific to Atlantic coasts. Current range includes southern Peru, Bolivia, Chile, Paraguay, Argentina, Uruguay, and southern Brazil.

Habitat

Tuco-tucos live in many habitats: grasslands, semi-arid lands, coastal dunes, forest meadows, and steppes, and from the sea level up to 13,120 ft (4,000 m) in the Andes. They perform almost all their activities underground, except for some foraging and, eventually, young dispersal.

Tuco-tucos dig tunnel systems that are exclusive for each individual (solitary) or for multiple animals (social). Their burrows are at depths varying 11.8–118 in (30–300 cm), built as central tunnels with branching secondary tunnels, and have

The Talas tuco-tuco (*Ctenomys talarum*) molds the walls of its tunnels by urinating on the soil and then packing it into place. (Photo by Aníbal Parera. Reproduced by permission.)

multiple holes communicating with the surface usually closed with soil plugs that can be open or closed at will. The tunnel system then acts not only as an anti-predator defensive device, but also allows the animal to maintain a humidity level always near 100% and an almost stable temperature level through the year.

Behavior

Tuco-tucos are mostly solitary animals. Individuals get together only during the mating season for copulation and, after pregnancy, the pups remain with the mother for a few months before dispersing. Some species have been suggested as social, but that condition is confirmed only for *Ctenomys sociabilis*.

Ctenomys uses sounds, odors, and touch to communicate with each other. Tactile communication appears at close contact. Urine and feces act as chemical signals. General knowledge about them is scarce.

Vocalizations have been reported for many *Ctenomys* species, both solitary and social. Solitary animals have limited repertoires of four to six different signals. The common name of these animals (tuco-tuco) is an onomatopoeic representation of their territorial/warning vocalizations that can be heard from fairly great distances outside their burrows. Most common vocal signals for solitary animals are territorial, aggressive, male courting (guttural sounds), female-mounting acceptance, and pup contact/isolation calls (with a "crying" quality).

Azara's tuco-tuco (*Ctenomys azarae*) has stiff hairs on its feet to help move dirt. (Photo by Gabriel Rojo. Reproduced by permission.)

The majority of the solitary species of *Ctenomys* are territorial and they maintain separate burrows, using warning signals. In social animals, each colony maintains their burrow system independent from others, also using signals. Solitary animals are very aggressive. Social animals also have aggressive behaviors, but they can be more tolerant.

Tuco-tucos are thought to be polyrhythmic in their activity patterns, alternating many activity periods with resting or immobility throughout the day. They seem to be basically di-

The Azara's tuco-tuco's (*Ctenomys azarae*) claws are more developed on the forelegs. (Photo by Gabriel Rojo. Reproduced by permission.)

The Talas tuco-tuco's (*Ctenomys talarum*) eyes are close to the top of its head, allowing it to remain unexposed while surveying its surroundings. (Photo by Aníbal Parera. Reproduced by permission.)

urnal, at least for foraging outside their burrows. Nevertheless, the current information available is very scarce. No migratory patterns are known.

Feeding ecology and diet

Tuco-tucos are strictly herbivorous and exhibit a generalist feeding strategy. They feed both on aerial and subterranean (root) parts of grasses, herbs, and shrubs.

They do not drink water; all the water they need is obtained from the plants they eat. They perform fecal reingestion (second passage of fecal pellets through the digestive tract) and have special kidney adaptations. Reingestion and kidney adaptations might be related to water economy and to the recovering of some particular nutrients.

Some species feed aboveground, while other species harvest the food outside and gather it into their burrows to feed.

Reproductive biology

Courtship, mating, and pup lactation occur inside the burrows.

Courtship begins with aggressive postures and continues with an intense exchange of chemical, tactile, and acoustic signals. Long pre-copulatory interaction periods and, in general, more than one copulation occur before ejaculation because of

Despite their resemblence to pocket gophers, Azara's tuco-tucos (*Ctenomys azarae*) do not have external cheek pouches. (Photo by Gabriel Rojo. Reproduced by permission.)

their induced ovulator condition. In induced ovulators, strong stimulation of the female during copulation is needed. The mating system is polygynous.

Gestation takes about 100 days. Two to six pups per litter are born fully developed, and the lactation period duration is about two months. In general, males do not participate in pup care.

One or two reproductive periods per year may appear. In species with only one reproductive period, it occurs during the austral winter.

Conservation status

Some tuco-tucos are common (*Ctenomys talarum* and *C. mendocinus*), others are restricted to typical localities. The IUCN lists *C. magellanicus* as Vulnerable, and *C. latro*, *C. mattereri*, and *C. sociabilis* as Lower Risk/Near Threatened. No other species are listed.

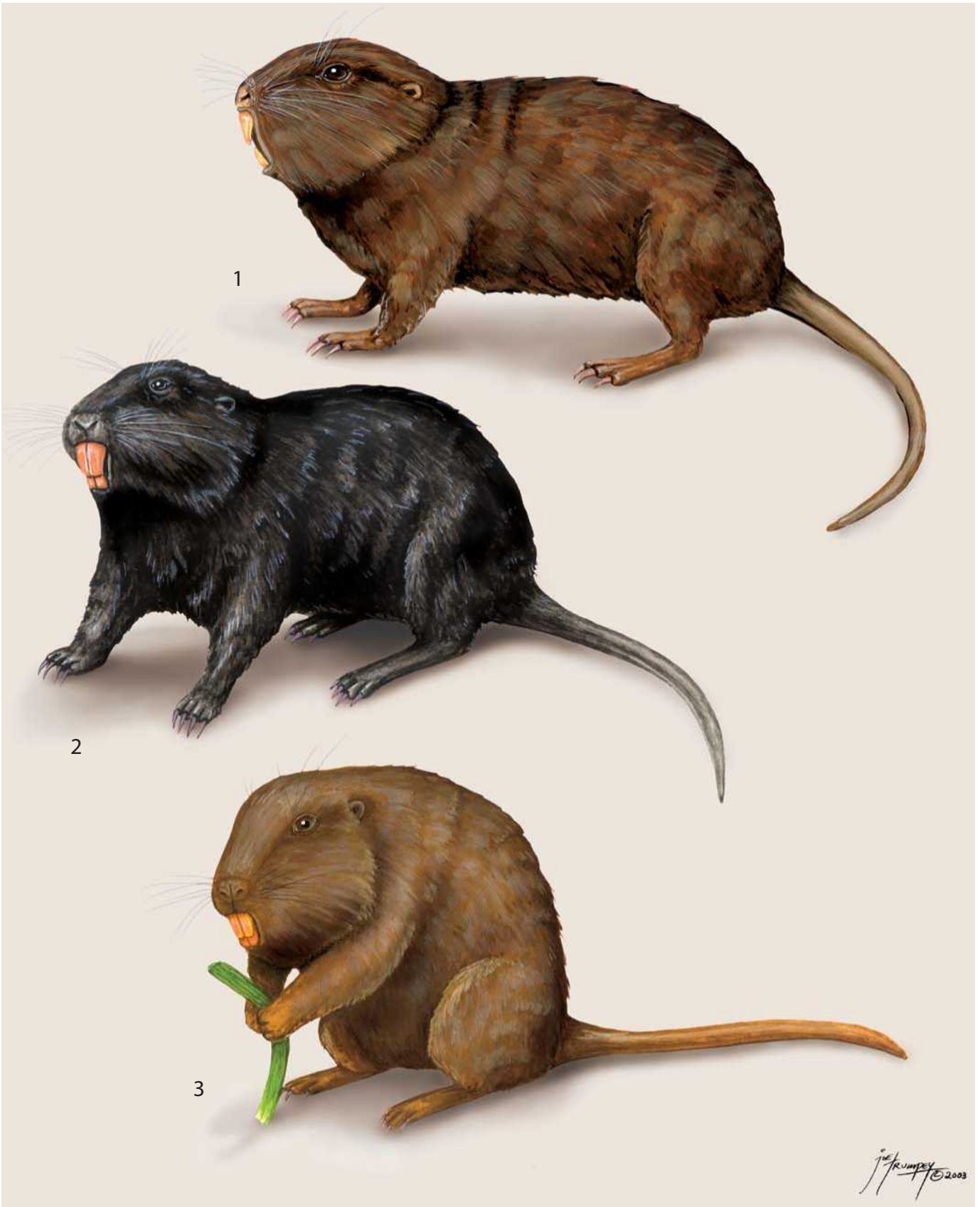
The decline of some populations is mostly due to urbanization, floodings (natural or artificial), or vulcanism.

Population estimates are variable, from one individual per acre (2.5 individuals per ha) (*C. opimus*) to 84 individuals per acre (207 individuals per ha) (*C. talarum*).

No conservation efforts are currently known.

Significance to humans

Tuco-tucos appear in many South American indigenous myths and legends (i.e., Tehuelches and Tobas indigenas). Tehuelches and Onas people eat them. *Ctenomys* is considered a pest in Argentina. Tuco-tucos may cause problems to humans because they consume crops and roots of timber trees. They can also affect human building activities because of their removal of soil.



1. Social tuco-tuco (*Ctenomys sociabilis*); 2. Rio Negro tuco-tuco (*Ctenomys rionegrensis*); 3. Pearson's tuco-tuco (*Ctenomys pearsoni*). (Illustration by Joseph E. Trumpey)

Species accounts

Pearson's tuco-tuco
Ctenomys pearsoni

TAXONOMY
Ctenomys pearsoni Lessa and Langguth, 1983, Colonia Department, Uruguay. No subspecies recognized.

OTHER COMMON NAMES
Spanish: Tucu-tucu de Pearson.

PHYSICAL CHARACTERISTICS
Average head and body length is 7.5 in (19 cm); weight is 7 oz (200 g). Brown reddish pelage with a white collar under and white patches lateral to neck.

DISTRIBUTION
Southwestern Uruguay and Entre Rios Province, Argentina.

HABITAT
Coastal sand dunes and grasslands.

BEHAVIOR
Solitary; territorial; aggressive; conspicuous territorial vocalizations. Leaves the burrow only to forage.

FEEDING ECOLOGY AND DIET
Includes grasses, herbs, shrubs, and roots.

REPRODUCTIVE BIOLOGY
Only one litter per year. Litter size two to four pups. Probably polygynous. Sex ratio unbalanced in favor of females. Frequent female vocalizations during courtship.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Rio Negro tuco-tuco
Ctenomys rionegrensis

TAXONOMY
Ctenomys rionegrensis Langguth and Abella, 1970. No subspecies recognized.

OTHER COMMON NAMES
Spanish: Tucu-tucu de Rio Negro.

PHYSICAL CHARACTERISTICS
Head and body length 6–10 in (15–25 cm); weight 3.5–25 oz (100–700 g). Three pelage forms: black; brown grayish; and dark-backed (brown grayish with a mid-dorsal black band).

DISTRIBUTION
Occurs in a restricted area of southwestern Rio Negro Province, Uruguay, and in local populations east and west of Entre Rios Province, Argentina.

HABITAT
Grasslands.

BEHAVIOR
Presumed colonial. Variable aggressive behavior.

FEEDING ECOLOGY AND DIET
Feeds on grasses, herbs, and roots.

REPRODUCTIVE BIOLOGY
Assumed to be polygynous. Probably two litters per year. Litter size is two to four pups. Male and female vocalizations during courtship.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Social tuco-tuco
Ctenomys sociabilis

TAXONOMY
Ctenomys sociabilis Pearson and Christie, 1985, Neuquén Province, Argentina. No recognized subspecies.

OTHER COMMON NAMES
Spanish: Tuco-tuco social.

PHYSICAL CHARACTERISTICS
Head and body length is 6.7–9.8 in (17–25 cm); weight is 6.3–8.3 oz (180–235 g). Brown reddish, dark-backed. Light orange patches lateral to the nose.

DISTRIBUTION
Very restricted. Southern Neuquén Province, Argentina.

HABITAT
Andean pre-cordillera steppe at the edges of meadow patches.

BEHAVIOR
Socially organized in groups of two to six related females sharing the same burrow system. All individuals participate in digging. Males disperse from natal group at the age of four to eight months. Distinctive high-pitched vocalization.

FEEDING ECOLOGY AND DIET
Includes grasses and roots. All group members participate in foraging.

REPRODUCTIVE BIOLOGY
Only one male per colony, suggesting a polygynous-harem reproductive system. All females that share a colony nest are producing milk when lactating pups are present.

CONSERVATION STATUS
Not listed by the IUCN, but considered in critical danger by the Argentine Society of Mammalogists.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Southern tuco-tuco *Ctenomys australis*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Buenos Aires Province, eastern Argentina.	Likely vegetarian.	Not listed by IUCN
Bolivian tuco-tuco *Ctenomys boliviensis*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Central Bolivia, western Paraguay, and Formosa Province, Argentina.	Likely vegetarian.	Not listed by IUCN
Colburn's tuco-tuco *Ctenomys colburni*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Extreme western Santa Cruz Province, Argentina.	Likely vegetarian.	Not listed by IUCN
Emily's tuco-tuco *Ctenomys emilianus*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grass plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Neuquén Province, Argentina, at the base of the Andes.	Likely vegetarian.	Not listed by IUCN
Mottled tuco-tuco *Ctenomys latro*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Tucumán and Salta Provinces, northwestern Argentina.	Likely vegetarian.	Lower Risk/Near Threatened
Magellanic tuco-tuco *Ctenomys magellanicus*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Extreme southern Chile and southern Argentina.	Likely vegetarian.	Vulnerable

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Natterer's tuco-tuco *Ctenomys nattereri*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Mato Grosso, Brazil.	Likely vegetarian.	Lower Risk/Near Threatened
Goya tuco-tuco *Ctenomys perrensis*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Corrientes, Entre Ríos, and Misiones Provinces, north-eastern Argentina.	Likely vegetarian.	Not listed by IUCN
Salta tuco-tuco *Ctenomys saltarius*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Alta and Jujuy Provinces, northern Argentina.	Likely vegetarian.	Not listed by IUCN
Collared tuco-tuco *Ctenomys torquatus*	Upperparts gray or creamy buff through brown to almost black; underparts are paler. Stiff hair fringes on the hind that form comb-like bristles. Head and body length 5.9–9.8 in (15–25 cm); tail length 2.4–4.3 in (6–11 cm); weight 3.5–24.7 oz (100–700 g).	Prefer sandy, somewhat dry soil in coastal areas, grassy plains, forests, and the altiplano to 13,120 ft (4,000 m). Dig burrows with a long main tunnel and several short passages. Generally one litter per year.	Uruguay, northeastern Argentina, and extreme southern Brazil.	Likely vegetarian.	Not listed by IUCN

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Other

Gabriel Francescoli's Webpage. <http://eto.fcien.edu.uy/gaboeng.htm>.

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Octodonts
(Octodontidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Octodontidae

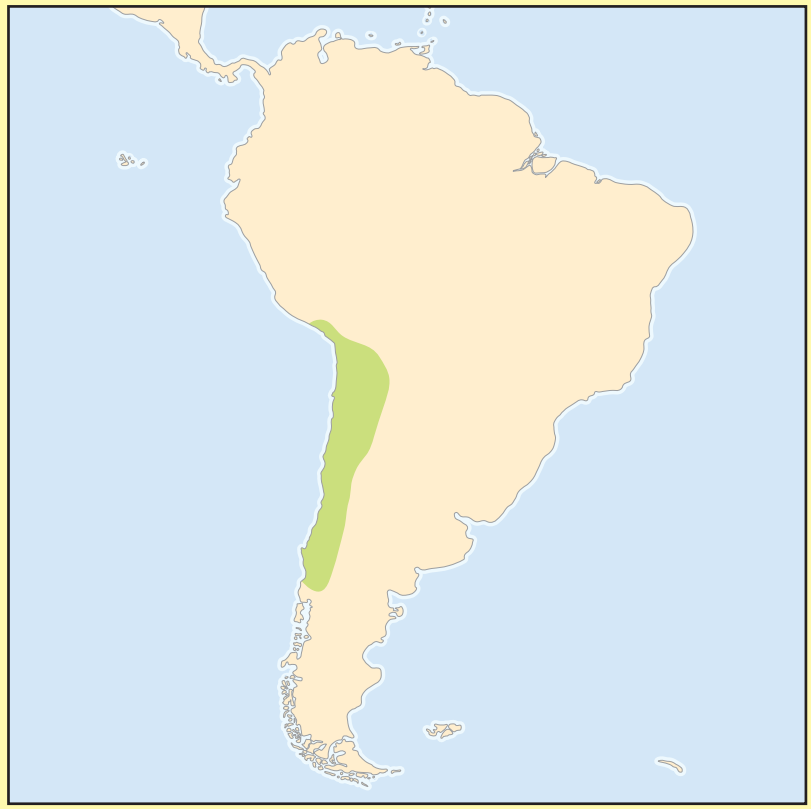
Thumbnail description
Smallest of hystricognath rodents; classic figure-eight pattern on occlusal surface of molar teeth; diverse ecologically and morphologically; specializations for burrowing in many forms

Size
Head and body length 5.0–8.7 in (125–221 mm); tail 1.5–7 in (40–180 mm); 2.8–10.6 oz (80–300 g)

Number of genera, species
8 genera; 12 species

Habitat
Scrubland, savanna, arid, semiarid, montane, and coastal areas

Conservation status
Vulnerable: 2 species



Distribution
Southwest Peru, Chile, Argentina, and southwest Bolivia

Evolution and systematics

Members of the family Octodontidae are considered to represent some of the most morphologically primitive species of the suborder Hystricognathi. Depending upon the assignment of fossils to the family, the fossil record for the family extends from either the early Miocene or early Oligocene to recent. All recent systematic treatments place the families Octodontidae, Capromyidae, Ctenomyidae, Echimyidae, Myocastoridae, and Abrocomidae in the monophyletic (sharing a common ancestry) superfamily Octodontoidea. A molecular phylogenetic study in 2003 by Honeycutt and others suggested that the families Octodontidae and Ctenomyidae, commonly known as tuco-tucos, share a common ancestry, followed by an association with a group containing the families Myocastoridae, Echimyidae, and Capromyidae.

Speciation within the family was influenced by environmental changes occurring in the Pliocene and Pleistocene. Within the family, species of octodontids are chromosomally diverse ranging in diploid chromosome number from a low of 38 to a high of 102. The red viscacha rat, *Tympanoctomys barrerae*, has the highest diploid number, and in 1999, Gallardo and others provided genetic evidence for this species being a tetraploid with a genome size twice that seen in related species. Honeycutt and others provided evidence for relationships among genera within the family. Two major groups were observed, one representing the desert specialists from Argentina, *Octomys* and *Tympanoctomys*, and the other containing *Octodontomys* and a group represented by *Octodon*, *Aconaemys*, and *Spalacopus*, three genera restricted to Chile. The latter two genera contain species adapted for semi-fossorial and fossorial lifestyles, and according to the molecular data, they are each other's closest relatives. Although in 1987 Contreras and others questioned the species-level distinction between *O. lunatus* and *O. bridgesi*, estimates of genetic and phylogenetic divergence between these forms support these taxa as being distinct species. In 1994, Hutterer named a new species, *Octodon pacificus*, restricted to Mocha Island off the coast of Chile. Evidence from standard karyotypes and morphological comparisons by Gallardo and Mondaca in 2001 and the molecular phylogenetic study of Honeycutt and others support species-level status for the two currently recognized subspecies of *Aconaemys*, *A. fuscus fuscus*, and *A. fuscus porteri*. Mares and others in 2000 described two new genera and species, *Pipanacoctomys aureus* and *Salinoctomys loschalchalerosorum*, both of which are desert specialists occurring in perisaline

A degu (*Octodon degus*) emerging from underneath a rock. (Photo by S. R. Maglione/Photo Researchers, Inc. Reproduced by permission.)

shrublands in Argentina. These two new species are most closely related to *Tympanoctomys barrerae*.

Physical characteristics

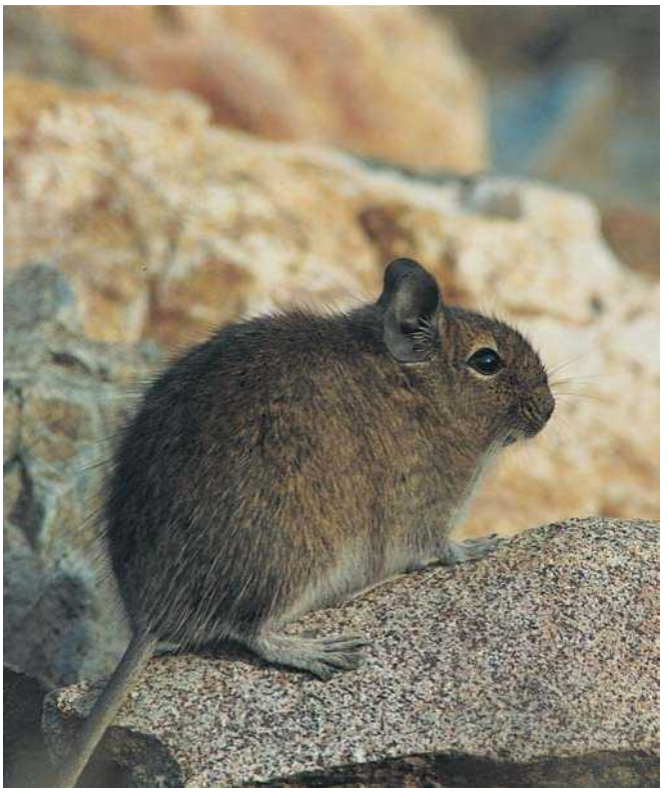
A figure-eight cusp pattern on the cheek teeth is the major diagnostic characteristic for the family. Members of the family are rat-like in appearance with stocky bodies, short legs, relatively large heads, and rounded ears. Relative to other families of hystricognath rodents, octodontids are small, not exceeding a head and body length of 7.7 in (195 mm) and a weight of 10.6 oz (300 g). The fur is dense and silky, and the dorsal pelage varies in color from pale gray to black. The ventral pelage is lighter, appearing almost white in some species. The coruro, *Spalacopus cyanus*, has the darkest pelage with many individuals being entirely black, and species living in arid regions tend to have paler-colored pelage. Species show little digit reduction, and have clawed digits for digging as well as long bristles between the digits. With the exception of coruros and rock rats of the genus *Aconaemys*, most species have relatively long tails that are distinctly tufted.

Distribution

Members of this family occur primarily in the southern cone of South America and, according to Contreras and others in 1987, most species occur between 16°S and 41°S latitude. Redford and Eisenberg in 1992 described the family's distribution as encompassing primarily areas in Bolivia, Chile, and Argentina, and eight of the 12 currently recognized species have ranges that are restricted almost exclusively to the western side of the Andes in Chile. Several species occur in Andean zones at higher elevations ranging 9,840–16,400 ft (3,000–5,000 m), whereas others maintain distributions from near sea level in coastal areas up to approximately 3,940 ft (1,200 m).

Habitat

Members of the family are diverse in terms of ecology and morphology. All species construct burrow systems under either shrubs or rocks, and coruros and rock rats are the most modified for a subterranean lifestyle. Degus of the genus *Octodon* are terrestrial, but are capable of climbing low-lying trees and shrubs. Most species prefer scrub habitat occurring in coastal, montane, and desert regions. This habitat varies in elevation from sea level to Andean regions ranging in elevation 9,840–16,400 ft (3,000–5,000 m). Most areas where species occur have shrub and grasses that are patchily distributed and intermixed with some rocks. The genera *Tympanoctomys*, *Salinoctomys*, and *Pipanacoctomys* are restricted to arid regions in Argentina characterized by desert plants with high salt content. Some species of rock rats occur in *Nothofagus* and *Araucaria* forests.



Degu (*Octodon degus*) live in rock piles near Reserva Nacional Las Chinchillas, Chile. (Photo by Fletcher & Baylis/Photo Researchers, Inc. Reproduced by permission.)

A degu (*Octodon degus*) among family members showing social behavior of fur scratching. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

A degu (*Octodon degus*) mother with babies. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

Behavior

Degus are diurnal, whereas most species appear to be nocturnal. Studies of activity patterns of coruros appear contradictory. Reig's field observations in 1970 indicated that coruros were active during the day, whereas Begall and others in 2002 observed nocturnal activity patterns in captive coruros. Several species are social, forming colonies occupying a communal burrow system. According to Fulk in 1976, colonies of degus usually consist of two to four adult males and females that share a common burrow system. Individuals within a colony defend territory and display a wide array of social activities related to social grooming, play, and courtship. Coruros also form colonies that occupy a mutual burrow system. Begall and others in 1999 observed one colony containing 26 individuals, whereas Torres-Mura and Contreras in 1998 indicated that the typical colony consisted of either one or more pairs of adults and their young. The colonial species display a diverse repertoire of vocalizations associated with alarm calls and other social interactions. Although little is known about them, rock rats appear to be colonial, while the remaining species are solitary. Both the degu and the chozchoz, representing the genus *Octodontomys*, take dust baths.

Feeding ecology and diet

All species are herbivorous, and with the exception of cururos, most species forage aboveground. Species living in less arid environments feed on a variety of plant materials, including grasses, leaves, bark, fruits, and forbs. Highly fosso-

The degu (*Octodon degus*) is also known as the South American bush rat. (Photo by J-C Carton. Bruce Coleman, Inc. Reproduced by permission.)

rial forms like cururos feed on underground portions of plants, and desert-adapted species like the red viscacha rat are adapted for feeding on the stems and leaves of plants rich in salt. In 1997, Mares and others described adaptations that allow the red viscacha rat to feed on halophytic plants. This species has bundles of hairs on each side of the mouth that function as an extra pair of incisors for the removal of salt from leaves. Other species feed on fruits of cacti, seeds, and other plant materials.

Reproductive biology

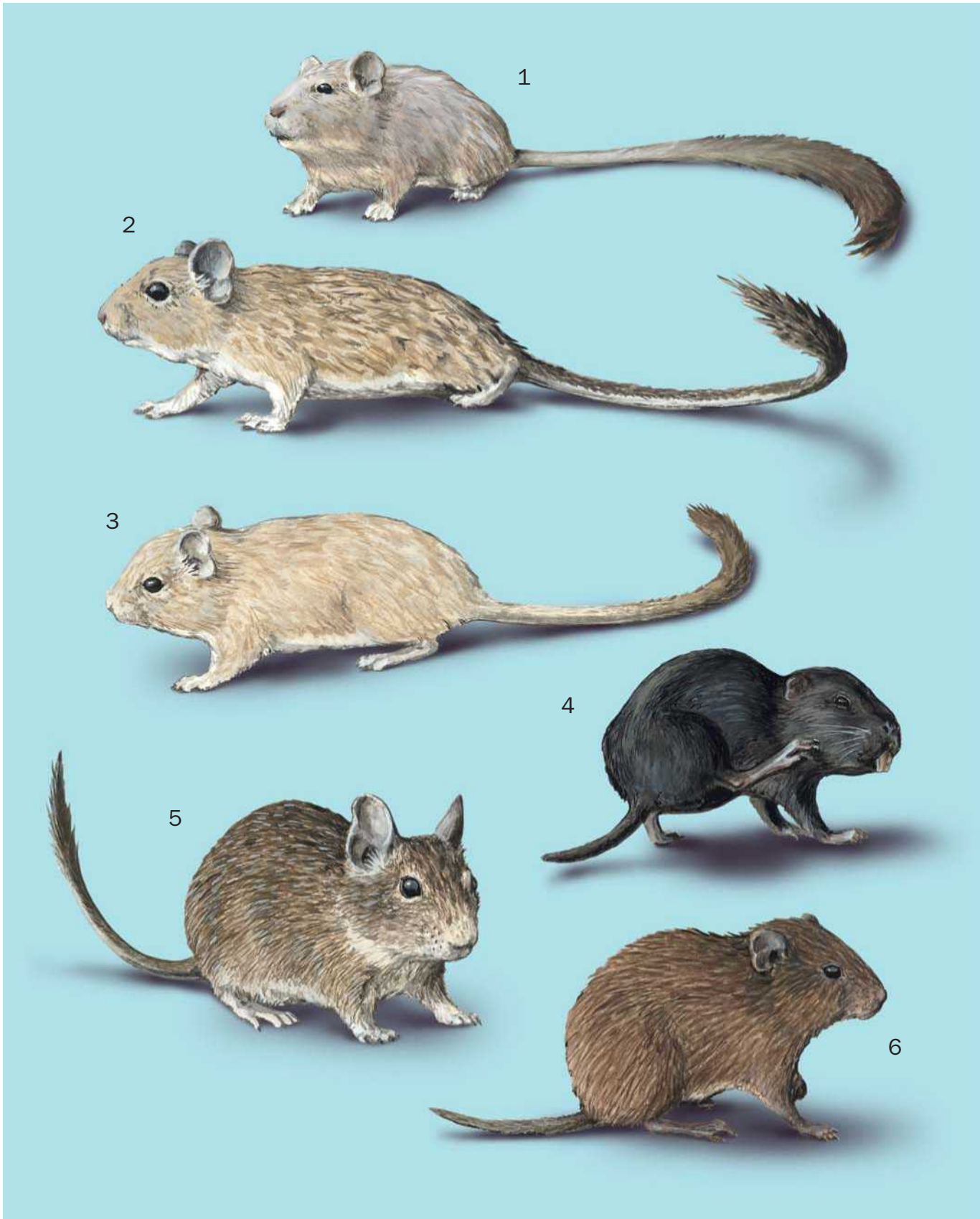
For their body size, octodontids have a long gestation period ranging from 77–105 days. Young are precocial and weaned at an early age. The average litter size ranges between two and five offspring, and the females of many species are capable of postpartum estrus. The viscacha rat of the genus *Octomys* produces multiple litters per year, whereas coruros, red viscacha rats, and degus appear to be more seasonal in their breeding patterns. The mating system for octodontids are not known.

Conservation status

Most species of octodontids are locally common and not listed as species of concern by either IUCN or CITES. Two species, *Octodon pacificus* and *Tympanoctomys barrerae*, are listed as Vulnerable by IUCN, primarily because they display restricted distributions and habitat specializations that make them susceptible to extinction in the near future. In the case of *O. pacificus*, populations are confined to forest habitats, and recent agricultural activities associated with clear-cutting for cultivation are contributing to loss of habitat. Given the restricted distributions of *Salinoctomys* and *Pipanacoctomys*, these new species probably should be considered potential candidates for listing.

Significance to humans

Both degus and coruros are considered potential agricultural pests. According to Torres-Mura and Contreras, coruros can damage tuberous plants like potatoes, and in their 1975 review, Woods and Boraker suggested that degus cause damage to a variety of cash crops, including orchards, grains, and vineyards.



1. Red viscacha rat (*Tympanoctomys barrerae*); 2. Chozchoz (*Octodontomys gliroides*); 3. Viscacha rat (*Octomys mimax*); 4. Coruro (*Spalacopus cyanus*); 5. Degu (*Octodon degus*); 6. Rock rat (*Aconaemys fuscus*). (Illustration by Brian Cressman)

Species accounts

Red viscacha rat
Tympanoctomys barrerae

TAXONOMY
Tympanoctomys barrerae (Lawrence, 1941), La Paz, Mendoza Province, Argentina.

OTHER COMMON NAMES
English: Plains viscacha rat.

PHYSICAL CHARACTERISTICS
Head and body length averages 5 in (128 mm); tail 5.7 in (145 mm); weight 5 oz (143 g). Enlarged tympanic bullae and head. Dorsal pelage pale, white hind feet, and tail darker and possessing longer hairs near the tip.

DISTRIBUTION
Restricted to arid area the Mendoza Province in Argentina.

HABITAT
Occupies arid regions characterized by shrubs and halophytic (salt-rich) vegetation. Plants usually patchily distributed.

BEHAVIOR
Shows physiological and morphological adaptations to arid climates. Constructs complex burrow system and caches food. Nocturnal and solitary.

FEEDING ECOLOGY AND DIET
Herbivore that specializes on diets consisting of leaves and stems from plants with high salt content, specifically *Heterostachys ritteriana*. Uses lower incisors and bristle brush located on each side of the mouth to remove excess salt prior to ingesting plant material.

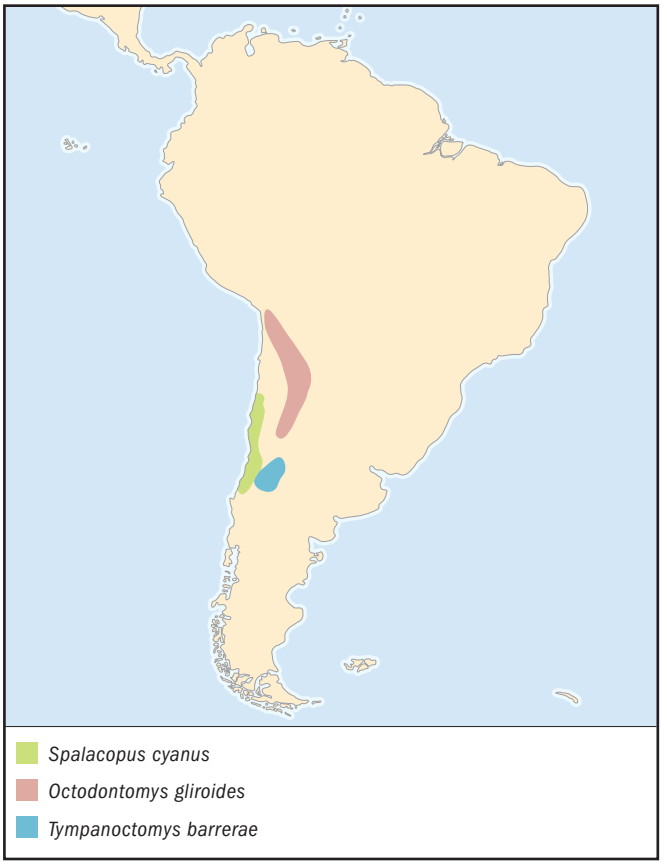
REPRODUCTIVE BIOLOGY
Precocial young that eat solid food within days of being born.

CONSERVATION STATUS
Listed as Vulnerable by IUCN as a result of restricted range and specialized habitat requirements.

SIGNIFICANCE TO HUMANS
None known. ◆

Rock rat
Aconaemys fuscus

TAXONOMY
Aconaemys fuscus (Waterhouse, 1842), Valle de las Cuevas, Mendoza Province, Argentina.



OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 5.3–7.4 in (135–187 mm); tail 2.2–2.7 in (55–70 mm); males 4.2 oz (120 g), females 4.7–5.3 oz (135–152 g). Dark brown dorsally, with bi-colored tail and stout body. Fewer specializations for fossoriality. Hind feet with fringe of hairs.

DISTRIBUTION
Occurs in Andean regions of Chile and Argentina between 33° and 41°S latitude.

HABITAT
Montane scrub habitat as well as forests consisting of *Nothofagus* and *Araucaria*.

BEHAVIOR
Nocturnal and colonial. Semi-fossorial producing runways.

FEEDING ECOLOGY AND DIET
Herbivorous feeding on roots and other vegetation. Caches food.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Abundant where it occurs, not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Coruro
Spalacopus cyanus

TAXONOMY
Spalacopus cyanus (Molina, 1782), Valparaiso Province, Chile.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 4.5–6.5 in (115–165 mm); tail averages 1.9 in (49 mm); 1.7–5.3 oz (50–150 g). Body stocky with short tail, and brown to black pelage. Specialized for digging with large incisors, claws on digits, large front feet, and small ears.

DISTRIBUTION
Occurs west of the Andes in central Chile between approximately 27°S and 36°S latitude.

HABITAT
Occupies complex, communal burrow system. Fossorial, and prefers more temperate coastal and montane areas with shrub cover that does not exceed 60%.

BEHAVIOR
Fossorial-excavating burrow systems with complex arrangement of tunnels and multiple openings that are not plugged. Forms colonies containing up to 26 individual adults and young. Highly vocal, with individuals producing a series of trills and other calls associated with socializing and warning. In field, observed to be diurnal, whereas lab colonies display nocturnal activities.

FEEDING ECOLOGY AND DIET
Herbivorous, foraging below on tubers and stems. Especially fond of the lily, *Leucoryne ixiodes*. Caches food in burrow system.

REPRODUCTIVE BIOLOGY
Reproduces twice per year with average litter size of two. Gestation is 77 days.

CONSERVATION STATUS
Common locally. Subspecies *S. c. maulinus* considered Endangered by Chilean Red List.

SIGNIFICANCE TO HUMANS
Considered an agricultural pest in some areas. ◆

Chozchoz
Octodontomys gliroides

TAXONOMY
Octodontomys gliroides (Gervais and d'Orbigny, 1844), La Paz, La Paz Department, Bolivia.

OTHER COMMON NAMES
Spanish: Rata cola pincel.

PHYSICAL CHARACTERISTICS
Head and body length 6.3–7.1 in (161–182 mm); tail 5.1–7 oz (130–180 mm); 3.5–7 oz (100–200 g). Pelage is thick with grayish dorsal color and white venter. Tail bicolored and tufted. Ears relatively large and auditory bullae enlarged.

DISTRIBUTION
Higher elevations in north Chile, southwest Bolivia, and northwest Argentina.

HABITAT
Occupies burrows in xeric scrub areas comprised of various cacti, bushes, and rocks.

BEHAVIOR
Nocturnal species. Can be solitary or live in small groups. Vocalizes and bathes in dust.

FEEDING ECOLOGY AND DIET
Forages aboveground on fruits of cacti and acacia pods as well as other plants.

REPRODUCTIVE BIOLOGY
Gestation approximately 101 days and litter size ranges from one to three. Seasonal breeder producing two litters per year.

CONSERVATION STATUS
Considered common, not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Viscacha rat
Octomys mimax

TAXONOMY
Octomys mimax Thomas, 1920, La Puntilla, Catamarca Province, Argentina.

OTHER COMMON NAMES
Spanish: Rata cola peluda.

PHYSICAL CHARACTERISTICS
Head and body length 5.5–6.7 in (140–170 mm); tail 5.9–7 in (151–180 mm); 4.2–5 oz (121–144 g). Dorsal pelage pale, under parts white, and a tufted tail that is partially bi-colored. Large auditory bullae.

DISTRIBUTION
Argentina in parts of the Monte desert in Catamarca and several provinces including San Juan, La Rioja, and Mendoza.

HABITAT
Higher altitudes along the slopes of the Andes in desert scrub habitat. Ecologically converges on the North American wood rat genus *Neotoma*.

BEHAVIOR
Burrows under rocks and is nocturnal. Appears to be solitary.

FEEDING ECOLOGY AND DIET
Herbivorous feeding on a variety of plant materials, including seeds and cacti.

REPRODUCTIVE BIOLOGY
Produce several litters per year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Degu
Octodon degus

TAXONOMY
Octodon degus (Molina, 1782), Santiago, Santiago Province, Chile.

OTHER COMMON NAMES
Spanish: Chozchoris, rata de las cercas, bori.

PHYSICAL CHARACTERISTICS
Head and body length 9.8–12.2 in (250–310 mm); tail 2.9–5.1 in (75–130 mm); 6.0–10.5 oz (170–300 g). Compact body and large head. Dorsal color brown and ventral side light yellow, with black tufted tail. Digits with claws, with little digit reduction. Hind feet with bristles protruding beyond claws.

DISTRIBUTION
Western slope of Andes in Chile between Vallenar and Curico.

HABITAT
Usually restricted to elevations at 3,937 ft (1,200 m) and below in shrub and savanna habitats ranging from subtropical to semiarid. Burrows placed at the base of bushes and rocks and prefers microhabitats that are thermally less stressful.

BEHAVIOR
Diurnal species active in mornings and afternoons. Constructs multi-chambered and colonial burrow systems housing several adults and young. Highly social with allogrooming among males and females, group huddling, and complex vocalizations consisting of warning alarms and other calls.

FEEDING ECOLOGY AND DIET
Herbivorous diet consisting of forbs, grasses, leaves, and bark of shrubs. Animals forage aboveground and cache food within the burrow system. Individuals capable of climbing to forage.

REPRODUCTIVE BIOLOGY
Generally breeds twice per year, but demonstrates variation relative to the number and timing of litters. Sexual maturity of females reached in six months, gestation is 90 days, and average litter size is five. Young are precocial, and females experience postpartum estrus.

CONSERVATION STATUS
Common throughout its range in Chile; not threatened.

SIGNIFICANCE TO HUMANS
Potential animal model for studying human diseases such as cataracts and diabetes mellitus. Known to harbor some diseases threatening to humans. Agricultural pest in some areas. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Sage's rock rat *Aconaemys sagei*	Brown fur with a bicolored tail. Head and body length 5.5–7.3 in (14–18.7 cm), tail length 2.1–3.1 in (5.5–8 cm), weight 2.9–3.8 oz (83–110 g).	High Andes and coastal mountains. Fossorial. Burrow systems are complex and shallow.	Southern Argentina.	Likely herbivorous.	Not listed by IUCN
Bridges's degu *Octodon bridgesi*	Upperparts grayish to brownish, sometimes with an orange cast. Underparts creamy yellow. Tail tip has a black brush. Head and body length 4.9–7.7 in (12.5-19.5 cm), tail length 4.1–6.5 in (10.5-16.5 cm). Larger than *O. degus,* whose weight is 5.9–10.6 oz (170–300 g).	Coastal mountains. Fossorial with a complex burrow system.	Andes of northern and central Chile.	Likely herbivorous.	Not listed by IUCN
Moon-toothed degu *Octodon lunatus*	Upperparts grayish to brownish, sometimes with an orange cast. Underparts creamy yellow. Tail tip has a black brush. Head and body length 4.9–7.7 in (12.5-19.5 cm), tail length 4.1–16.5 in (10.5-16.5 cm). Larger than *O. degus,* whose weight is 5.9–10.6 oz (170–300 g).	Coastal mountains. Fossorial with a complex burrow system.	Andes of central Chile.	Likely herbivorous.	Not listed by IUCN

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Rodney L. Honeycutt, PhD

Chinchilla rats
(Abrocomidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Abrocomidae

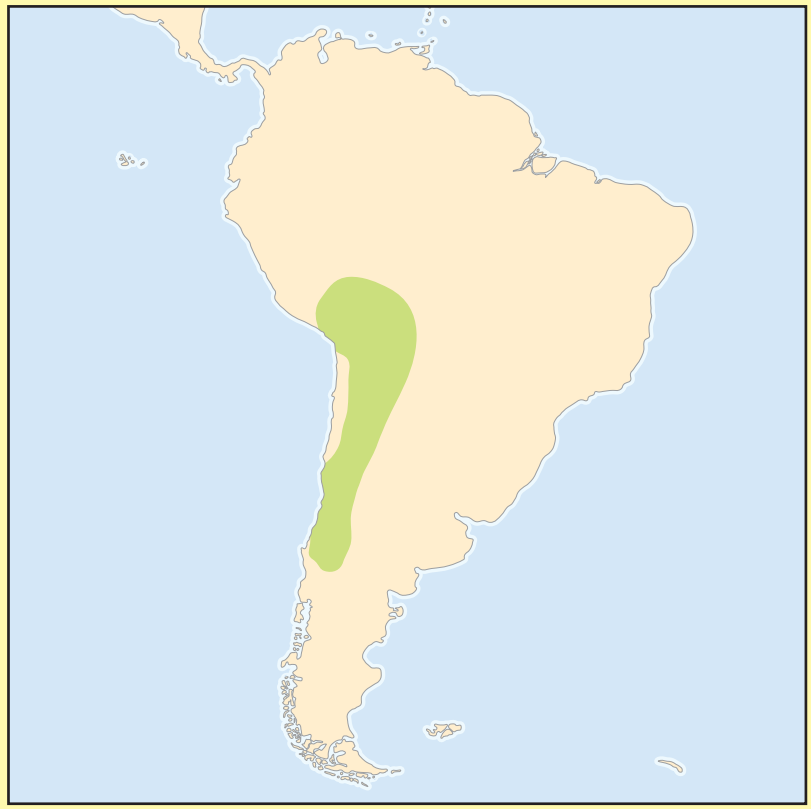
Thumbnail description
Similar in appearance to members of the chinchilla family, but for a more elongated head and ears, which presents a more rat-like appearance

Size
6–10 in (15–25 cm) from the tip of the nose to the rump; tail 2.5–6 in (6.0–14.5 cm); 7–11 oz (200–300 g)

Number of genera, species
2 genera; 6 species (1 species presumed extinct)

Habitat
From sea level to elevations up to 16,000 ft (5,000 m); rock crevices and underground tunnels; small shrubs and trees

Conservation status
Vulnerable: 1 species



Distribution
Coastal regions and Andes mountains of South America, encompassing southern Peru, northern Chile, northwestern Argentina, and central Bolivia

Evolution and systematics

The chinchilla rats, or chinchillones (genus *Abrocoma*), belong to the Abrocomidae family, in the order Rodentia. Within the genus *Abrocoma*, there are three species. The two best-studied are the ashy chinchilla rat (*Abrocoma cinerea*) and Bennett's chinchilla rat (*Abrocoma bennettii*). In 1990, a third species was designated, namely the Bolivian chinchilla rat (*Abrocoma boliviensis*). Another species, *Abrocoma vaccarum*, has been the subject of only a few academic reports and is considered a systematic development, rather than a true species.

In 1999, a new genus, *Cuscomys*, was described in the Peruvian Andes. As of 2003, two species are included in the genus. Of these, one (*Cuscomys oblativa*) is presumed to be extinct, and is represented only by remains discovered in burial sites in Peru. The other species is the Ashaninka rat, *Cuscomys ashaninka*. To date, only the recently-killed corpse of a single member of the species has been discovered. Until further specimens are recovered, information concerning *Cuscomys* is pending, and this species designation is not widely accepted.

The evolutionary history of the family Abrocomidae dates back to the Early Miocene Epoch (from 23.8 million to 16.4 million years ago), in what is present-day Argentina. Evolutionary diversification of the octodont rodents, which led to the development of the six families, including Abrocomidae, is thought to have had its genesis after the separation of the South American continent from other continental masses.

Physical characteristics

Abrocoma have large eyes and ears on an elongated head. The ears are round rather than pointed. However, the nose assumes the typical long and pointed rat-like countenance. The cylindrical tail is covered by short and fine hairs, unlike the bushier and squirrel-like tail of true chinchillas. Another distinguishing feature is the double pair of nipples present on the upper belly of females.

Members of the genus *Abrocoma* have four digits on the forelimbs and five digits on the hindlimbs. Soles are uncov-

A captive ashy chinchilla rat (*Abrocoma cinerea*). (Photo by Dr. R. E. Martin/Mammal Images Library of the American Society of Mammologists.)

ered, while the tops of the feet are fur-covered. Small claws are present on the fore and hind feet. The claws are not exceptionally powerful, owing to their hollow structure. However, some stiffness is provided in the middle three toes of the hind feet by protruding upper hairs that act to form a grooming or utility comb.

Chinchilla rats are covered in fur that is gray or gray-brown in color. The belly is yellowish white or brown. The silky, thick fur resembles that of the highly prized fur of the family Chinchillidae, but is not as woolly in texture. Indeed, chinchilla rats are a source of false fur sold to unsuspecting buyers by unscrupulous merchants.

For its size, the members of *Abrocoma* possess a long intestinal tract. The combined small and large intestines coil for 8.2 ft (2.5 m), and the caecum extends for a further 7.9 in (20 cm). The intestines and other internal organs are well protected by the 17 pairs of ribs. No other rodent has as many ribs.

Distribution

Chinchilla rats are distributed throughout the Andes from southern Peru to west central Argentina, northern Chile, and into Bolivia. Depending on the species, they range from the foothills of the west coast of Peru and Chile, to the 12,000–15,000 ft (3,660–4,570 m) elevations of the Altiplano of western Bolivia and southeastern Peru.

Abrocoma cinerea dwells exclusively in the Altiplano, and is found from southeastern Peru to the north of Chile and Argentina. In contrast, *A. bennettii* prefers the coastal foothills of Chile. As implied by its name, *A. boliviensis* is found in Bolivia, specifically at higher elevations, up to 10,000 ft (3,050 m) in the country's central region.

Habitat

All three species of *Abrocoma* are agile climbers of rocks, shrubs, and even small trees. They can make their dens in crevices in the rock- or cliff-face. Sometimes these crevices are supplemented by the construction of sidewalls that can reach up to 10 ft (3 m) high. The walls are built of feces that are bonded together using urine and other fluids. When dry, the walls become almost as hard as the surrounding rock. Underground tunnels can also provide a home. The tunnel entrances are typically concealed under a rock or at the base of a bush.

Behavior

Chinchilla rats are thought to be colonial. A field study observed a half dozen *A. cinerea* burrowing within 59 ft (18 m) of one another, and small colonies can even occupy a single burrow. Further attesting to their colonial proclivity have been observations of co-dwelling degu, another rodent that has similar size and behavior.

Both males and females are nocturnal, and keep to their burrows or crevices by day.

Communication includes the issuing of a grunt prior to or following an attack, a higher-pitched squeak when under pursuit, and a gurgling sound when being groomed.

The ashy chinchilla rat (*Abrocoma cinerea*) communicates through grunts and squeaks. (Photo by Hernán Torres. Reproduced by permission.)

Feeding ecology and diet

Diet for these herbivores consists of plant material such as buds, leaves, nuts, seeds, stems, and fruit. The search for food can even lead them to climb bushes and low-lying trees. Being nocturnal, the search for food occurs at night.

Reproductive biology

Little is known about reproduction in *Abrocoma*. Gestation times have been documented for *A. cinerea*, ranging from 115 to 118 days, with litters of one to two young. Litters of up to six have been described, and indeed may be more the norm, as shown by field work that collected pregnant females in Chile with embryo counts of four, five, and six.

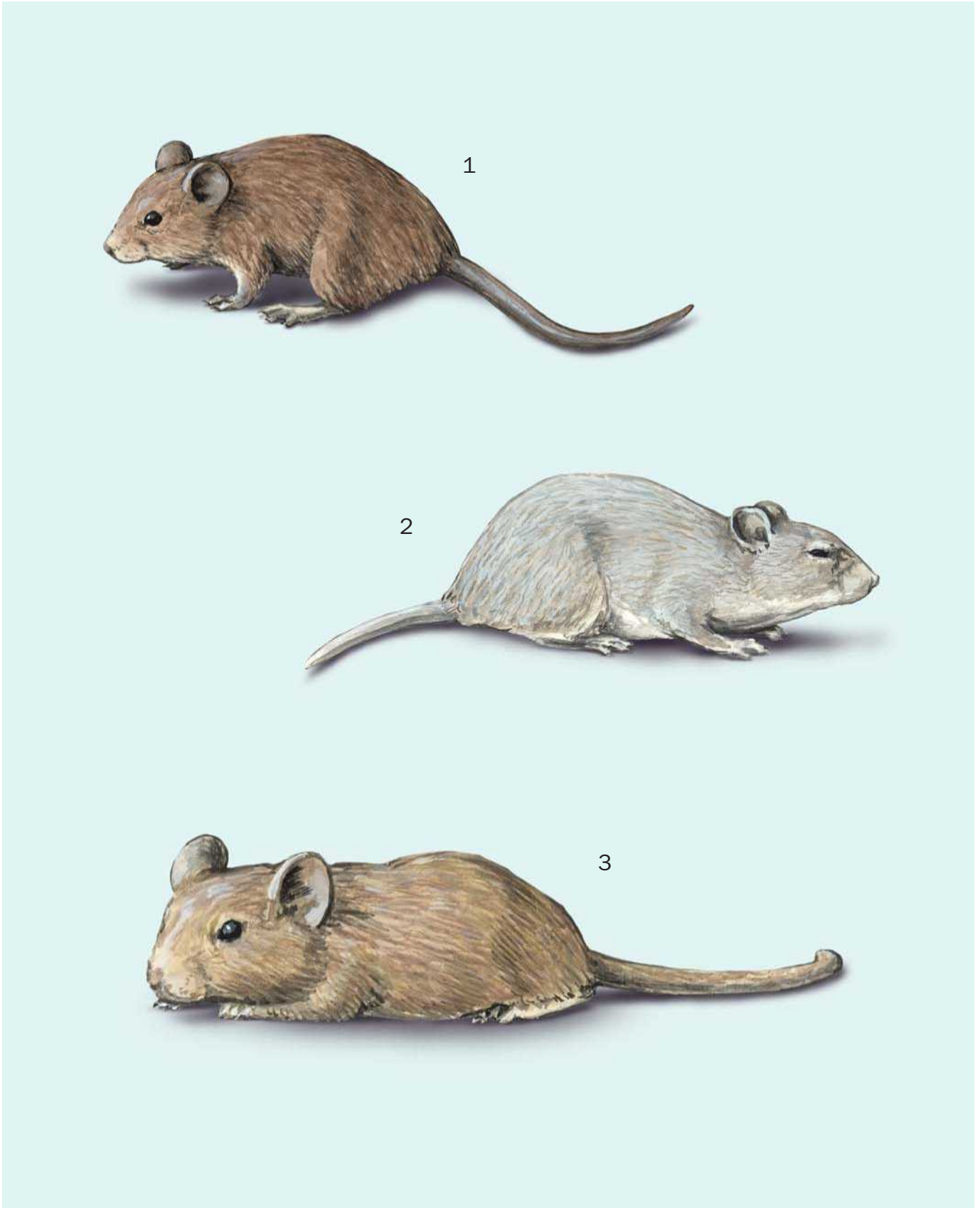
Pregnant *A. cinerea* females, or females with newborns, have been collected during the months of April, the end of July and August, and at the beginning of June. Mating would have occurred in the early months of the year. Details of mating are unknown.

Conservation status

The Bolivian chinchilla rat (*Abrocoma boliviensis*) is Vulnerable; the other species are not listed by the IUCN. Hunting and destruction of their habitats, in order to secure the fur, is responsible for declining populations. The fur, which resembles the prized fur of the true chinchilla, is sold to the unsuspecting buyer.

Significance to humans

Other than as a supply of fur for unscrupulous marketers, the species of chinchilla rat have no outstanding significance to humans. The fur itself has no marked economic value.



1. Bolivian chinchilla rat (*Abrocoma boliviensis*); 2. Ashy chinchilla rat (*Abrocoma cinerea*); 3. Bennett's chinchilla rat (*Abrocoma bennettii*). (Illustration by Brian Cressman)

Species accounts

Ashy chinchilla rat
Abrocoma cinerea

TAXONOMY
Abrocoma cinerea Thomas, 1919, Cerro Casabindo, Jujuy Province, Argentina.

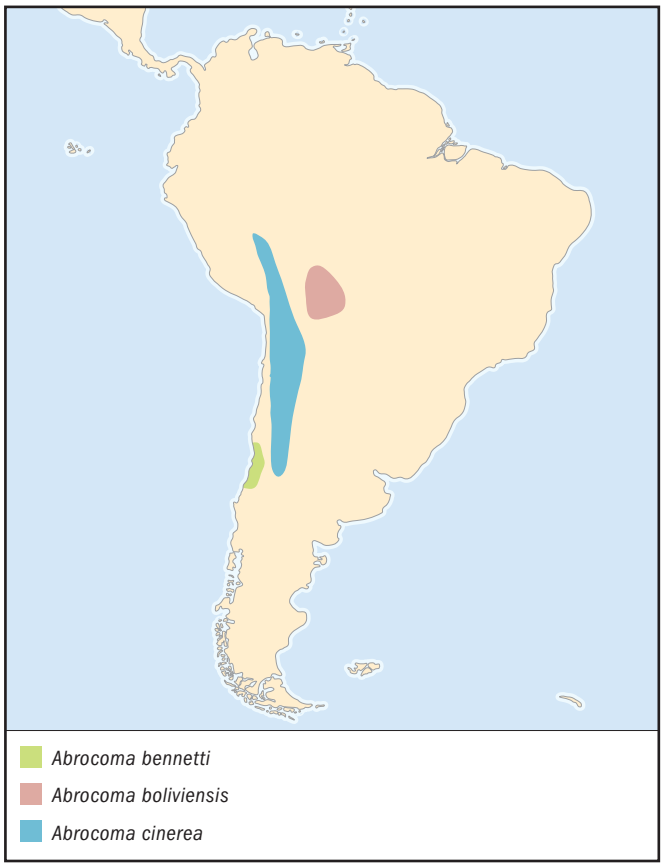
OTHER COMMON NAMES
English: Chinchilla rat; French: Rat chinchilla; German: Chinchillaratte; Spanish: Ratón chinchilla de cola corta.

PHYSICAL CHARACTERISTICS
6–10 in (15–25 cm) from tip of nose to rump; tail 2.4–7.2 in (6–18 cm) long; 7.1–10.6 oz (200–300 g). Fur is silver-gray above and lighter below.

DISTRIBUTION
Altiplano of the South American Andes, from southern Bolivia and Peru into the central region of Chile.

HABITAT
Rocky regions at elevations of 12,000–16,400 ft (3,700–5,000 m). Typically live in burrows that are built under rocks or at the base of a shrub.

BEHAVIOR
Live in colonies of up to six individuals. Burrows can be very close together. Communicate using a variety of sounds.



FEEDING ECOLOGY AND DIET
Herbivorous; the diet includes seeds, fruits, and nuts. They are nocturnal feeders.

REPRODUCTIVE BIOLOGY
Mate in January or February. Gestation period is 115 to 118 days. Litters are typically one or two young. Other details unknown as of 2003.

CONSERVATION STATUS
Not listed by the IUCN, but presumed rare as a result of overhunting and habitat destruction.

SIGNIFICANCE TO HUMANS
No economic significance or importance, other than to unscrupulous merchants. ◆

Bennett's chinchilla rat
Abrocoma bennettii

TAXONOMY
Abrocoma bennettii Waterhouse, 1837, Aconcagua Province, Chile.

OTHER COMMON NAMES
French: Chinchilla du Chile; German: Chilenische Chinchillaratte; Spanish: Ratón chinchilla común.

PHYSICAL CHARACTERISTICS
7.5–9.8 in (19–25 cm) from the tip of the nose to the rump; tail 5.3–7.0 in (13–18 cm) long; up to 12.3 oz (350 g). Fur is brownish above and lighter below.

DISTRIBUTION
Altiplano of the Chilean Andes.

HABITAT
Rock crevasses and tunnels are used as burrows.

BEHAVIOR
Live in colonies of about six individuals. Burrows can be very close together. Often live in the same burrow with the degu (*Octodon degus*), another rodent of similar size and habits. Communicate using a variety of sounds.

FEEDING ECOLOGY AND DIET
Herbivorous; the diet includes seeds, fruits, stems, buds, leaves, and nuts. They are nocturnal feeders, and can climb trees in search of food.

REPRODUCTIVE BIOLOGY
Details of mating and reproductive behavior are ill-understood. If similar to *A. cinerea*, a gestation period of approximately 116 days and a litter size of one to six is expected.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted for its faux-chinchilla fur. ◆

Bolivian chinchilla rat

Abrocoma boliviensis

TAXONOMY
Abrocoma boliviensis Glanz and Anderson, 1990, Department of Santa Cruz, Bolivia.

OTHER COMMON NAMES
French: Chinchilla de Bolivie; German: Bolivienische Chinchillaratte.

PHYSICAL CHARACTERISTICS
6–10 in (15–25 cm) from tip of nose to rump; tail 2.4–7.2 in (6–18 cm) long; 7.1–10.6 oz (200–300 g). Fur is brownish above and lighter below.

DISTRIBUTION
Central Bolivia.

HABITAT
Inhabits rocky and shrubby mountainous regions at an elevation of about 8,200 ft (2500 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumed to be herbivorous and a nocturnal feeder.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

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Brian Douglas Hoyle, PhD

Spiny rats
(Echimyidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Echimyidae

Thumbnail description
Rat- to cat-sized rodents with large heads, and (in many species) spines in the fur of their backs; even species lacking spines, however, have another echimyid character: the presence of only four toes and a vestigial pollex (thumb)

Size
Head and body 4.13–18.9 in (10.5–48.0 cm); tail 0.2–16.5 in (0.5–42.0 cm); weight 0.46–2.9 lb (210–1,300 g)

Number of genera, species
20 genera; 78 species

Habitat
Rainforests, savannas, agricultural habitats, swamps, parks, and beach vegetation

Conservation status
Extinct: 3 species; Critically Endangered: 1 species; Vulnerable: 5 species; Lower Risk/Near Threatened: 9 species; Data Deficient: 5 species

Distribution
Central and South America

Evolution and systematics

The Echimyidae is one of the families of rodents with an evolutionary center in South America, and members of the family are still actively speciating in several genera (especially *Proechimys*). Four genera formerly present in the West Indies became extinct by the nineteenth century. The family shows remarkable convergent evolution with other rodent lineages, including a giant spiny rat (*Chaetomys*) that so closely resembles a porcupine that zoologists classified it with porcupines for many years until its true affinities were recognized. One of the most abundant and successful families of Neotropical mammals, virtually every type of lowland habitat has at least one echimyid species in it, and many have more than six. Though the least specialized echimyid genera (such as *Proechimys* and *Hoplomys*) have spines, the evolutionary trend within this family is to lose these. Thus, the more advanced and specialized genera lack spines in their fur. Fossil echimyids are known from the late Oligocene to Miocene and Pleistocene to recent. Several fossil forms reached considerable size. The family is closely related to the Capromyidae (Hutias) by the now-extinct Heteropsomyinids, the Caribbean spiny rats.

Spiny rats (*Proechimys* sp.) have stiffened guard hairs on their backs and rumps. (Photo by Tom McHugh at Bronx Zoo/Photo Researchers, Inc. Reproduced by permission.)

Physical characteristics

With the exception of those in the genera *Isothrix* and *Trichomys* and those in the subfamily Dactylomyinae, all

members of this family have spines in their fur, most notably on the mid-back and rump. Each spine consists of a single modified hair, and may be fine and needle-like or broad and stout. No matter what their shape or size, these spines narrow at the base to a narrow waist where they emerge from the skin.

The forefoot characteristically has only four functioning toes, with the fifth (the pollex, equivalent to the human thumb) being vestigial. The head is often large in proportion to the body, the nose is prominent, and the snout is blunt. The ears are small in proportion to the body. Many terrestrial genera have the ability to shed their tails. The family name is derived from the Greek *ekhinos*, a hedgehog, and *mus*, a mouse.

Distribution

Southern Honduras to northern Argentina.

Habitat

Primarily rainforest, though there are also species (e.g., *Caterodon* and *Trichomys*) adapted to more open and seasonally deciduous habitats.

Behavior

Generally nocturnal and burrow-using. Limited sociality, though *Clyomys* is colonial. Arboreal echimyid species use calls rather than scent marks to denote territories, a characteristic that is unusual in rodents.

Feeding ecology and diet

Members of this family are mostly unspecialized vegetarians, with some insects being eaten. Some species (e.g., *Kannabateomys amblyonyx*) have become specialized feeders on bamboo.

Reproductive biology

Echimyids do not follow the familiar rodent pattern of producing many low-investment young. Instead the litter size is small, the young are born well developed, and parental care is strong.

Conservation status

The IUCN lists one species as Critically Endangered (*Makalata occasius*); five species as Vulnerable (*Chaetomys subspinosus*, *Clyomys bishopi*, *Diplomys rufodorsalis*, *Echimys chrysurus*,

A spiny rat (*Thrichomys apereoides*) with young. (Photo by Claus Meyer/Minden Pictures. Reproduced by permission.)

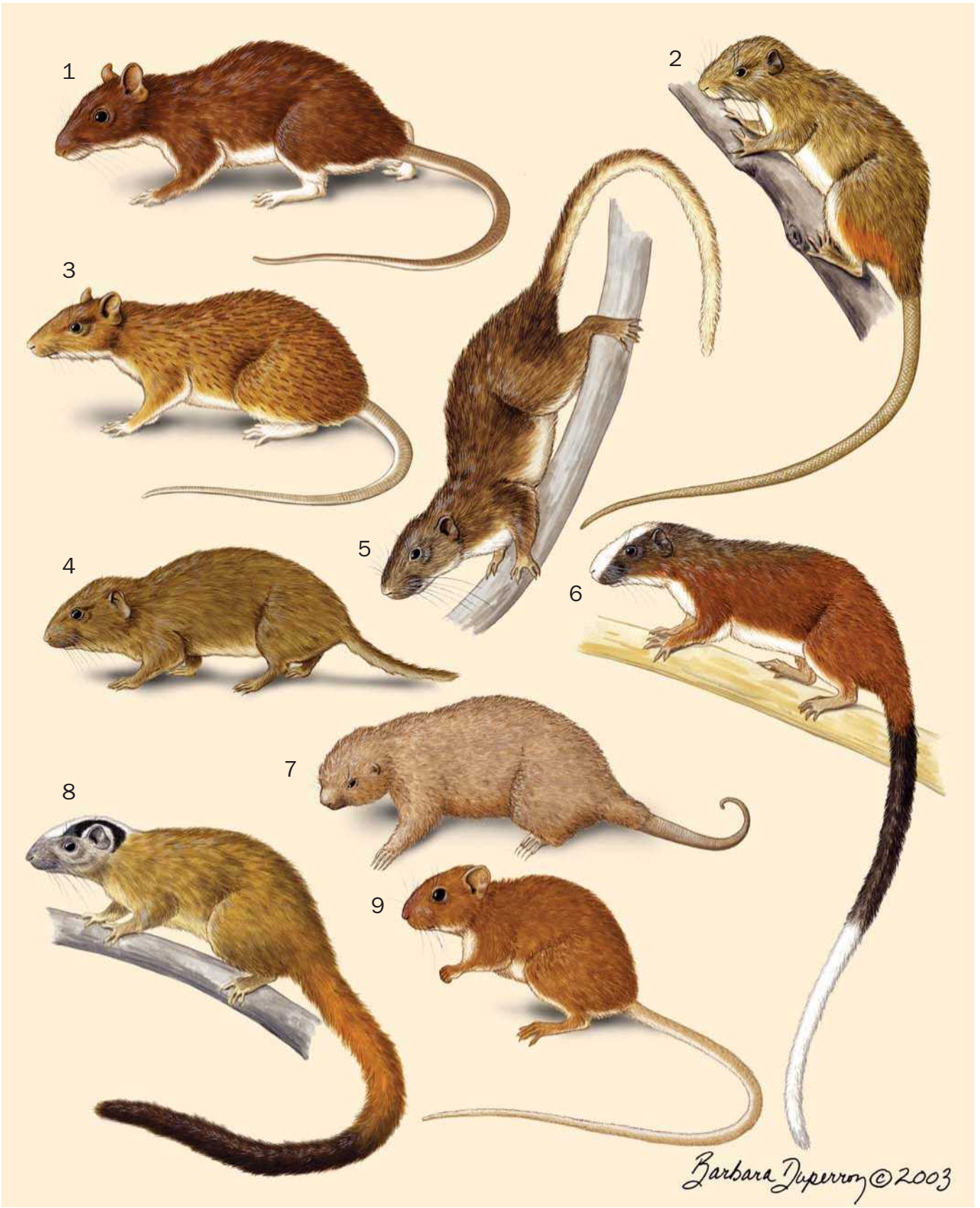
A male Venezuelan spiny rat (*Proechimys amphichoricus*) on a tree branch. (Photo by Rexford Lord/Photo Researchers, Inc. Reproduced by permission.)

E. thomasi); nine species as Lower Risk/Near Threatened (*Carterodon sulcidens*, *Diplomys caniceps*, *Echimys blainvillei*, *Isothrix bistriata*, *I. pagurus*, *Olallamys albicauda*, *O. edax*, *Proechimys albispinus*, *P. gorgonae*); and five species as Data Deficient (*Dactylomys peruanus*, *Echimys pictus*, *E. rhipidurus*, *Mesomys didelphoides*, *M. obscurus*).

Significance to humans

Some species are hunted, and others are considered agricultural pests. Several species have been used as laboratory animals and some of the rarer ones have been used as flagship conservation species for habitat preservation.

A close-up of a spiny rat (*Proechimys* sp.). (Photo by Hans Reinhard/OKAPIA/Photo Researchers, Inc. Reproduced by permission.)



1. Spiny rat (*Proechimys semispinosus*); 2. Amazon bamboo rat (*Dactylomys dactylinus*); 3. Armored rat (*Hoplomys gymnurus*); 4. Cerrado rat (*Caterodon sulcidens*); 5. Southern bamboo rat (*Kannabateomys amblyonyx*); 6. White-faced arboreal spiny rat (*Echimys chrysurus*); 7. Thin-spined porcupine (*Chaetomys subspinosus*); 8. Toro (*Isothrix bistriata*); 9. Montane bamboo rat (*Olallamys albicauda*). (Illustration by Barbara Duperron)

Species accounts

Spiny rat
Proechimys semispinosus

SUBFAMILY
Eumysopinae

TAXONOMY
Echimys semispinosus (Tomes, 1860), Esmeraldas, Ecuador.

OTHER COMMON NAMES
German: Igelratten; Spanish: Sacha cui (Peru); Surinamese: Maka alata.

PHYSICAL CHARACTERISTICS
The size of a house rat or white lab rat, but with a proportionately larger head and smaller ears. Fur (especially on the back and rump) is bristly to the touch due to the presence of stiffened, flattened hairs. Above is an orangish brown, and below is pure white. The tail is naked and is often pale toward the end. A weakness in the fifth vertebra of the tail means that, like lizards, *Proechimys* rats can break off the tail as distraction technique against predators. A rare recessive gene means that some "spiny" mice actually lack spiny fur.

DISTRIBUTION
Southern Honduras to coastal Colombia and Peru, only west of the Andes in South America.

HABITAT
Forest, often near waterways. Prefer dense vegetation, especially around treefalls.

BEHAVIOR
P. semispinosus does not dig its own burrow, but uses available depressions, including cavities in rocks, holes in logs, or burrows of other animals. This species is nocturnal, with a small home range, 0.2–3.7 acres (0.1–1.5 ha), with that of the female being smaller than the male's range. Population density fluctuates seasonally, nearly quadrupling at the end of the rainy season. There is considerable overlap in home ranges, with only burrows specifically defended, and only against members of the same species and sex. Females make a variety of birdlike twitterings to their young as they follow her around the territory.

FEEDING ECOLOGY AND DIET
Members of this family are important seed predators, eating both fallen fruit and the cached fruit of agoutis and acouchis. They also feed on fungi, including those fungi with symbiotic mycorrhizal associations with forest trees. For such fungi, they act as important dispersal agents. Members of this species will habitually take foods back to the same spot to eat them, resulting in small piles of debris that, when collected, can reveal to biologists what the animals have been eating.

REPRODUCTIVE BIOLOGY
Opportunistic breeders, these animals will breed throughout the year if conditions permit. The litter size ranges between three and six young, a large litter for an echimyid. However, in typical echimyid fashion, the young are large (birth weight 0.7 oz, or 22 g), though not as well coordinated and furred as in other genera. The estrous cycle lasts some 23 days, and gestation is 60–65 days. Weaning occurs in three to four weeks and puberty is reached in five months. Wild individuals commonly survive more than two years. Often the most numerous terrestrial mammal in a rainforest, *Proechimys* species provide important food sources for small carnivores such as ocelots and jaguarondis as well as for bushmasters and other snakes.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Trapped for meat by rural residents. ◆

Armored rat
Hoplomys gymnurus

SUBFAMILY
Eumysopinae

TAXONOMY
Echimys gymnurus (Thomas, 1897), Cachavi, Esmereldas Province, Ecuador.

OTHER COMMON NAMES
English: Thick-spined rat; German: Lanzenratte; Spanish: Rata espinosa.

PHYSICAL CHARACTERISTICS
Head and body length 8.6–12.5 in (22–32 cm); tail 5.9–9.8 in (15–25 cm); weight 7.7 oz to 1.7 lb (218–815 g). Males are considerably bigger (up to 38%) than females. This terrestrial

rodent has very thick and well developed spines, especially on its back where they are up to 1.1 in (3 cm) long and 0.08 in (2 mm) in diameter. Spines on the back are white at the base and tipped with black. On the flanks, they are tipped with orange and banded to the base with dusty orange and black. The spines are loosely fixed to the skin and fall out when the pelage is brushed the wrong way. There is soft fur interspersed with the spines and lying beneath them. Spines are most strongly developed on the mid-back, rump, and thighs. The belly lacks spines and is white. Members of this species can drop their tails to distract predators.

DISTRIBUTION
Southern Honduras through western Colombia to northwest Ecuador. Not found east of the Andes.

HABITAT
Hoplomys gymnurus lives in grassy clearings in rainforest, brush, and deserted farm lands, and has not been recorded at altitudes above 2,625 ft (800 m). The species shows a distinct preference for cooler moist areas, and in dryland forests is found only in forests in moister steep ravines.

BEHAVIOR
The territory is very small and is often centered around a decaying log, under which it may hide in the burrow it digs. This consists of a small chamber with dry leaves at the bottom of a short simple shaft. This species makes runways in dense vegetation.

FEEDING ECOLOGY AND DIET
The diet consists of fruits, seeds, and browse, but insects are also eaten.

REPRODUCTIVE BIOLOGY
Litter size of two to three. Reproduction is seasonal. Young are born furred, with open eyes and the ability to walk. This species may be monogamous, with a territory shared by a mated pair.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Cerrado rat
Carterodon sulcidens

SUBFAMILY
Eumysopinae

TAXONOMY
Echimys sulcidens (Lund, 1841), Lagoa Santa, Minas Gerais, Brazil. First described in 1841 from remains in fossil owl pellets. The first live specimen was found in 1851. Very few have been found since.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head and body length 6.1–7.9 in (15.5–20 cm). Tail 2.7–3.1 in (6.8–8 cm). Yellow-brown above, flanks grayish, with a reddish throat and neck. Under parts are yellowish with a white midline blotch. The tail is thin, and black above and pale yellow below. Fur on the back has spines and bristles. Spines are flexible and end in long hairlike projections.

DISTRIBUTION
The central uplands of Brazil.

HABITAT
Cerrado vegetation (a grassland with sparse trees and seasonal rains that looks a lot like the African savanna).

BEHAVIOR
This species digs a shallow burrow in soil between pockets of dense vegetation, and lines this burrow and the chamber at the bottom with leaves and grasses. Emerges late afternoon or early evening to feed.

FEEDING ECOLOGY AND DIET
Not known. May feed on roots and herbs.

REPRODUCTIVE BIOLOGY
Breeds in late dry season. Further information is not yet known.

CONSERVATION STATUS
Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Toro
Isothrix bistriata

SUBFAMILY
Echimyinae

TAXONOMY
Isothrix bistriata Wagner, 1845, Río Guaporé, Brazil.

OTHER COMMON NAMES
English: Yellow-crowned brush-tailed tree rat.

PHYSICAL CHARACTERISTICS
Fur long and soft, no spines. Upperparts are yellowish gray, orange, or pale yellow below. Head has a pale yellow crown, extending onto neck. Below this is a wide black stripe that nearly merges on nape. The tail is long and thickly furred, with orange-yellow fur closer to the rump and black toward the end. Feet are short and broad with strong claws.

DISTRIBUTION
Amazon and Orinoco basin rainforests, as well as eastern Peru and Bolivia.

HABITAT
Primary forest, near streambanks.

BEHAVIOR
This species is nocturnal, and feeds in trees in a squirrel-like manner. It dens in a hole in a small tree (often a dead palm) some 33 ft (10 m) from a favored tall tree, and spends afternoons with its head sticking out of the den hole. Some levels of sociality are possible, as small groups have been observed foraging together.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Little known. Litter size is probably one.

CONSERVATION STATUS
Lower Risk/Near Threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

White-faced arboreal spiny rat
Echimys chrysurus

SUBFAMILY
Echimyinae

TAXONOMY
Myoxus chrysurus (Zimmerman, 1780), Suriname.

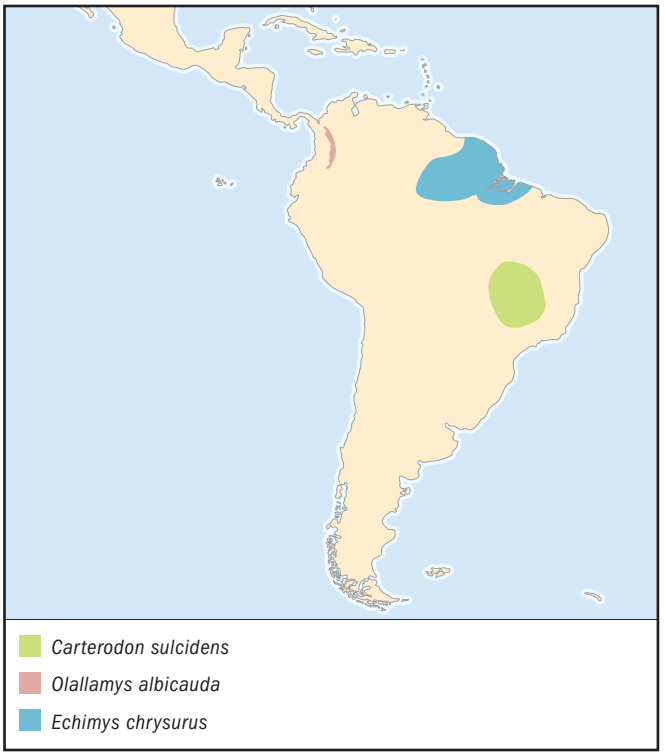
OTHER COMMON NAMES
Portuguese: Conoco, sauia banderira.

PHYSICAL CHARACTERISTICS
Fur is bristly and spiny, with the upper parts brownish red, while the belly and throat are buff colored. A broad white blaze runs from the nose to behind the ears. The last three-quarters of the tail is white with a yellowish tip. Paws are white.

DISTRIBUTION
Guanas and northeastern Brazil.

HABITAT
In dense vegetation along riverbanks and in flooded areas. Uses upper stories of vegetation.

BEHAVIOR
The same size as a familiar European/North American squirrel, but does not move like one, slinking along branches rather than bounding. This species builds nests of dry leaves in hollow trunks or tree holes, and usually maintains two holes. *Echimys chrysurus* is nocturnal, and may live in small groups, which may be an extended family. Individuals give loud territorial calls at night.



FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Young born fully furred and with eyes open. Litter size one or two.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Amazon bamboo rat
Dactylomys dactylinus

SUBFAMILY
Dactylominae

TAXONOMY
Echimys dactylinus (Desmarest, 1817), upper Amazon.

OTHER COMMON NAMES
English: Singing rat; Spanish: Cocopitzu (Ecuador), pacamama (Peru).

PHYSICAL CHARACTERISTICS
The head and body are 11.8 in (30 cm), with a tail measuring approximately 15.7 in (40 cm). Weight is 1.3–1.7 lb (600–750

g). Stocky in appearance with square muzzle. Head is grayish beige with darker stripe between ear and eye. Back and flanks are grayish with a rusty wash, grading to pure rusty orange on base of tail and thighs. Underfur is black, and belly, chest and throat are white. The fur is soft and lacks spines and bristles. Only the base of the tail is haired. The paws are remarkably primate-like, with the third and fourth digits expanded in length and width for climbing (hence the genus name, which means "hand mouse"). Unlike almost all other rodents, the underside of the paws lack pads, and are broad and covered with hundreds of grip-enhancing, stud-like tubercles. Males have a gland in middle of the chest, which imparts a strong musky smell. The eye has a horizontal pupil, like a goat.

DISTRIBUTION
Lowland Amazon of southern Colombia, Eastern Ecuador, Peru and Brazil. Other members of the genus are known to occur in altitudes up to 5,900 ft (1,800 m).

HABITAT
Formerly in thick vegetation of tree falls and along river sides, this species is now common in forested areas disturbed by logging. Shows a strong preference for areas rich in vines and bamboo clumps.

BEHAVIOR
This species is nocturnal, beginning activity at dusk and finishing before dawn. It spends the day in vine-rich vegetation, and has two to three regular resting sites, often in leaf masses caught in palm crowns. The home range is small, recorded as 0.6 acres (0.23 ha). Movements are slow and cautious, and this species does not move far per night—as little as 148 ft (45 m). *Dactylomys dactylinus* occurs in pairs, and both sexes give a staccato territorial "boop...boop...boop" call during the evening. The call, amplified by the unusually enlarged larynx, is a series of deep-pitched staccato pulses well-adapted to maximum propagation in dense vegetation. The male does much of the calling, though a pair may duet. Calls are especially common in early evening, an hour or so after dusk. Males mark stems with the chest gland. If two males meet, they will make an "explosive quacking," as an appeasement call.

FEEDING ECOLOGY AND DIET
Eats young bamboo shoots, leaves, and stems, plus a variety of other plants and fruits, and some insects. The gut has an enlarged large intestine with a pseudo-caecum. This increases the passage time of food and allows more energy and nutrients to be extracted. At 1.3–1.5 lb (600–700 g), *Dactylomys* is the smallest of the Neotropic's specialized arboreal folivores; if it were any smaller, it would not be able to offset the heat loss from a small body with the slow rate at which energy is received from its poor-quality food.

REPRODUCTIVE BIOLOGY
Litter size is two.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The object of or a character in a number of local legends. ◆

Southern bamboo rat
Kannabateomys amblyonyx

SUBFAMILY
Dactylominae

TAXONOMY
Dactylomys amblyonyx (Wagner, 1845), São Paulo, Brazil.

OTHER COMMON NAMES
German: Bambus-Fingerratte; Spanish: Rata de las Taquaras (Argentina).

PHYSICAL CHARACTERISTICS
An individual *Kannbaetomys amblyonyx* weighs up to 1.3 lb (600 g), and its back, flanks, and head are a dull orangey-buff, while its under parts are off-white. Fur is thick and soft, lacking bristles, and the tail is thickly haired. The third and fourth digits are greatly elongated and expanded to provide a wide, strong grip when climbing thick round bamboo stems. Claws are modified into nails. The muzzle is squarish.

DISTRIBUTION
Southeastern Brazil (Cerea, Rio Grande, Parana, and Rio Grande do Sul), northeastern Argentina (Missones Province), and southeastern Paraguay.

HABITAT
Bamboo thickets along stream banks.

BEHAVIOR
Kannbaetomys amblyonyx is nocturnal, solitary, slow moving, and highly territorial. The species makes loud territorial calls, defending its patch of bamboo. Individuals are found outside bamboo stands only when moving from one patch to another (every few years, plants in a bamboo stand will flower simultaneously and then die). If found on the ground in their territory, they are avoiding troops of foraging capuchin monkeys (*Cebus apella*), which may harass them and even kill them. There is no overlap in territories of individuals. The home range size varies from 1,780 to 11,820 ft^2 (165–1,098 m^2). Radio-collared individuals traveled an average of 843 ft (257 m) a night. In native *Guada* bamboo, *K. amblyonyx* is reported to make large, complex nests. In stands of introduced bamboo they do not make nests, but have three to four regular resting sites in dense patches of stems and leaves. They leave and enter such areas half an hour before sunset and sunrise. The animal's slow movements and small territory size are reflective of its poor-quality food.

FEEDING ECOLOGY AND DIET
Climbs bamboo stems during the night to eat succulent shoots, young stems, and young leaves. Prefers the native giant bamboo *Guada*, but is also able to eat the introduced *Phyllostachys* and *Bambusa tuloides*.

REPRODUCTIVE BIOLOGY
Litter size one or two. Subadults may travel with mother for a period after weaning.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Formerly considered to be threatened by habitat destruction, but now considered to be more adaptable and capable of using alien bamboos. Is being used by conservation groups as a charismatic species to promote conservation of groves of native

giant bamboo and the rich bird fauna (27 habitat specific species) associated with this habitat, and who are less adaptable than the bamboo rat. ◆

Montane bamboo rat
Olallamys albicauda

SUBFAMILY
Dactylominae

TAXONOMY
Thrinacodus albicauda (Günther, 1879), Medellin, Antioqua Department, Colombia. *Thrinacodus* had been used since the animals' original description until American zoologist Louise Emmons pointed out that this name had already been given to a fossil shark. Under the rules governing the naming of animals, no two may share the same name, so the species was given a new name. The new name celebrated the Ecuadorian collector Carlos Olalla and his four sons Alfonso, Manuel, Ramón, and Rosalino, who collected mammals all over the Amazon and elsewhere in South America between 1922 and 1969.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Seven to 9.5 in (18 to 24 cm) in body length, with a tail up to 13.7 in (35 cm). Fur on the back and flanks is reddish, and the belly fur is yellowish white. The thick soft fur lacks spines, but possesses other internal characteristics of the family.

DISTRIBUTION
Northwest and central Colombia.

HABITAT
Groves of *Chusquea* bamboo in the montane forests of the Colombian Andes, 6,560–7,550 ft (2000–2,300 m) in altitude.

BEHAVIOR
Nocturnal and arboreal, with the long tail used as a balancing pole. These animals make a whistling cry.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Lower Risk/Near Threatened due to habitat destruction.

SIGNIFICANCE TO HUMANS
None known. ◆

Thin-spined porcupine
Chaetomys subspinosus

SUBFAMILY
Chaetomyinae

TAXONOMY
Hystrix subspinosa (Olfers, 1818), Cameta, Para, Brazil. Formerly classed with the Neotropical porcupines (Erythrozontidae), but now recognized as an echimyid and as a remarkable example of parallel evolution. Characteristics that led to this reassessment included the retention of deciduous premolars throughout life and the lack of an internal carotid artery.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Rabbit-sized and weighing some 2.87 lb (1.3 kg), *C. semispinosus* has its back covered with long thin bristles. On the head, neck, and shoulders, these are more spine-like. Like sloths, this species has low levels of muscle mass for its body size.

DISTRIBUTION
A small portion of Atlantic Coastal Rainforest in southeastern Brazil, in the states of Sergipe, Bahia, Espirito Santo and Rio de Janeiro. Not seen after 1952, but was rediscovered in 1987.

HABITAT
Rainforest and secondary scrub, cocoa plantations.

BEHAVIOR
Nocturnal, arboreal, solitary, and slow moving. Spends the day asleep and nearly 70% of the night resting between bouts of moving, feeding, and grooming. Tail is probably not fully prehensile, but capable of a tight grip and so assists in climbing. Like a sloth, descends to ground to defecate and urinate. Lethargic life in keeping with ingestion and digestion of poor quality, hard-to-digest forage.

FEEDING ECOLOGY AND DIET
Leaves, plus some insects and fruit.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Vulnerable. However, ability to live in modified habitats may mitigate the fact that it has a very restricted distribution in an area of very rapid deforestation.

SIGNIFICANCE TO HUMANS
None known. Eats cocoa pods but punitive hunting not reported. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Rufous tree rat *Diplomys labilis*	Upperparts rusty brown, reddish, or orange buffy mixed with black; underparts buffy, reddish, or reddish white. Head and body length 9.8–18.9 in (25–48 cm); tail length 7.9–11 in (20–28 cm).	Forests or clearings, near water. Nocturnal.	Panama, western Colombia, and northern Ecuador.	Grass, sugar cane, bananas, other fruits, and nuts.	Not threatened
Armored spiny rat *Makalata armata*	Upperparts dark yellowish brown, heavily lined with black; back speckled with yellow. Spines are pale gray at the base and darker at the top. Underparts pale yellowish or grayish brown with no spines. Short tail, many lose their tails. Head and body length 6.7–8 in (17–20.2 cm); tail length 7.2 in (18.2 cm); weight 5.2–11.2 oz (147–317 g).	Lives in trees, preferably along rivers.	Andes of northern Ecuador and Colombia, Venezuela, Guianas, Amazon Basin of Brazil, Tobago, and Trinidad.	Grass, sugar cane, bananas, other fruits, and nuts.	Not listed by IUCN
Bishop's fossorial spiny rat *Clyomys bishopi*	Upperparts grayish brown and black, mixed with rufous; underparts whitish or buffy. May have grayish patches at throat, chest, or belly. Fur is bristly. Head and body length 4.1–9.1 in (10.5–23 cm); tail length 2.2–3.4 in (5.5–8.7 cm); weight 0.74–1.4 oz (21–39 g).	Live in clearings. Build burrows and appear to live in communities.	São Paulo, Brazil.	Grass, sugar cane, bananas, other fruits, and nuts.	Vulnerable
Guiara *Euryzygomatomys spinosus*	Upperparts drab brown; underparts whitish. Hands and feet are brown. Spines present on back. Head and body length 6.7–10.6 in (17–27 cm); tail length 2–2.2 in (5–5.5 cm). Males may be somewhat larger than females.	Areas covered with grass or bushes, preferably near water. Nocturnal and apparently fossorial.	Southern and eastern Brazil, northeastern Argentina, and Paraguay.	Grass, sugar cane, bananas, other fruits, and nuts.	Not listed by IUCN
Tuft-tailed spiny tree rat *Lonchothrix emiliae*	Upperparts dark brown, buffy spots in shoulder region; sides are tawny; underparts are pale tawny. Spines present on back; belly is somewhat spiny. Tail is mostly furless, but tufted at the end. Head and body length about 7.9 in (20 cm); tail length about 7.5 in (19 cm).	Lives in forests and is likely arboreal.	Central Brazil, south of the Amazon River.	Grass, sugar cane, bananas, other fruits, and nuts.	Not threatened
Brazilian spiny tree rat *Mesomys didelphoides*	Upperparts various shades of brown; spines may have dark brown and pale buffy bands. Underparts orangish, pale buffy, or whitish. Spines present on back. Brown, tufted tail. Head and body length 5.9–7.9 in (15–20 cm); tail length 4.4–8.7 in (11.3–22 cm).	Lives in forests at elevations of 295–6,400 ft (90–1,950 m) and is likely arboreal.	Brazil.	Grass, sugar cane, bananas, other fruits, and nuts.	Data Deficient
Punare *Thrichomys apereoides*	Upperparts dull brown; underparts grayish to white. Soft fur, with no spines or bristles; hairy tail. Head and body length 7.9–11.4 in (20–29 cm); tail length 7.1–8.7 in (18–22 cm); weight 10.6–15.9 oz (300–450 g).	Rocky and thickly vegetated areas, and swamps. Generally active at twilight.	Eastern Brazil and Paraguay.	Cotton seeds or fruits, coconuts, and cacti.	Not threatened

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Adrian A. Barnett, PhD

Hutias
(Capromyidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Capromyidae

Thumbnail description
Medium to large stockily built rodents with broad rounded heads

Size
14–32 in (36–80 cm); 1.1–18.7 lb (0.5–8.5 kg)

Number of genera, species
8 genera; at least 24 species

Habitat
Forest, woodlands, scrub, cliffs, and mangroves

Conservation status
Extinct: 6 species; Critically Endangered: 6 species; Vulnerable: 4 species; Lower Risk/Near Threatened: 2 species

Distribution
Caribbean

Evolution and systematics

The Capromyidae represents a Caribbean radiation of the south and central American Hystricognath rodents closely allied to the Myocastoridae (coypu) and Echimyidae (spiny rats). Some subfamilies have been varyingly classified across all three families and the Myocastoridae is still included within the Capromyidae by some authorities.

Extensive extinction has occurred within this family and a number of additional species are known from Holocene fossil deposits. The exact extinction date of many is unclear and the possibility exists that some species believed to be extinct may still exist on small islands within the Caribbean.

The number of species is difficult to accurately assess with so many recent extinctions. Some sources cite as many as 33 species, although some of these are only known as sub-recent fossils. The status and correct taxonomic determination of many species is still unclear and the family is in need of taxonomic revision.

Physical characteristics

Hutias have many typical Hystricognath (caviomorph) features. They are heavily built rodents with broad rounded heads. They have relatively small eyes and short rounded ears. Tail length varies from around 80% of the head and body in *Mysateles* down to only 10% in *Geocapromys*. In *Mysateles* the tail is partially prehensile. The fur is generally thick but harsh and varies from dark, almost blackish, to very pale gray. Most species are paler ventrally.

Distribution

The entire family is endemic to the Caribbean. Many species have very restricted distributions to either a single or small group of islands. Extant species still occur on or in the cays around Cuba, Jamaica, the Bahamas, and Hispaniola. Three species are known only from their type localities, one of which, *Mysateles garridoi*, is known only from a single specimen. Only two species are considered to be relatively common where they occur, *Capromys pilorides* and *Mysateles prehensilis*.

Habitat

Hutias generally inhabit forested or rocky areas where they are mainly arboreal. They are known to climb well and use tree holes and rock crevices as dens. *Mesocapromys auritus* and *M. angelcabrerai* are known to build large obvious stick nests in areas of mangrove forest, some of which may be communal.

Most species are nocturnal, although *Capromys pilorides* is reported to be both nocturnal and diurnal. *Geocapromys ingrahami* occurs at densities of up to 30 individuals per hectare on East Plana Cay in the Bahamas occupying rough limestone cliffs and scrub. Very little ecological data exists on most species.

Behavior

They are generally regarded as living in social family groups, agonistic encounters are few and individuals appear

A Cuban hutia (*Capromys pilorides*) in the trees of Zapatas Swamp, Cuba. (Photo by Animals Animals ©Red Levin. Reproduced by permission.)

not to be territorial. Reports of a solitary social structure may result from displaced individuals or very small families. *Geocapromys* and *Capromys* are tolerant of conspecifics in captivity and will live in loose groups. Communal nesting has been reported in both *Mesocapromys* and *Plagiodontia* in the wild. Social groups frequently groom each other and a variety of low vocalisations are used.

Runs in and around natural rock crevices and fecal deposits often reveal the presence of hutias. The large stick nests of some *Geocapromys* in the branches of mangrove forest can also reveal the presence of hutias in an area.

The Bahamian hutia (*Geocapromys ingrahami*) was thought to be extinct until 1966. (Photo by Tom McHugh at the Bronx Zoo/Photo Researchers, Inc. Reproduced by permission.)

Of all hutias, the Jamaican hutia (*Geocapromys brownii*) has the shortest tail. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Hutias are generally herbivorous feeding on a variety of bark, leaves, and fruits. They also occasionally eat lizards and other small animals. The stomach of *Capromys* is highly complex for a rodent, comprising three chambers each separated by a constriction. They possess open rooted molars and premolars that continue to grow throughout life.

The Jamaican hutia (*Geocapromys brownii*) lives in limestone rich environments. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

A Hispaniolan hutia (*Plagiodontia aedium*) rests on a tree branch. (Photo by Tom McHugh/Pt. Defiance Zoo, Tacoma/Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

Hutias give birth to small litters of highly precocial offspring following a relatively long gestation. The estrous cycle is normally 10 days, although in *Capromys* it has been reported as 16 days. Gestation in all species is between 110–150 days. A single infant is normal but litters of up to three for *Geocapromys brownii* or even six for *Capromys pilorides* have been known.

Young are highly precocial and mobile at birth, in most species weighing around 5–10% of adult weight. Breeding is probably aseasonal in the wild and up to two litters a year may be produced.

Conservation status

Hutias are highly threatened and many of the species are highly restricted island endemics. Two of the eight genera are totally extinct and a third, *Isolobodon*, is known only from skeletal remains and is most likely also extinct. Of the 13 extant species, only two are considered secure and the remaining 11 are all threatened or Near Threatened. In 2002 the World Conservation Union (IUCN) considers six of these to be Critically Endangered.

The major threats are hunting for food, deforestation of habitat for agriculture, and the introduction of cats, mongoose, and black rats. Despite most hutias being protected by law urgent conservation action is required to safeguard their survival.

Significance to humans

Hutias have long been used as a food source by native peoples in the region. Indeed, several species are known from skeletal remains in kitchen middens. They were moved between islands by people and possibly even partially domesticated. Some extinctions occurred prior to the arrival of Europeans in the region although these have accelerated since this time.

1. Prehensile-tailed hutia (*Mysateles prehensilis*); 2. Jamaican hutia (*Geocapromys brownii*); 3. Hispaniolan hutia (*Plagiodontia aedium*); 4. Cuban hutia (*Capromys pilorides*). (Illustration by Brian Cressman)

Species accounts

Cuban hutia
Capromys pilorides

TAXONOMY
Capromys pilorides (Say, 1822), Cuba.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
18–35 in (46–90 cm); 6.6–18.7 lb (3–8.5 kg). Thick fur is darker gray to black above and lighter below.

DISTRIBUTION
Mainland Cuba and many of the islands and cays in the Cuban archipelago.

HABITAT
Forest, mangrove, scrub, and rocky areas.

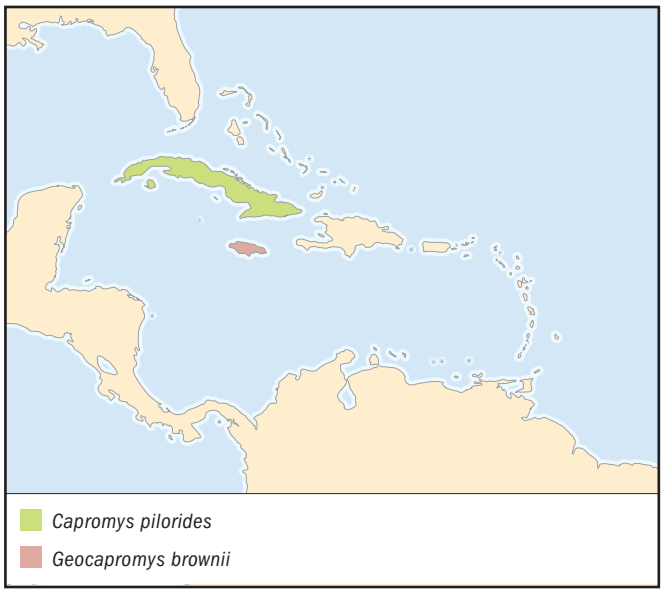
BEHAVIOR
Mainly arboreal and diurnal, living in extended family groups, sometimes at high density.

FEEDING ECOLOGY AND DIET
Bark, leaves, fruits, and some small vertebrates.

REPRODUCTIVE BIOLOGY
Litters of one to six young are born fully furred with their eyes open at birth. Gestation period varies from 110–140 days.

CONSERVATION STATUS
Not threatened; the only comparatively common species of hutia.

SIGNIFICANCE TO HUMANS
Extensively hunted for food. ◆



Jamaican hutia
Geocapromys brownii

TAXONOMY
Geocapromys brownii (Fischer, 1829), Jamaica.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
16–20 in (40–50 cm); 2.2–4.4 lb (1–2 kg). Fur is darker gray to black above and lighter below.

DISTRIBUTION
Jamaica.

HABITAT
Scrub and rocky areas.

BEHAVIOR
Nocturnal and secretive, living in social groups which nest communally in the cracks and fissures in the rocks.

FEEDING ECOLOGY AND DIET
Bark, foliage, and fruits.

REPRODUCTIVE BIOLOGY
Litters of one to three young are born fully furred with their eyes open at birth. The gestation period is around 120 days.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Extensively hunted for food. ◆

Hispaniolan hutia
Plagiodontia aedium

TAXONOMY
Plagiodontia aedium Cuvier, 1836, probably Haiti. Three subspecies have been recognized.

OTHER COMMON NAMES
None known.

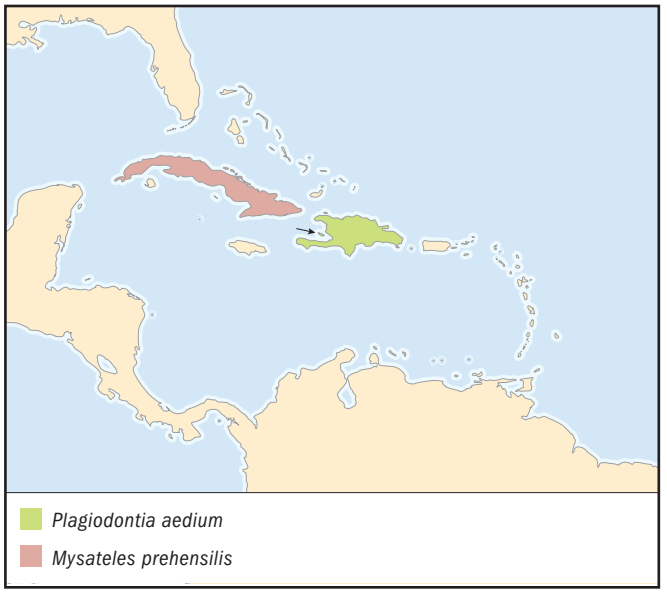
PHYSICAL CHARACTERISTICS
17–22 in (43–56 cm); 2.2–3.3 lb (1–1.5 kg). Fur is darker above and lighter below.

DISTRIBUTION
Hispaniola, La Gonave Island.

HABITAT
Forested hillsides and ravines.

BEHAVIOR
Nocturnal and mainly arboreal, living in pairs or small groups.

FEEDING ECOLOGY AND DIET
Leaves, fruits, and roots.



REPRODUCTIVE BIOLOGY
Litters of one to two highly precocial youngsters born after a gestation of around 120–150 days.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Hunted for food and agriculture has encroached upon its habitat. ◆

Prehensile-tailed hutia
Mysateles prehensilis

OTHER COMMON NAMES
None known.

TAXONOMY
Mysateles prehensilis (Poeppig, 1824), Cuba.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
22–30 in (55–75 cm); 3.1–4.2 lb (1.4–1.9 kg). Fur is darker gray to black above and lighter below.

DISTRIBUTION
Cuba.

HABITAT
Forest and mangrove.

BEHAVIOR
Arboreal and partly diurnal, they climb exceptionally well and have partially prehensile tails.

FEEDING ECOLOGY AND DIET
Leaves, bark, and fruit.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not threatened; one of only two non-threatened species of hutia.

SIGNIFICANCE TO HUMANS
Widely hunted for food. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Eared hutia *Mesocapromys auritus* English: Large-eared hutia	Upperparts a variety of buff, yellow, red, gray, brown, and black shades; underparts usually paler. Coat has long, coarse guard hairs and softer underfur. Hairy tail. Head and body length 8.7–19.7 in (22–50 cm); tail length 5.9–11.8 in (15–30 cm); weight 17.6–24.7 oz (500–700 g).	Forests or rocky areas. Seem to be basically arboreal.	Las Villas Province, Cuba.	Leaves, bark, fruits, lizards, and other small animals.	Critically Endangered
Dwarf hutia *Mesocapromys nanus*	Upperparts a variety of buff, yellow, red, gray, brown, and black shades; underparts usually paler. Coat has long, coarse guard hairs and softer underfur. Hairy tail. Head and body length 8.7–19.7 in (22–50 cm); tail length 5.9–11.8 in (15–30 cm); weight 17.6–24.7 oz (500–700 g).	Forests or rocky areas. Seem to be basically arboreal.	Matanzas Province, Cuba.	Leaves, bark, fruits, lizards, and other small animals.	Critically Endangered
Black-tailed hutia *Mysateles melanurus* English: Bushy-tailed hutia	Upperparts a variety of buff, yellow, red, gray, brown, and black shades; underparts usually paler. Coat has long, coarse guard hairs and softer underfur. Hairy tail. Head and body length 8.7–19.7 in (22–50 cm); tail length 5.9–11.8 in (15–30 cm); weight 17.6–24.7 oz (500–700 g).	Forests or rocky areas. Seem to be basically arboreal. May be nocturnal.	Eastern provinces of Cuba.	Leaves, bark, fruits, lizards, and other small animals.	Lower Risk/Near Threatened
Bahamian hutia *Geocapromys ingrahami* English: Ingraham's hutia	Upperparts yellowish gray, dark brown, or blackish; underparts buffy gray or dusky brown. Short, dense fur, and short, rounded ears.	Small, semi-arid island of East Plana Key, Bahamas. Almost completely nocturnal, feeding at night.	East Plana Key, Bahamas.	Bark, small twigs, and leaves.	Vulnerable
Samana hutia *Plagiodontia ipnaeum*	Living species of the genus have short, dense fur with upperparts brownish or grayish and underparts buffy. Likely larger than 2.8 lb (1,267 g).	Forests from sea level to 6,560 ft (2,000 m). Likely nocturnal and arboreal.	Hispaniola.	Likely vegetation and small animals.	Extinct
Puerto Rican hutia *Isolobodon portoricensis*	Similar in size to *Plagiodontia.*	No information on this possibly extinct species.	Hispaniola and offshore islands; introduced on Puerto Rico, St. Thomas, St. Croix, and Mona Islands.	Likely vegetation and small animals.	Critically Endangered
Imposter hutia *Hexolobodon phenax*	Similar in size to *Capromys pilorides.*	No information on this extinct species.	Hispaniola and La Gonave Island.	Likely vegetation and small animals.	Extinct

Resources

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Mike J. R. Jordan, PhD

Giant hutias
(Heptaxodontidae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Heptaxodontidae

Thumbnail description
Very large island rodents with distinctively shaped molars

Size
31–440 lb (14–200 kg)

Number of genera, species
4 genera, 5 species

Habitat
Lowland and montane tropical rainforest

Conservation status
All species are presumed extinct

Distribution
Several islands of the Greater and Lesser Antilles

Evolution and systematics

The native rodents of the West Indies, living and extinct, are an extraordinarily diverse group. They are sorted by taxonomists into four families, 15 genera, and about 60 species, including family Heptaxodontidae, with four genera and five species.

Only Pleistocene and Recent (post-Pleistocene to present) fossils and subfossils are known for the Heptaxodontidae, most of these recovered from caves. The Heptaxodontidae most likely arose in isolation on the islands of the Antilles from an ancestral species that rafted from the mainlands of the Americas. Taxonomists have tried to link the family with the families Myocastoridae (nutria), Chinchillidae (chinchillas and viscachas), Capromyidae (hutias), and Dinomyidae (pacaranas and related species).

At least one genus, *Quemisia*, may still have been extant when Native Americans first occupied the islands, in 7000 B.C., while *Clidomys* and *Amblyrhiza* apparently became extinct during the Pleistocene Epoch before the arrival of humans on the Antilles.

Physical characteristics

The skulls of heptaxodontids are massive, resembling those of the nutria (Myocastoridae). The rostrum (snout) was massive, the bullae (bones of the inner ear) were small, and many of the skulls bear sagittal crests (bony ridges on the top of the skull to provide added anchorage for strong jaw mucles).

The cheek teeth, or molars, were strongly hypsodont ("high-crowned"), each having four to seven laminae (layers), set more or less parallel while arranged at angles to the long axis of the skull. *Quemisia* and *Elasmodontomys* had teeth and jaw adaptations for propalinal (side-to-side) chewing.

The skulls and postcranial bones suggest that the Hepataxodontidae had heavy-set bodies. All species were considerably larger than the general run of rodents today. *Amblyrhiza* was nearly the size of a black bear (*Ursus americanus*).

Distribution

Amblyrhiza inhabited the islands of Anguilla and St. Maarten when both islands were part of a much larger, dry landmass now called the Anguillan Bank. *Quemisia* lived on Hispaniola, *Elasmodontomys* in Puerto Rico, and *Clidomys* in Jamaica.

Habitat

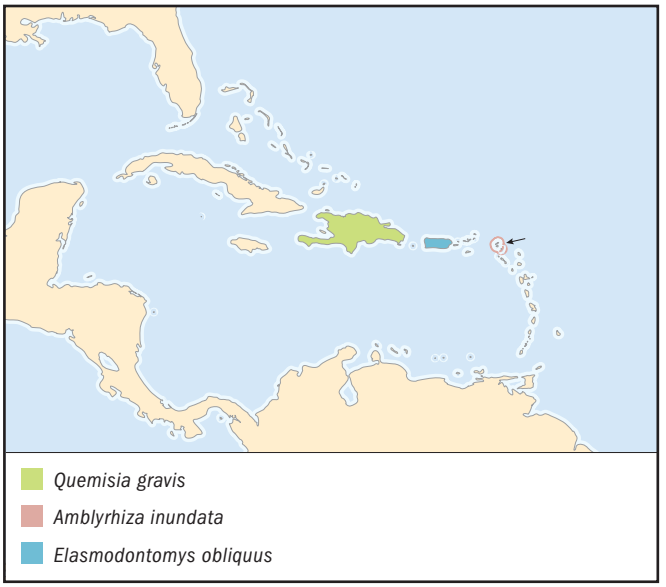
Probably lowland and montane tropical rainforest.

Behavior

Nothing is known.

Feeding ecology and diet

Unknown. Most likely predominantly or completely herbivorous.



Reproductive biology

Nothing is known. Mammals in the size range of the Heptaxodontidae, on islands with limited areas and resources, would have tended toward smaller litters.

Conservation status

All heptaxodontid species are considered extinct. The presence of remains of some species among human refuse and artifacts suggests that they were hunted as food by Native Americans, who began settling the Antilles in 7000 B.C. *Clidomys* and *Amblyrhiza* probably became extinct long before the Native American colonization.

Some living heptaxodontids were probably present when the first Europeans began settling the West Indies in A.D. 1500. Early Spanish explorers briefly described an animal slightly larger than a hutia (Capromyidae) that was a source of food for the aboriginals, who called the creature "quemi," and which may have been a heptaxodontid.

Significance to humans

Some species used as food source for Native Americans. The remains of Heptaxodontidae allow valuable scientific insight into the dynamics of adaptive evolution on islands.

Puerto Rican giant hutia (*Elasmodontomys obliquus*). (Illustration by Barbara Duperron)

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Anguilla-St. Martin giant hutia *Amblyrhiza inundata*	Some individuals reached the size of an American black bear (*Ursus americanus*). Adult sizes vary from a low of about 110 lb (50 kg) to a high of about 440 lb (200 kg). The distinctive, obliquely orientated laminae on the molars average out at 35° from the long axis of the skull.	Probably lived in tropical rainforest. Behavior is unknown.	Remains have been found on the islands of Anguilla and St. Martin in the northern Lesser Antilles.	Unknown, but presumably herbivorous.	Extinct
Hispaniolan giant hutia *Quemisia gravis*	Weight about 31 lb (14 kg), about the same size as *Elasmodontomys*. It had an unusual twisting of the enamel pattern of the molars. The obliquely orientated laminae on the molars average out at 55° from the long axis of the skull.	Probably tropical rainforest. Behavior is unknown.	Hispaniola. The species is known only from bones found in caves near St. Michel in Haiti and Samana Bay in the Dominican Republic.	Unknown, but presumably herbivorous.	Extinct
Puerto Rican giant hutia *Elasmodontomys obliquus*	A large, terrestrial rodent with a heavy-set body and a body weight of 31 lb (14 kg). The flat-topped skull resembles that of a nutria (*Myocastor coypus*). The short bones of its digits indicate that it was terrestrial and not arboreal. The obliquely orientated laminae on the molars average out at 45° from the long axis of the skull.	Probably lowland and montane tropical rainforest. Behavior is unknown.	The species is known only from bones recovered from cave deposits in Puerto Rico.	Unknown, but presumably herbivorous.	Extinct

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Kevin F. Fitzgerald, BS

Coypus
(Myocastoridae)

Class Mammalia
Order Rodentia
Suborder Hystricognathi
Family Myocastoridae

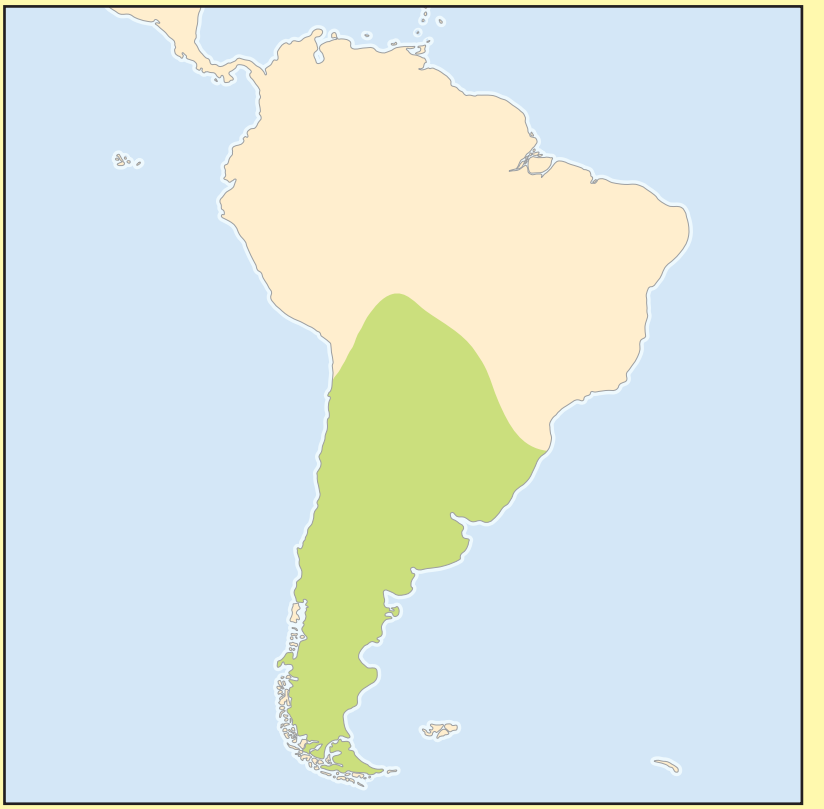
Thumbnail description
Large, semi-aquatic rodent with a reddish to yellowish brown outercoat and a thick, gray undercoat

Size
Head and body length 1.4–2.1 ft (43.0–63.5 cm), tail 0.8–1.4 ft (25.5–42.5 cm), weight 11–22 lb (5–10 kg), can occasionally reach 37 lb (17 kg), with males generally larger than females

Number of genera, species
1 genus; 1 species

Habitat
Prefers remote, shallow inland bodies of water such as ponds, slow-moving rivers, lakes, and swampy or marshy areas

Conservation status
Not threatened



Distribution
Native to southern South America, introduced to Europe, Asia, Africa, and North America

Evolution and systematics

The coypu (from the native South American Araconian word *koypu*) is also known as the nutria (from the corrupted Spanish word *lutra*, meaning "otter"). It is sometimes also referred to as the South American beaver. The geological range is the late Oligocene epoch (about 38 million to 24 million years ago) to the Recent in South America.

Originally considered a subfamily of the Hutias (Capromyidae), coypus have more recently been distinguished from the other rodents due to their large size and strong, broad, orange-colored incisors.

The taxonomy for this species is *Myocastor coypus* (Molina, 1782), Rio Maipo, Santiago Prov., Chile.

Coypu (*Myocastor coypus*). (Illustration by Michelle Meneghini)

Physical characteristics

The stout body of the coypu is highly arched. Its four legs are relatively short and hairless, with the two hind feet much longer than the two forelimbs. The hind feet each contain five digits, with webbed toes except between the

fourth and fifth toes (the skinless fifth toe is used for grooming the fur), while the forefeet each have four long, flexible, non-webbed toes and a non-functioning thumb. Its strong claws are sharp. The tail is scaly and sparsely haired, except at and around the base. The coypu is often confused with the muskrat, but it is much larger and has a terete (cylindrical) tail as opposed to the laterally compressed (flat) tail of the muskrat.

Its coat consists of two types of hair: (1) an outercoat (or outer fur) that is soft, dense, reddish brown to yellowish brown in general coloration, containing long, coarse bristles (or guard hairs) that are coarser in texture on the back; and (2) an undercoat (or under fur) that is thick, dark gray in color, and denser on the abdomen, also called nutria (the fur that is valuable as pelts). Also on the lower parts of the body is the stomach fur, which is pale yellow and is not as coarse as that of the upper parts. The outercoat almost completely hides the undercoat.

The head is large and sturdy, and somewhat triangular in shape. The facial features include 20 strong teeth ([I1/1 C0/0 P1/1 M3/3] $\times$ 2 = 20). Its large, broad, and conspicuously orange-colored front incisors continue to grow, while the extremely high-crowned cheek teeth are semi-rooted and decrease in size as they converge toward the front. The coypu can close its lips behind the incisors, thus allowing it to gnaw while underwater. Its small black eyes are set near the upper part of the head. The coypu has small, rounded ears and well-developed auditory senses. Near the chin and around the nose and mouth is white fur, and on each side of the face are a few whiskers that are longer and more sensitive than the adjoining white fur. Fat glands (used for lubrication while grooming) are located at the corner of the mouth and near the anus.

A female coypu has four pairs of thoracic mammae. These are located high on the sides of the body so that the mother can lie on her stomach while in the nest as she nurses her young, or to allow them to nurse while she is feeding in shallow water.

A coypu (*Myocastor coypus*) resting on log. (Photo by Animals Animals ©Peter Weimann. Reproduced by permission.)

A copyu (*Myocastor coypus*) chewing on vegetation. (Photo by Animals Animals ©Peter Weimann. Reproduced by permission.)

Distribution

The coypu is native to the temperate zones (southern parts) of South America ranging from central Bolivia and southern Brazil to Paraguay, Uruguay, and Tierra del Fuego in Chile and Argentina. It was introduced to North America, northern Asia, eastern Africa, and Europe mostly for the value of its furs or to control evasive aquatic plant species. The animal is not well adapted to cold conditions, often becoming more active during the warmer days (rather than during the colder nights) and tending to huddle together in burrows with other coypus on cold nights.

Habitat

The coypu lives in rainforests, temperate deciduous forests, grasslands, specifically in swamps and marshes and near the banks of lakes, streams, and rivers. Considered terrestrial, however it actually spends most of its time in the water, being an excellent swimmer and diver. The coypu lives in burrows that are built in and around the water. It is especially fond of areas with abundant vegetation along the banks. The coypu normally prefers freshwater, but it will inhabit brackish and saltwater (such as the population of the Chonos Archipelago in Chile).

Behavior

Coypus usually live together in pairs, although they frequently form large colonies of two to 13 animals usually consisting of related adult females, their offspring, and a large

A coypu (*Myocastor coypus*) mother checking on a youngster. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

A coypu (*Myocastor coypus*) in the Anuahac National Wildlife Refuge in Texas, USA. (Photo by Animals Animals ©Joyce & Frank Burek. Reproduced by permission.)

male. A young adult male may be occasionally solitary. Both the male and the female will generally remain in the same territorial area for their entire lives. A coypu can swim well due to webbed toes on the hind feet, and spends most of its time in the water. It is able to remain underwater for as many as five to 10 minutes. On a regular basis, it carefully cleans and lubricates its fur with its fore feet, wiping the fat glands at the corners of its mouth. It then grooms and arranges the fur throughout its body.

A coypu (*Myocastor coypus*) rests on feeding platform. (Photo by C. C. Lockwood. Bruce Coleman, Inc. Reproduced by permission.)

The coypu often takes over the hole of other animals, usually muskrats. When it digs its own burrow, it prefers a location near water along a sloping bank that is usually at a 45–90% inclination. Self-built burrows can be simple tunnels 4–10 ft (1.2–3.0 m) long or complex systems that contain branching passages that extend 50 ft (15 m) or more and chambers that hold simple nests composed of various types of vegetation. The burrow's entrance is built above the water level. When unable to dig its burrow in the ground, the coypu carefully builds a simple surface nest of reeds, either on land or in shallow water. It builds winter resting platforms near dense vegetation that are 20–30 in (51–75 cm) wide and 6–9 in (15–23 cm) above the water level. It also makes runways through the grass in order to wander on numerous, curvy trails up to 590 ft (180 m) from its den. The average territorial range for a female is about 6 acres (2.5 ha), while for a male it is about 14 acres (5.7 ha); however, home ranges can vary anywhere from 6 to 445 acres (2.5–180 ha). The population density is usually 1.1–6.4 animals per acre (2.7–16.0 animals per ha), but can be smaller or much larger than these values.

The coypu is most active at night just before sunset and a few hours before dawn, where its main activities are feeding, grooming, and swimming; during the day it is commonly seen but is not so active. It is a very shy and fearful creature at the first sign of the smallest disturbance, which quickly sends it

A litter of young coypus (*Myocastor coypus*) resting on a log in Lake Martin, Louisiana, USA. (Photo by John Eastcott & YVA Momatuik/Photo Researchers, Inc. Reproduced by permission.)

seeking shelter in the water, in its burrow, or in other hiding places. When in a safe environment, the coypu is gregarious and very social to other members of its community.

Predators of the coypu include wild cats, large birds of prey (such as bald eagles), red wolves, large snakes (like the anaconda and cottonmouth), alligators, and humans. Turtles, snakes, birds of prey, and other swamp animals may eat juvenile coypus. When confronted with an enemy, it will dive into the water, being more graceful in water than on land (where it is sometimes awkward and clumsy). If unable to quickly reach water when confronted with danger, it can run and jump fast for short periods of time.

Feeding ecology and diet

The coypu will eat almost any available terrestrial or aquatic green plant. It has been called "an eating machine" for its huge appetite for all types of plants. The coypu is primarily an herbivore, feeding on aquatic plants such as rushes, spikerush, arrowhead, pickerel week, smartweed, bur reed, three-cornered grass, cattail, bullwhip, alligator weed, and duckweed. It also eats leaves, roots, stalks, and stems, along with bark, clover, and cultivated crops (if available nearby) such as rice, sugarcane, soybeans, and corn. It forages for food on land and in the water. A Maryland (United States) study determined that roots are its most important food. The coypu will also eat insects, bivalve mollusks, mussels, snails, and earthworms (but seemingly only in England and South America). It is fond of foods that can be gnawed and chewed, which wears down its teeth. The animal eats about one-fourth of its own weight in

A coypu (*Myocastor coypus*) in duckweed in Louisiana, USA. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

food each night, munching throughout most of the night rather than eating large meals. The digestive organ easily breaks down cellulose particles, which are then adapted for use in the body. When preparing to eat, the coypu often brings its food to a feeding site. It usually sits on a riverbank while holding food in its fore feet before transfering it to its mouth. In other cases, it uses vegetation, branches, and other floating materials as a platform to sit upon while eating (and resting and grooming). It also competes for food with native fur-bearing animals such as the muskrat, beaver, and various waterfowl. In its native habitat of South American marshes and coastal lakes, the coypu is well adapted to regular periods of flood and drought. Its ability to breed quickly allows its populations to stabilize well after frequent environmental upsets caused by drought and flood cycles. However, without these regular cycles to regulate its population size, the number of coypus can quickly grow out of control.

Reproductive biology

The coypu is generally polyestrous in captivity and sometimes in the wild, where mating occurs usually two or three times during the year. It is a very successful procreator. The estrous cycle is variable but generally lasts for about 24–26 days, with a period of receptivity lasting one to four days. The intervals between estrous cycles last from five to 60 days. Ovulation may be induced. The gestation period is long, lasting a little over four months (specifically, 127–139 days). In Chile, the young are born in the spring and in the summer. There is a post-partum estrus within one to two days of giving birth. A female usually give birth to a litter of three to six young (with an average of five, and with one to 13 having been recorded). Factors influencing the size of the litter include availability and type of food, weather conditions, enemies, and diseases. Miscarriages are unusually high in this female rodent, with about one-third of the litters being lost during pregnancy.

A well-developed newborn is born with hair and teeth, open eyes, and able to swim as soon as it dries off (usually within a few hours). Birth weight is about 7.9 oz (225 g) and a newborn is able to survive on its own after about five days of nursing, but usually remains dependent on its parents for six to 10 weeks. The youngster rapidly gains weight during the first five months. The mother's lactation period lasts some eight weeks. A young coypu is sexually mature at about three to four months if born in warmer months and at about six to seven months if born during cooler months. In the wild, there is an 80% mortality rate in the first year of life, and only a few animals live more than two to three years. However, its life span can be six to nine years and some animals have been reported to live for 10 years.

Conservation status

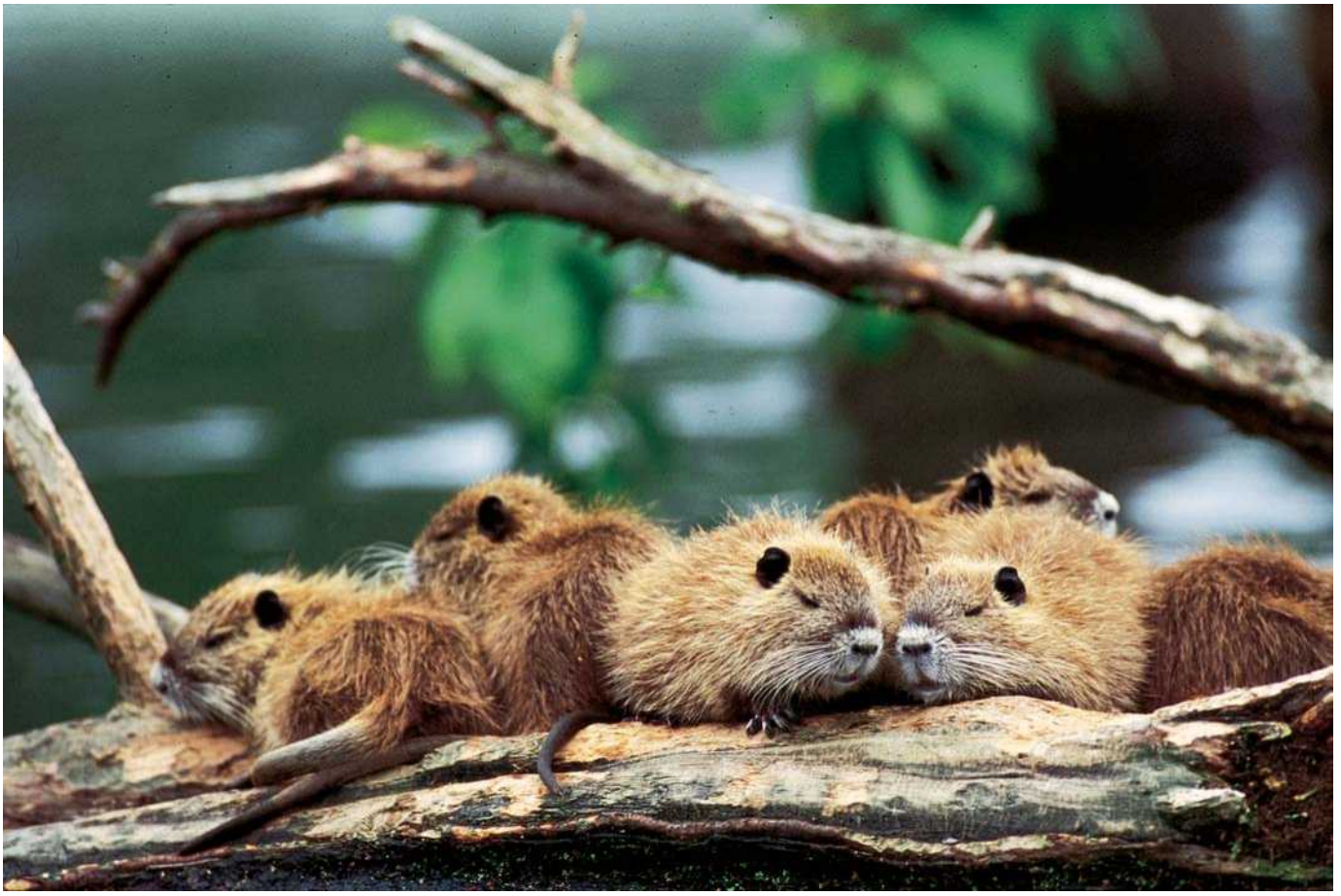
Generally coypus are common, with no special status. The coypu population was severely reduced in the past, mainly during the early nineteenth century as a result of intensive hunting for its valuable, velvet-like undercoat. Demand for its fur continues to the present, but not as much as in the past because its fur is no longer considered as attractive as it used to be. It is rapidly disappearing along many rivers and lakes in Argentina. The species became rare in many of its natural habitats during the height of its being hunted for its fur, but by the early 1900s, efforts were started to regulate hunting and to establish captive breeding farms. Such farms were established within its natural habitat and in other parts of the world. Some animals escaped or were deliberately introduced in such areas as the United States (especially the Gulf coast states, along the West coast to Washington, and the East coast to Maryland), Canada (mostly the southern parts), England, Holland, France, Germany, Scandinavia, Japan, Asia Minor, the Caucasus, and central Asia. By the 1950s, the capture of coypus was prohibited in Argentina and Uruguay, and the nutria pelt trade also became illegal. (The name nutria is generally used when referring to its pelt.) Coypu populations in those countries started to recover following these actions. Most of the present fur trade is presently supplied by nutria farms, and by coypus that have become wild in North America, England, and Russia.

Significance to humans

The fur of a farm-bred coypu is valued because of its luxurious, fine, soft undercoat, which is processed by furriers (by first removing the coarser bristles in order to leave the undercoat exposed). It is also hunted for its meat mostly in its native lands, although farm-raised meat is much more convenient. There is no direct benefit from coypu populations in its non-native habitat. Some were introduced in some habitats to control invasive aquatic plant populations, but its appetite for all plant species made its presence at those areas more damaging than beneficial.

The coypu is considered a pest in some places because its burrows often damage dikes, irrigation facilities, and natural plant communities. Burrows can also weaken riverbanks. The coypu population often competes with native wildlife, and also eats and sometimes destroys cultivated crops such as rice. Parasites from coypus have been reported such as trematodes, cestodes, nematodes, biting lice, and mites. Diseases and viruses from coypus have also been reported, such as leptospirosis, hemorrhagic septicemia, and paratyphoid. In wetlands, its large appetite has severely damaged many habitats. On barrier islands where coypu feed on sea oats, the stability of sea dunes has been threatened.

In the 1930s, coypus were introduced to fur farms in southeast England. Escaped individuals adapted quickly to the new habitat and caused considerable damage to riverbanks and root crops. An eradication campaign in the 1960s resulted in the extermination of most of the wild population (approximately 40,000 animals caught), but a string of mild winters in the 1970s brought significant growth. A more committed eradication campaign in the early 1980s resulted in 35,000 captured individuals, with the last coypu caught in England in 1989.



A litter of young coypus (*Myocastor coypus*) sleeping on log in Lake Martin, Louisiana, USA. (Photo by Animals Animals ©Eastcott/Momatiuk. Reproduced by permission.)

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William Arthur Atkins

Lagomorpha
(Pikas, rabbits, and hares)

Class Mammalia

Order Lagomorpha

Number of families 2

Number of genera, species 12 genera; 91 species

Photo: A snowshoe rabbit (*Lepus americanus*) in its summer coat. (Phoyo by Rolf Kopfle. Bruce Coleman, Inc. Reproduced by permission.)

Evolution and systematics

The evolution and systematics of the Lagomorpha (pikas, rabbits, and hares) has a rich tradition of controversy, prompting one paleontologist to author a paper several decades ago entitled, "What, if anything, is a rabbit?" The problem, however, is not defining the limits of what constitutes a lagomorph (expanding "rabbit" to include pikas and hares), but rather determining the position of lagomorphs within the mammals. Lagomorphs represent a well-defined grouping, and although they were originally classified within the Order Rodentia, even in this alignment lagomorphs were separated into the Duplicendentata whereas the "true" rodents were classified as Simplicendentata. This distinction was based on the second small peg-like upper incisors that sit behind the primary incisors in all lagomorphs, while rodents possess only a single upper incisor.

In 1912, Gidley proposed that the duplicendentates be raised to a separate order, the Lagomorpha. The existence of the Lagomorpha and Rodentia orders has been adopted as standard terminology, but unfortunately this separation did little to solve the problem of relationship of lagomorphs with other mammals. For example, Gidley proposed the independence of the lagomorphs because he thought they showed significant differences from the rodents (above and beyond dentition) and believed they showed more affinities with ungulates, perhaps the Artiodactyla. Simpson, however, maintained that the lagomorphs and rodents should be recognized together and coined the term Glires to represent a clade made up of the two orders. According to this view, lagomorphs and rodents share a common ancestor, although Simpson was the first to admit that the relationship implied by Glires was "permitted by our ignorance, rather than sustained by our knowledge." Through the years the issue of whether or not lagomorphs belong in the Glires with the rodents was hotly debated, and lagomorphs were variously linked with a variety of other mammalian taxa.

We are now fortunate to have molecular techniques to complement an increased knowledge of fossil lagomorphs, and there has been a flurry of investigations in the past 10 years (many since 2000) that specifically address the evolutionary placement of the lagomorphs. Unfortunately, the results of these studies are as contradictory as in earlier times when we had fewer data. A majority of studies using molecular sequence data significantly support the Glires clade, incorporating the Lagomorpha and Rodentia. In these cases, Glires is apparently a sister taxon to Primates, Dermoptera (flying lemurs), and Scandentia (tree shrews). In addition, morphological data analyzed in a similar manner define Glires with 100% support. However, other molecular studies specifically reject the grouping of Lagomorpha and Rodentia, while others are ambiguous on the issue. One investigator put it this way: "The rabbit wanders about in the mitochondrial protein tree, undecided whether to join the carnivore-perrisodactyle-cet-artiodactyle clade, the primate branch, or neither." Other studies link lagomorphs with the tree shrews or the Xenarthra (armadillos). It is likely that the lack of support for the Glires clade in some molecular studies reflects poor taxon sampling within the lagomorphs and rodents. While the jury is out until there can be resolution among these various molecular approaches, a parsimonious conclusion is that the lagomorphs are indeed linked with rodents—as Glires—in their evolutionary history.

A complementary question is how long ago did the lagomorphs become an independent lineage? Again, here we are assisted by both molecular and paleontological data, and the

A collared pika (*Ochotona collaris*) sunning in Denali National Park, Alaska, USA. (Photo by John Hyde. Bruce Coleman, Inc. Reproduced by permission.)

results are surprising. Until recently it was assumed that the major lineages of mammals diversified in the early Tertiary. Now, there is strong evidence from molecular data that lagomorphs were independent as long ago as the Cretaceous. Some reports using molecular sequence data indicate that the lagomorphs split from the rodents 64.5 million years ago (mya), others push the date back to over 100 mya. The variability in these molecular approaches, however, stems from their use of different genes, sampling, and methods, such that an unambiguous time of divergence between lagomorphs and rodents is not presently possible. In addition, a form with lagomorph characteristics, *Alymlestes kielanae*, has been uncovered in central Asia and dated to nearly 85 mya, thus pushing back the paleontological clock for lagomorphs. Thus, lagomorphs apparently became independent far earlier than had previously been assumed, and this independence likely occurred during the Cretaceous.

A significant fossil record of two rodentiform taxa (called eurymylids and mimotonids) is found in the Paleocene. The mimotonids appear to be primitive lagomorphs, whereas the eurymylids are linked with ancestral rodents (although in earlier treatments they were often classified as lagomorphs). These forms appear to be too advanced along their respective specialized lines to be ancestors, thus confirming that the Glires separated sometime during the Cretaceous. The most primitive representative of the mimotonids was Mimotoma, a rabbit-like animal similar to Alymlestes, but with a rabbit dental formula. Like rabbits it had two upper incisors, although the second incisor was still large and functional, while in modern-day rabbits it is small. Mimotoma was the likely ancestor to Mimolagus, an Eocene form that possessed many more lagomorph-like characteristics. Alymlestes, Mimotoma, and Mimolagus are all Asian forms, thus confirming an Asian center of origin for lagomorphs.

The first true rabbits (Leporidae) appear in the lower Eocene in Asia (Lushilagus, Shamolagus) and slightly later in North America (Mytonolagus). Lushilagus possesses teeth very similar to Mimotoma, and modern lagomorph dentition could easily have been derived from these teeth. These early forms lacked the limb proportions that characterize modern rabbits; they more closely resembled modern pikas. From this point it is possible to derive the lineages leading to both of the modern-day families of lagomorph, the Leporidae (rabbits and hares) and the Ochotonidae (pikas). The split into these two families occurred about 37 mya, or near the Eocene-Oligocene transition. By the middle Oligocene the first pika, represented by *Desmatolagus gobiensis*, was found in Asia, and other pikas soon appeared in Europe. Pikas would eventually flourish and reach their zenith in the Miocene. Geographically most pika evolution was restricted to Asia, Europe, and North America, but some forms reached Africa in the Miocene. Today, pikas are represented by a single genus, Ochotona, distributed in Asia and North America. Twenty-five extinct genera of ochotonids have been described, one of which, Prolagus, occupied Europe until historical times before becoming extinct.

By the early Oligocene a variety of true rabbits were found in Asia and North America, and the family would eventually spread throughout most of the world. Thirty-one extinct genera of leporids have been described, and today the family is represented by 11 extant genera.

The chapters on the Leporidae and Ochotonidae detail the evolution of these families, respectively. However, one important observation highlights the evolution of the lagomorphs. There are relatively few lagomorph species compared with the closely related rodents (over 2,000 rodents versus only 91 lagomorphs), and this discrepancy has never been adequately explained. Furthermore, morphologically there has been significantly less innovation (fewer specialized adaptations) in lagomorphs than in rodents. The term lagomorph means "hare shaped" and this description adequately serves to portray all species in the order.

Physical characteristics

The key characteristic of the lagomorphs, the one that led them to be classified originally in the duplicidentata, is the presence of a second peg-like upper incisor that nestles in behind the first large continually growing incisor. A third incisor forms, but is lost before birth or shortly thereafter. There is a single layer of enamel in the front incisors of rabbits in contrast to the double layer in rodents. This enamel layer surrounds the incisor on all sides (unlike in rodents) and is not colored by stored pigments, as are rodent incisors. The lower incisors in lagomorphs can occlude directly with the main upper incisors (as in rodents), but they can also "slide" behind the upper ones to press against their flat surface, thus allowing an efficient cropping mechanism. Canines are absent, and there is a gap (the diastema) between the incisors and the molars. The occlusal plane of the cheek teeth is not parallel with the zygomatic arch in lagomorphs, whereas this surface and the arch are parallel in rodents. The cheek teeth are rootless and hypsodont with two transverse ridges (unlike the several transverse ridges on rodent cheek teeth). Pikas have 26 teeth; leporids, 28. Lagomorphs have a fenestrated

skull one with areas of thin lattice-like bones, a feature particularly well developed in some leporids.

Lagomorphs, especially the leporids, are quick on their feet and/or fast runners. Leporids have long legs and large hind feet, and the tibia and fibula are fused distally to add strength and reduce weight to the leg. The soles of lagomorph feet are covered with hair (except the distal-most toe pads in pikas). The hairs on the soles of the feet are rectangular when viewed in cross-section. The foot posture is digitigrade while running, but plantigrade during slow movements. No lagomorphs are able to grasp food with their paws. Ears are huge to relatively large (even pika ears are large for their body mass compared with most rodents), and tails are short and, in pikas, not visible. Lagomorphs have soft rather long fur, and the color is normally reddish to gray-brown. The gut is large, in particular the caecum, and all lagomorphs practice coprophagy (reingestion of feces). A pseudo-cloaca is present such that there is one opening for reproduction, urine and feces.

General body shape differs between representatives from the two families. Pikas are egg-shaped, roughly 5–8 in (13–20 cm) long, and weigh 3–10 oz (80–300 g). Leporids are more angular and larger, ranging in length from 10–30 in (25–75 cm) and in weight from 14 oz to 13.2 lb (0.4–6.0 kg).

Distribution

Lagomorphs are distributed around the world, as native or introduced species. The pikas once had a broad distribution across most of Eurasia, North America, and into Africa. Currently, however, they are found only in the mountains of the inter-montane west in North America and in Alaska, and across much of Asia primarily in the high mountains of Central Asia, but also south into the northern Middle East and across Russia from the Urals to the East Coast. An isolated population also occurs on Hokkaido in northern Japan.

The leporids currently have a far greater geographic distribution, being found naturally throughout the world with the exception of Australia, New Zealand, and other islands of Oceania, Madagascar, southern South America, and most of Amazonia. The European rabbit (*Oryctolagus cuniculus*) and the European hare (*Lepus europaeus*) have been introduced widely in particular to areas not naturally occupied by rabbits. Thus, Australia, New Zealand, southern South America, and over 500 oceanic islands now are home to these invaders.

Habitat

Pikas occupy two distinctly different habitats. The two North American pikas and roughly half of the species in Asia live in rocks or boulder fields and do not dig burrows. These pikas utilize vegetation found in meadows at the talus edge or growing in small patches within the rocks. In special circumstances rock-dwelling pikas are "fooled" into occupying areas with the general physiognomy of rock piles, but which are not, such as heaps of fallen logs.

A marsh rabbit (*Sylvilagus palustris*) in saltmarsh of Honeymoon Island State Park, Florida, USA. (Photo by Animals Animals ©Maresa Pryor. Reproduced by permission.)

The remainder of the pikas, all Asian species, live in meadow, steppe, shrub, or open desert environments where they dig burrows. Rarely are two burrowing species found in the same locality, but a burrowing pika can occur in meadow habitat that abuts the habitat of a talus-dwelling pika.

The true hares (genus *Lepus*) in general prefer open country high arctic tundra, steppe, agricultural pasture, tropical savanna, and desert. Within these habitats some form of cover (shrubs or rocks) is needed for protection from predators (in particular, birds of prey). Hares also use cover for protection from the elements, and generally run into the open to avoid predators. A few *Lepus* spp. live in forests, such as the snowshoe hare (*L. americanus*), Manchurian hare (*L. mandshuricus*), and some populations of mountain hare (*L. timidus*).

No single vegetative community typifies the habitat of cottontail rabbits (genus *Sylvilagus*). Some are found in marshy areas (*S. aquaticus*, *S. palustris*), many occupy forested regions (e.g., *S. brasiliensis*, *S. cunicularius*, *S. graysoni*, *S. insonus*), and other brushy situations (e.g., *S. bachmani*, *S. floridanus*, *S. mansuetus*, *S. nuttallii*, *S. transitionalis*). The closely related pygmy rabbit (*Brachylagus idahoensis*) requires big sagebrush (*Artemisia tridentata*) habitat for its existence.

Several rabbits are endemic to Africa. The riverine rabbit (*Bunolagus monticularis*) specializes on dense riparian growth along seasonal rivers in the central Karoo region of South Africa. All three species of rockhare (genus *Pronolagus*) are true to their common name, being restricted to

With the ability to reach speeds up to 64 mi (103 km) per hour, the Arctic hare (*Lepus arcticus*) is able to outrun many of its predators. (Photo by Mark Bradley/Boreal Nature Photos. Reproduced by permission.)

rocky situations in association with grass or scrub vegetation. The bunyoro rabbit (*Poelagus marjorita*) also is associated with rocky outcrops occurring in moist savanna or open shrub woodlands.

The hispid hare (*Caprolagus hispidus*) of India and Nepal is dependent on early successional riverine communities, typically comprised of tall dense grasslands. Both *Nesolagus* spp. from Sumatra and southeast Asia occupy dense tropical forest. The Zacatuche or volcano rabbit (*Romerolagus diazi*) of the highlands of central Mexico lives in open pine forests with an understory of thick bunch grass called zacaton. The zacaton is required for food, cover, and protection for this species. The Amami rabbit (*Pentalagus furnessi*) of Japan lives in primary forest, but also has been found to occupy forest edges and secondary forests. Finally, the common European rabbit (*Oryctolagus cuniculus*) is a denizen of open grasslands with well-drained, loosely compacted soils for constructing their warrens, although it is eminently adaptable and found in nontypical situations.

Behavior

Social organization, territoriality, and behavior

The pikas have two sharply contrasting forms of social organization. Those species that inhabit rocky or talus habitats are extremely unsocial. In the American pika (*Ochotona princeps*), males and females hold separate territories of comparable size and rarely interact. Rock-dwelling pikas in Asia tend to live in pairs on a communal territory, but they still avoid one another and engage in few social encounters. Territory size for rock-dwelling pikas is variable, and largely dependent on the quality of vegetation adjoining the talus; the lower the quality of surrounding vegetation the larger the territory. For most species territory size is large, compared to the size of its occupant(s), and average sizes range from approximately 600–2400 yd^2 (500–2,000 m^2). Most rock-dwelling pikas are rather pugnacious and chase conspecifics whenever they are encountered. Neighboring adult males and females suppress this aggressive urge some of the time, and adults do not always chase their own young.

In contrast, burrowing pikas are among the most social of mammals. These animals live in family burrow systems functioning as a family territory. As the summer breeding season progresses and young from sequential litters are weaned, the density on these family territories becomes high. In the plateau pika (*Ochotona curzoniae*) approximately 10 families occupy each hectare, and each family may be comprised of up to 30 pikas, yielding regional densities of 120 per acre (300/ha). Affiliative social interactions are frequently expressed among family members, including such behaviors as nose-rubbing, sitting-in-contact, boxing, wrestling, and grooming. Aggression, generally in the form of a long chase or fur-flying fight, is reserved for pikas that wander off of their family territory and into the domain of their neighbors.

Variability in social organization is also seen in the leporids. Most hares and rabbits live solitary lives and are nonterritorial. Some form temporary feeding aggregations, and the Arctic hare (*Lepus arcticus*) can be seen in huge herds. Territories are defended by the largely solitary European hare (*L. europaeus*). Most representatives of the *Sylvilagus* spp. occupy relatively stable overlapping home ranges of only a few acres, and several species have a male dominance hierarchy which controls the social structure of their population.

Unlike any other leporid, the European rabbit (*Oryctolagus cuniculus*) is extremely social. Defended territories are usually small (approximately 2.5 acres [1 ha]) and made up of a "warren"—an interconnected maze of burrows. A warren usually consists of six to 12 adults controlled by a dominant male who sits at the top of a strict linear hierarchy of dominance. Most rabbits remain in the area of their warren for life.

Communication and senses

The dominant form of communication in lagomorphs is olfactory—all species have a keen ability to detect odors. In turn, all lagomorphs have glands on their cheeks, chin, and/or groin areas that are used to rub pheromones on their coat during grooming, or to deposit scent marks on rocks or shrubs. Urine and feces are also used to transmit olfactory messages. Individual animals broadcast these pheromones to advertise their reproductive status or to demarcate their territorial boundary.

Very few lagomorphs are vocal. Some hares and rabbits communicate by thumping their big hind feet, and hares can

expel a deep grumbling sound. The piercing shriek given by leporids when in distress is legendary. But, only the Zacatuche (*Romerolagus diazi*) and pikas (genus *Ochotona*) are truly vocal. Rock-dwelling pikas utter a restricted repertoire of calls, just a short call used to advertise their territory and alert neighbors of the presence of predators and a long-call (or song) given by males during the breeding season. Burrowing pikas express a rich variety of calls, including whines, trills, and muffle-like sounds, that complement their social milieu, and males also give a breeding season long-call.

While vocal communication is restricted in most lagomorphs, they still possess an acute sense of hearing. Hares in particular, but all lagomorphs, have large ears that assist in detecting predators.

Pikas have small eyes and do not seem to rely significantly on their sense of vision. On the other hand, leporids are known for their large laterally set eyes that provide a nearly circular field of vision. This arrangement provides for restricted visual acuity (which the animals do not need, as their food is sedentary), but enhances their ability to detect motion from all angles in order to avoid the approach of predators. Many leporids, in particular those living in open habitats, flash the white underside of their fluffy tails during flight to alert conspecifics of the presence of predators. Interestingly, species living in forested habitats have dark tails and do not use this form of communication.

Activity patterns

With the exception of the nocturnal steppe pika (*Ochotona pusilla*), all pikas are diurnally active. When temperatures are warm, pikas tend to restrict their activity to early morning and late afternoon hours.

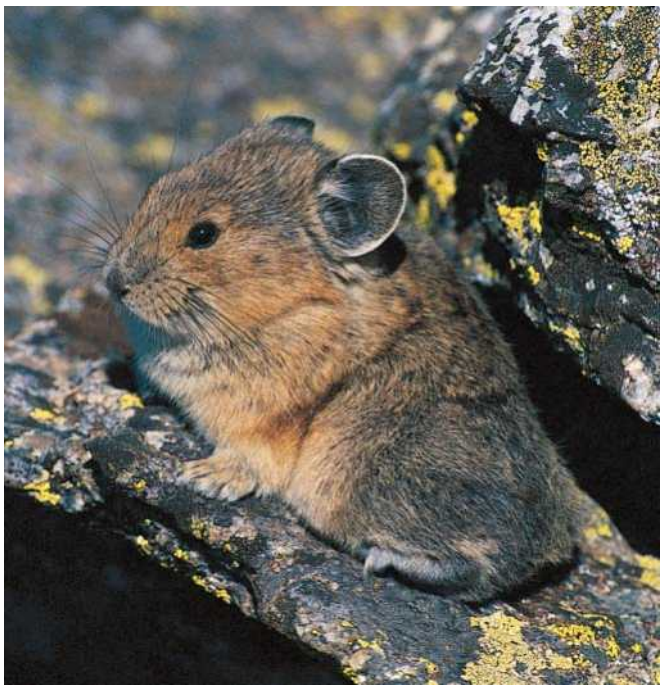
Most leporid activity occurs at night, although many species can also be seen active during the day particularly at dawn and dusk. For example, one might classify the European rabbit (*Oryctolagus cuniculus*) as noctural, but its preferred feeding time is dawn.

Migratory movements

No lagomorphs migrate. The term is sometimes associated with rare mass movements of some hare species (for example the European hare) following highly unusual climatic events but these cases do not represent true migration.

Feeding ecology and diet

Lagomorphs are, with rare exception, strict herbivores. Unlike many rodents, they are unable to hold or process food



An American pika (*Ochotona princeps*) sunning among rocks in Colorado, USA. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

with their paws, instead relying on the clipping of vegetation and side-to-side mastication of vegetation using only their mouths. Lagomorphs are rather generalized herbivores, with a diet consisting primarily of grasses and herbs, but also fruits, seeds, roots, leaves, buds, and bark of trees. As no lagomorphs hibernate, their feeding ecology must accommodate the need to harvest vegetation year round, or in the case of pikas to store food when access to vegetation is restricted.

Most pikas live in northern or high altitude environments blanketed by snow during winter. They adapt to these conditions by harvesting vegetation during summer, a time of abundance, and storing it into a cache or hay pile to serve as a source of nutrition during winter. The folk story that pikas lay out their hay on rocks to cure before carrying it to their hay pile is untrue; pikas harvest their hay with great economy, sometimes making hundreds of trips per day to deposit their loads directly on their hay pile.

Although generalized herbivores, pikas can be highly selective of the foods they eat. During summer most rock-dwelling pikas maintain a heavily grazed zone in the meadow adjoining the talus (on which they hold their territories). This zone allows pikas to graze continually on growing grasses, and also to better see approaching predators. At the same time pikas forage for their hay piles at greater distances from the meadow-talus edge, and they primarily select forbs to carry back to their cache. Forbs are larger and more economical to carry than grasses, although grasses can also be gathered up and deposited on haypiles. Plants selected for haying are generally higher in nutrition than non-selected plants, and in most cases they are less likely to be poisonous. The exception is that some rock-dwelling pikas harvest plants that, while poisonous, also inhibit bacterial growth in the hay piles, thus preventing them from rotting. This is an apparent win-win situation for the pikas, as these plants help to preserve the hay piles and later can be eaten after the toxic chemicals degrade.

Pika hay piles can be huge or sometimes inconspicuous when tucked under large boulders. There can be variability in how hay piles are constructed even within a single population. Burrowing pikas that do not have rocks under which to tuck their hay sometimes make giant stacks over a yard high. These are exposed when the snow otherwise covers the landscape, and Mongolian herdsman in the range of the Daurian pika (*Ochotona dauurica*) take advantage of these efforts and graze their livestock preferentially in areas occupied by pikas. Some pikas apparently do not make hay piles, and normally these species live in areas without snow where they can forage year-round. Even pikas that make hay piles often construct snow tunnels to allow foraging on nearby vegetation blanketed by snow.

One of the only known instances in which a lagomorph survives by eating meat is found in an isolated population of the collared pika (*O. collaris*). These pikas live on nunataks, or small islands of rock in the middle of a sea of ice, protruding from the Seward Glacier in the Yukon, the world's largest non-polar ice field. It is remarkable to find pikas in this environment, and even more so that they can survive on the few plants that also hang on in this bleak place. These pikas eat the brains from birds that die while flying overhead and fortuitously fall on the nunataks giving them their slim margin for survival.

Leporids are generally feeding opportunists, eating a smorgasbord of plants from those that are available in the habitats in which they live. Plant resins have been identified as a deterrent in lagomorph herbivory and may play a role in the 10-year population cycle of snowshoe hares (*Lepus americanus*). Close inspection of the area surrounding creosote bushes (*Larrea tridentata*) in the deserts of the southwestern United States yields many clipped but uneaten branches. Apparently each branch contains different levels of alkaloids, and black-tailed jackrabbits (*L. californicus*) prune the shrub, taste to assess the alkaloid level, eat the palatable branches, and discard the remainder.

Given a selection of plants, most leporids choose those which are the most succulent, particularly during times of water stress. They also prefer plants in the pre-reproductive or early reproductive stages of development that have the greatest nutritive value. Like pikas, leporids select plants that are comparatively higher in moisture and crude protein. Given that plant quality and availability changes dramatically with the seasons, so does the diet of rabbits and hares. Most jackrabbits, for example, show preferences for shrubs in winter and for grasses and forbs in spring and summer. The tendency of rabbits and hares to gravitate toward the most nutritious plants also is responsible for their love of cultivated areas. Here agricultural crops, bolstered with nutrients from fertilizers, represent a cornucopia to lagomorphs, and often result in dramatic increases in their population density. On the other hand, in natural conditions hares often are close to

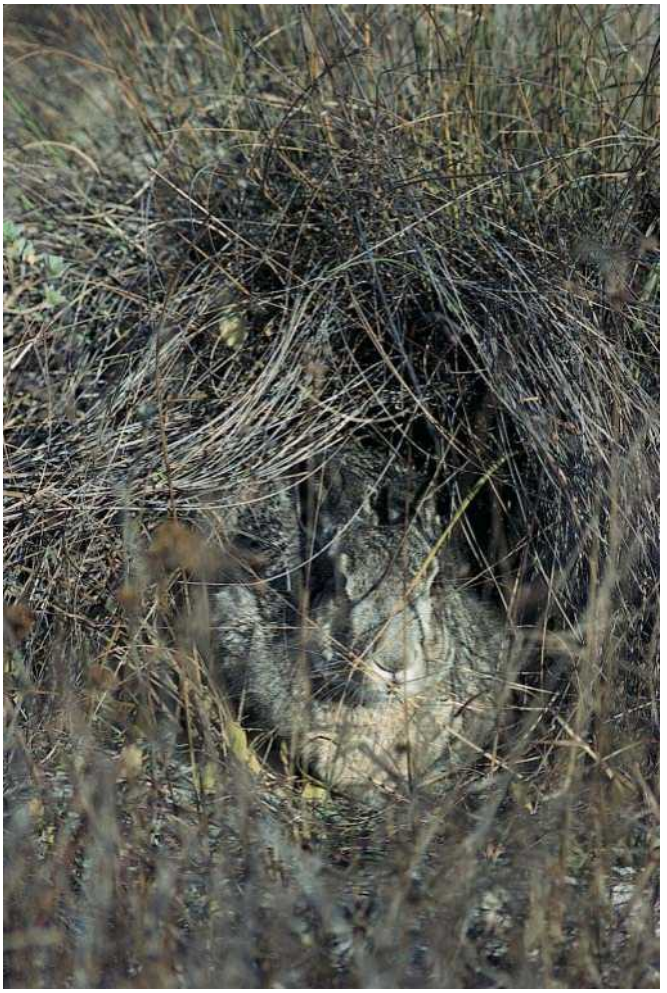
starvation when available food may be covered by snow and they are unable to harvest twigs sufficiently to meet their needs. In some areas it has been determined that hares will starve in winter when the diameter of twigs used for browse is greater than 1 in (3 mm).

Special dietary adaptations

Because generalized herbivores, such as lagomorphs, have such difficulty in acquiring food of a sufficient quality in terms of necessary vitamins and micro-nutrients they have been forced to develop specialized dietary adaptations. Lagomorphs possess a huge digestive system that appears specially constructed to deal with the large quantities of plant material they eat, much of which is difficult to digest. In particular, they feature a giant caecum up to 10 times larger than the stomach that branches off from the gut between the small and large intestines. This organ, its surface area enlarged by numerous divisions separated by a spiral fold of skin that runs through it, hosts a rich culture of bacteria and other microorganisms. Here, partially digested food (that not absorbed by the animal during passage through the small intestine), is broken down by these microorganisms, and in the process various vitamins (in particular vitamin B complex) and microbial proteins are manufactured. To be able to utilize these products, lagomorphs practice what is called coprophagy which literally means feces-eating. A soft feces is excreted from the caecum (called a caecotroph) and reingested. The reingested soft feces can then be digested in the stomach and small intestine yielding up to five times as many vitamins as in the original food. This process is such an integral part of lagomorph biology that if prevented from reingesting soft feces, a rabbit may develop malnutrition or die.

The caecotrophs, or soft feces, contrast with the normal hard round dry pellets characteristic of lagomorphs. These soft and hard feces are produced by a mechanical separation process, dependent on the size of food particles, in the small intestine. Fine food particles are shunted into the caecum, and large particles, basically those of poor quality, form the hard pellets and are passed quickly. When the separation mechanism ceases to act, fermented caecotrophs are excreted. The difference between the two feces types is not due to whether or not the food has passed once or twice through the gut, as is commonly assumed; some foods may be recycled numerous times. Within the leporids, there are two types of caecotroph: capsules (a spherical shape coated with a tough mucous membrane) found generally in rabbits and amorphous (without a surface membrane) most commonly found in hares.

Most of the literature on lagomorphs states that soft feces are excreted at night (sometimes even termed "night feces"), and that hard pellets are never eaten. Recent studies, however, show that lagomorphs regularly eat hard feces and that the timing of coprophagy, with respect to hard and soft feces, can be complex. Most feeding takes place at night in leporids, and during that time the separation mechanism is activated so that hard feces are formed and fine food particles are shunted to the caecum. In the morning, when animals cease feeding, hard pellets remain in the large intestine. These are excreted and reingested, after which soft feces are formed and reingested until early afternoon. Then the separation mechanism kicks in again to form hard feces that reach the anus in a few hours and are reingested in the afternoon. Thus, leporids feed on fresh food and ignore feces during the night, and excrete both hard and soft feces during the day and reingest these. This process is not as well known in pikas. Some caecotrophs are not eaten directly (perhaps when pikas have an abundance of fresh nutritious food and they are not necessary to achieve sufficient nutrition), and are deposited near the hay pile. These may be eaten later, or some grow a fungus after which the entire mass is reingested.



A black-tailed jackrabbit (*Lepus californicus*) in its nest. (Photo by Robert P. Carr. Bruce Coleman, Inc. Reproduced by pernssion.)

Reproductive biology

Most of our general knowledge of reproduction in lagomorphs comes from investigations on the European rabbit (*Oryctolagus cuniculus*). Rabbits are known to be reflex, or induced, ovulators. Females may come into heat and be attractive to males, but the act of copulation is needed to stimulate ovulation, which occurs about 12 hours after mating. It is assumed that this pattern is followed in other lagomorphs. Another interesting twist in lagomorph reproductive biology is the phenomena of "superfetation." In European

hares (*Lepus europaeus*), a female in late pregnancy can go into heat, mate, ovulate, and be impregnated and thus carry two litters of different age in her uterus at one time. This process naturally can lead to a rapid increase in the local population in a short time. Most pikas exhibit a post-partum estrus, thus initiating sequential litters back-to-back, with the same effect of truncating reproduction into as short an interval as possible—a particularly effective strategy given the short alpine summers experienced by most pika species.

Another interesting aspect of reproduction in lagomorphs is their apparent lack of parental care—in particular, the infrequency of nursing bouts initiated by mothers. Termed "absentee parental care" by Eisenberg, most mothers visit their young to nurse only about once every 24 hours. Fortunately lagomorph milk is extremely rich and the young are able to survive these long intervals between meals. This strategy may have arisen for mothers to avoid bringing their young, exposed in a shallow form, to the attention of predators.

Pikas do not express elaborate courtship or mating behavior. For both talus-dwelling (*Ochotona princeps*) and burrowing (*O. curzoniae*) pikas, males generally approach females, sniff the genital area briefly, and mount. Copulation lasts only a few seconds after which the pair separate. Rock-dwelling pikas tend to be monogamous; Asian forms live in pairs, and males and females in the American species generally occupy neighboring territories and show some familiarity with each other. Burrowing pikas live in family groups that also define their mating system. However, over-winter mortality is high and capricious, thus the availability of males and females within family territories can vary across the landscape. Most families begin the breeding season with one male and one female, thus demonstrating true monogamy. Some families have more adult females than males and are polygynous, whereas the reverse, a family with more adult males than females, yields a polyandrous mating system. All three types of mating systems can be found in adjoining family territories. Young pikas are born beneath tons of rock or deep in burrow systems, making observations of parental care difficult. Some captive studies and anecdotal field observations indicate that while pika mothers visit their young infrequently, they nurse more often than in the "absentee" system of most leporids. When young rock-dwelling pikas are weaned and appear on the talus, they are treated aggressively by their parents. Normally young avoid confrontations by choosing to be active at times when their parents are inactive and confining their movements to areas near the borders of adult territories. The opposite is true of newly weaned burrowing pikas. Fathers, and to a lesser degree mothers, are highly attentive toward their offspring and engage in numerous affiliative behaviors with them.

Reproduction is highly seasonal in all pikas beginning at the end of winter and extending through early summer. Timing and length of breeding season depends on altitude, latitude, that year's climate, and whether the species is a rock or burrowing form. Rock-dwelling pikas initiate two litters each year, although normally only one is successful. Litter size is small, generally three young (range of one to five), and not all of these are successfully weaned. Animals first breed as yearlings; gestation is 30 days. In contrast, burrowing pikas initiate many (up to five) sequential large litters (range of one to 12), and weaning success appears to be high. In some burrowing forms young mature quickly and breed initially in their season of birth. Gestation is approximately 20–21days. Thus, reproductive performance is greater in all dimensions in burrowing versus rock-dwelling pikas.

The most elaborate courtship pattern in lagomorphs has been described in the European hare. First, large mating groups aggregate from which animals seemingly pair off. Apparently these partners are faithful and live together for about one month. The extended courtship involves repeated chases and approaches, tail flagging, and contact. Copulation finally ensues, although lasting for less than 10 seconds. The pair separate with a giant leap by the female used to throw off the male. Vigorous pursuit and repeated copulations may follow. Most other hares and rabbits express a muted version of this behavior, and in some instances, copulation occurs without any preliminary courtship. In European rabbits mating is based on the dominance hierarchy within a warren; the mating system in most other species is either unknown or assumed to be based on either a dominance hierarchy or random encounters.

Hares are precocial (being born fully furred and with their eyes open) at birth. This condition follows a relatively long gestation period of about 40 days. Coupled with the lack of attention given young during the lactation period, there appears to be little in the way of parental care expressed toward young hares. Rabbits have a shorter gestation period of about 30 days, and their young are altricial (born without any fur and with their eyes closed) at birth. Mothers construct a nest, sometimes in a protected burrow dug for this purpose, lined with hair from their own belly and plant material to secure their young. The European rabbit enters a social world in the tightly knit warren, thus benefits from behaviors of parents

and others. Most other rabbits, however, do not receive substantial parental care and independently enter the world following weaning.

Leporids are legendary for their reproductive potential. Indeed, many species have many large litters each year, and young may reach sexual maturity at a relatively early age. However, lagomorphs live in a wide variety of ecosystems, and many of these are stressful and energy limited. In these conditions some species may not be as fecund. In the far north, where the summer breeding season is short, native hares (*Lepus othus*, *L. arcticus*) normally conceive only one large litter per year. In desert situations where some hares (*L. californicus*, *L. alleni*) may face a shortage of resources over an extended breeding season, litter sizes may consist of only one to three young, although they may produce four to seven litters each year. Latitude, and thus its effect on season length, may significantly influence litter size. For example, the Eastern cottontail (*Sylvilagus floridanus*) produces larger litters in the northern part of its range (average is 5.6), with a steady decline in litter size to the southern limit of the species (average is 3.1). Thus, seasonality and productivity of the habitat appear to be major influences on the fecundity of leporids.

Conservation

Currently the official IUCN Red List of Threatened Species lists 19 species of lagomorph as Threatened (IUCN categories of Critically Endangered, Endangered, or Vulnerable) out of 79 species for which complete assessments have been made (eliminating those species with Data Deficient or Not Evaluated; the IUCN/SSC Lagomorph Specialist Group has not had the opportunity to assess several new species recently described or assigned). The resulting 24% level of endangerment is equal to that for the class Mammalia as a whole. However, changes in assignment which are proposed, but not yet finalized, would change these numbers to 25 threatened species out of 86, or an endangerment level of 29%.

Most critical in this analysis is the level of endangerment found in those genera of lagomorphs with two or fewer species. The Lagomorpha contains seven monospecific genera and one genus with two species. Within this assemblage of the most phylogenetically unusual lagomorphs six of eight genera (75%), and seven of nine species (78%), are threatened with extinction.

Some of the most endangered mammals in the world are lagomorphs. The silver pika (*Ochotona argentata*) is known only from one 0.9 × 1.2 mi (1.5 × 2.0 km) patch of scrub located in the isolated Helan Shan mountains of central China. Similarly, the Ili pika (*O. iliensis*) lives in isolated cliffs in northwestern China, and several recent expeditions to assess its population have failed to relocate it at its type locality. Over 100 years past from the finding of Koslov's pika (*O. koslowi*) until it was recently rediscovered, and its habitat in central China is subject to widespread alteration. The pygmy rabbit (*Brachylagus idahoensis*) has declined severely throughout its range; in 2002, it disappeared from five of six known localities in the Columbia River population. The number of surviving riverine rabbits (*Bunolagus monticularis*) is estimated to be as low as 500 animals, its preferred habitat is disappearing, and none of its habitat is governmentally protected. Populations of the hispid hare (*Caprolagus hispidus*) are declining in the face of dramatic habitat loss throughout its range in Nepal and India. The Tehuantepec jackrabbit (*Lepus flavigularis*) is found in only three isolated populations in southern Mexico, each with only a handful of individuals. The only striped rabbits, two *Nesolagus* spp., are essentially unknown. The Sumatran rabbit (*N. netscheri*) has only been recorded a handful of times, and the only sightings in the past several decades were on film of two individuals captured by an automatic camera-trap in 1998. The newly found (first described in 2000) Annamite rabbit (*N. timminsi*) is best known for being found in a market in Laos as meat; its ecology is unknown. The Amami rabbit (*Pentalagus furnessi*) of Japan is the world's only black rabbit. Only 3,000 individuals remain on the two islands they inhabit and are threatened by an introduced mongoose and rampant deforestation. The volcanic highlands of central Mexico surrounding Mexico City host the 6,000 remaining zachatuche (or volcano rabbits [*Romerolagus diazi*]). Found on only 16 small patches of habitat, the zacatuche is being threatened by logging, burning of the zacaton grass on which it depends to enrich regrowth for cattle grazing, and thatch collection of zacaton for baskets. Only three specimens are known to science of the Omiltimi rabbit (*Sylvilagus insonus*) from the West Coast of Mexico, although in 1998 a barnyard dog retrieved another. Rigorous searches throughout its putative range already a protected area have failed to produce any additional sightings.

Significance to humans

Lagomorphs are economically and aesthetically important to humans in many ways. The pikas, normally living in remote pristine settings high in mountains or on the plateaus of Asia, represent wildness. The secretive yet engaging nature of these diurnally active creatures are enticing to ecotourists. Pikas have little history of direct economic importance to hu-

mans. They are too small to be utilized as food, although at times their soft fur has been used to make felt in central Asia. Also in central Asia, the soft feces of pikas is put through a distilling process and dried into a product called "mumio" that can be dissolved in water as a folk remedy to assist with the healing of broken bones or rheumatism. Some of the burrowing pikas are thought to compete with human economic interests and are poisoned. The Afghan pika (*Ochotona rufescens*) sometimes occupies agricultural areas, eating wheat or other crops and damaging apple, walnut, and other economically important trees. Other species (Pallas's pika [*O. pallasi*], Daurian pika [*O. dauurica*], plateau pika [*O. curzoniae*]) are believed to compete with livestock or to damage range lands. As an example of these control efforts, during the past four decades the plateau pika has been poisoned cumulatively over 80,000 sq mi (200,000 sq km) in Qinghai Province, China. Another perspective, however, on the role of the plateau pika is that it serves as a major keystone species for biodiversity on the Tibetan Plateau. When these pikas are poisoned other native species of endemic birds and predators that depend on the pikas for food disappear. The pikas also function to recycle soil and reduce erosion on degraded lands. While some control efforts continue, the tide is turning and this beneficial role of the plateau pika is being more widely acknowledged in China.

Leporids provide sport hunting, food, and fur worldwide. The cottontail rabbit (genus *Sylvilagus*) is the principal game animal in the United States; millions are hunted for sport each year. The pelt is sometimes used for clothing, and the meat is considered a delicacy. Snowshoe hares (*Lepus americanus*) have been a major component of the fur trade, particularly in Canada. Records of their pelts from the logs of the Hudson Bay Company extend back to early 1800s. Other hare species, both in North America and throughout the world, are also hunted for food and sport. In North America hares are not considered as desirable as cottontails. The European hare (*L. europaeus*) has declined in numbers and importance as a game species in recent years, and similar declines have been noted across Asia for other hare species. In Argentina, where it has been introduced, over six million European hares are hunted annually, and others are exported to Italy for sport hunting there.

Rabbits and hares also form an important link in ecological food chains; many predators rely on the abundance of the non-hibernating leporids in their diet, particularly during winter. One key example of this phenomenon is the linkage of numbers of the lynx with those of the snowshoe hare, which range from high to low population levels in a 10-year cycle. Leporids can also cause damage to ecosystems when their numbers are high, either girdling trees or consuming forage that could otherwise be available to livestock. Rabbits and hares are attracted to crop lands, reach high densities in these areas, and concomitantly are also considered an agricultural pest in certain areas.

The greatest damage done by a lagomorph has resulted from the human folly of introducing the European rabbit (Oryctolagus cuniculus) to areas throughout the world where there were no lagomorphs. The most dramatic example of such an alien introduction occurred in Australia. Here, 24 rabbits were introduced in 1859, and they rapidly increased and spread throughout most of the continent. In 1950 there were an estimated 750 million rabbits in Australia, and the damage that the rabbits have caused is legendary. Not only has the livestock industry been impacted, but the degradation to the habitat has led to the loss of many of Australia's unique native flora and fauna. The enterprising Australians have tried nearly everything to rid their land of this pest. The biological control agent, myxomytosis, initially proved to be highly effective, killing nearly all animals in most populations. However, rabbits have developed immunities and rebounded from this treatment. Additional innovative control techniques are in development.

The domestication of the European rabbit in southern Europe or Northern Africa in Roman times has led to a close connection between people and rabbits. The domestic rabbit now has over 100 varieties and serves as a lovable pet, and breeding stock for meat and fur.

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Organizations

IUCN Species Survival Commission, Lagomorph Specialist Group. Department of Biology, Box 871501, Arizona State University, Tempe, AZ 85287-1501 USA. E-mail: a.smith@asu.edu Web site: <http://www.ualberta.ca/dhik/lsg>

IUCN Species Survival Commission, Red List Programme Office. Web site: <http://www.redlist.org>

Andrew T. Smith, PhD

Pikas
(Ochotonidae)

Class Mammalia
Order Lagomorpha
Family Ochotonidae

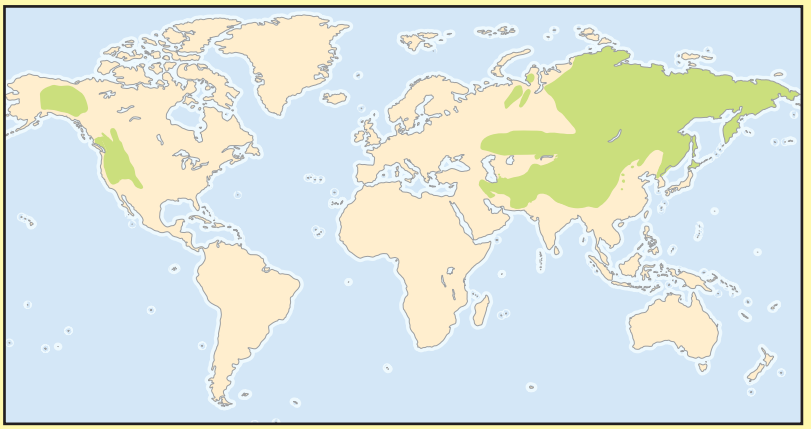
Thumbnail description
Small, egg-shaped herbivores with prominent round ears, small eyes, and no visible tail

Size
5–8 in (13–20 cm); 3–10 oz (80–300 g)

Number of genera, species
1 genus; 30 species

Habitat
Talus, meadow, and steppe

Conservation status
Extinct: 1 species; Endangered: 1 species; Vulnerable: 3 species; Lower Risk/Near Threatened: 2 species; Data Deficient: 2 species



Distribution
Mountains of western North America; primarily high mountains and steppe of central Asia

Evolution and systematics

Molecular evidence indicates that the family Ochotonidae (pikas) separated from the family Leporidae (the other family in the order Lagomorpha) 37 million years ago. Paleontological evidence closely matches this date, suggesting that the two families separated in the early Oligocene. All evidence points to an Asian origin for the family. Pikas spread to North America by the late Oligocene. Pikas quickly differentiated into many forms and became particularly diverse during the Miocene. During this time, representative genera were found in North America, Asia, and Africa. The first *Ochotona* appeared in the early Pliocene of Asia, and *Ochotona* first entered North America in the mid-Pliocene. *Ochotona* and *Prolagus*, the only other pika genus to reach historical times, are first found in Europe during the late Pliocene. *Prolagus* subsequently went extinct, leaving *Ochotona* as the only living representative of the family from a record of 25 fossil genera.

The close resemblance of all pika species makes it difficult to find external characters to tell them apart. Even using traditional morphological measurements on skull bones and dentition has not been sufficient to stem controversy over the systematic alignment of pika species; no two revisions of the genus are the same. Some subspecies have landed in as many as four different species. Molecular techniques have begun to clarify pika systematics, and a consensus is nearing, although the task is far from completed. Currently, 30 species of *Ochotona* are recognized.

Physical characteristics

All living pikas are very similar in appearance. They are small egg-shaped balls of fluff sporting thin, relatively large round ears and without a visible tail. Pikas range in size from the Gansu pika (*Ochotona cansus*), which weighs in at approximately 3 oz (80 g), to Glover's pika (*O. gloveri*), which can reach 10 oz (300 g). Most pikas are a brownish gray, and accents are most often in the red spectrum.

Distribution

Ochotona has a northern, Holarctic, distribution. In North America, they are found primarily at high elevations throughout the inter-montane west (American pika, *O. princeps*) or in the mountains of Alaska and the Yukon (collared pika, *O. collaris*). The remainder of the genus is found throughout central Asia, in the Himalayan massif and associated ranges, and across eastern Siberia to Sakhalin Island and onto Hokkaido Island, Japan. The steppe pika (*O. pusilla*) reaches west to the Ural Mountains, and one small population found to the west of this chain can be classified as European.

Habitat

There are two types of pikas: those that occupy rocks or piles of talus and those that live in meadow or steppe environments and construct burrows. This contrast in habitat type determines all aspects of behavior and reproduction in pikas, such that these traits are best treated together for each ecological type of pika.

Behavior

In general, rock-dwelling pikas are territorial as individuals or in pairs, relatively asocial (most are quite pugnacious), have a restricted recorded vocal repertoire of two calls, are long-lived (some reaching six years of age), and have relatively

A Daurian pika (*Ochotona dauurica*) emerging from its hole. (Photo by Fletcher & Baylis/Photo Researchers, Inc. Reproduced by permission.)

stable low-density populations over time. In contrast, burrowing pikas that occupy meadow or steppe habitats live in family burrow system territories, are extremely social, communicate by uttering a number of different vocalizations, have short adult life spans, and their populations undergo extreme annual fluctuations in size and may reach densities of up to 120 animals per acre (300/ha).

One similarity between the two types of pikas is the long-call, or song, given by adult males during the breeding season. The long-call consists of many repeated elements in a distinctive pattern for each species. There are, however, clear similarities between these calls in the rock-dwelling American pika (*Ochotona princeps*) and the burrowing plateau pika (*O. curzoniae*).

Throughout the day, most pikas are active about one-third of the time, and much of this is spent in quiet repose sitting atop a prominent rock surveying their surroundings. When they do patrol their territory, pikas often rub their cheek gland on rocks to advertise their presence. A quick vigorous chase normally ensues when another pika is encountered on their territory. Sometimes combatants actually make contact, with fur flying from the rump of the interloper. These chases are predictable when the interloper is an animal of the same gender or a non-neighbor of the opposite gender. However, chases are initiated only about half of the time when the animal encountered is a neighbor of the opposite gender. Otherwise, these opposite-sexed neighbors sit in a limbo of social tolerance, neither chasing nor engaging in any overt affiliative behavior that most likely defines a breeding pair.

Interestingly, these territories are not randomly spaced by gender across the talus. Instead, adjacent territories are generally occupied by a pika of the opposite sex. Pikas can live for up to six years of age and thus territory vacancies are uncommon. When they do occur, replacement is an animal of the same gender as the animal that died. Males will not allow settlement next door by another male, and similarly females chase off all available females. Female-female aggression ensures that their spacing is too far apart and the territories on talus are too large for any one male to control access to many females. Pika behavior controls the spacing of animals on the talus, and ultimately leads to a monogamous mating system. These dynamics ensure that the population structure of the pika is relatively stable over time.

Common predators of pikas are weasels and pine martens (genus *Mustela*). When a pika sees a predator, it utters an alarm call, a repetitive variant of the short call. Martens must capture pikas on the surface of the talus, as they are too big to fit in the cracks and crannies of the talus. When pikas first see a marten, they burst into an alarm call designed to warn neighbors (most of whom are close relatives) of the looming threat. If the predator is a weasel, then the pika often waits a few minutes before first giving the call. Weasels can follow pikas into their lairs in the rocks and, apparently, this latency to call allows the weasel time to clear out of the pika's territory before the pika alerts its neighbors of the threat.

The climate on the Tibetan plateau is frigid during winter and there is usually no snowpack (most precipitation occurs during summer) to insulate animals from these extreme

Pallas's pika (*Ochotona pallasi*) near Lake Khovsgol in Mongolia. (Photo by Joy Spurr. Bruce Coleman, Inc. Reproduced by permission.)

A collared pika (*Ochotona collaris*) eating vegetation in Alaska, USA. (Photo by Frank Krahmer. Bruce Coleman, Inc. Reproduced by permission.)

colds. The high degree of socialization, coupled with the philopatry of juveniles, has led to the conclusion that these family groups are selected to stay together during winter, when huddling may increase their average survivorship.

Nearly all mammalian carnivores and predacious birds on the Tibetan Plateau specialize on eating pikas. In response, plateau pikas utter an alarm call when predators are sighted. But, there are some unusual twists to this behavior. First, the call is very faint and barely audible from a short distance away. Apparently, it is designed only to warn immediate family members and not those from neighboring families. Second, the call is only given during the period of the first three days any new litter of juveniles is surface active. Giving the call may bring the predator's attention to the caller, and thus may be costly. After three days on the meadow, the young may be sufficiently experienced and no longer benefits sufficiently from an anti-predator alarm call. At this point, all the animals remain silent until the next litter surfaces.

A northern pika (*Ochotona hyperborea*) above the timberline. (Photo by © D. Robert & Lorri Franz/Corbis. Reproduced by permission.)

The American pika (*Ochotona princeps*) uses a "song" to warn others of danger. (Photo by © Robert Lindholm/Visuals Unlimited, Inc. Reproduced by permission.)

Feeding ecology and diet

Like all lagomorphs, pikas are generalized herbivores. Their most characteristic feeding behavior is the gathering of vegetation during summer that is stored in a centralized cache, or haypile, to serve as food during winter. Again like all lagomorphs, pikas excrete two types of feces and commonly reingest the soft viscous feces.

Pikas are most active during the mid- to late summer when they begin to gather vegetation with which to construct their haypile. At this time, a flurry of activity ensues with animals sometimes making one round-trip per minute to the adjoining meadow to pluck a long stem of a succulent herb. Commonly, a pika will sit on a rock briefly, utter a short call to proclaim its territory, rush to the meadow for a mouthful of vegetation, rush back, deposit the load, quickly give another call, and rush off again. The haypiles constructed by members of a pair are normally located on their territory closer to the territory of their pair mate rather than centered on their territory. Pikas forage for vegetation off of the talus, gener-

A Himalayan pika (*Ochotona* sp.) climbs on top of a rock, Ladakh, India. (Photo by Gertrud & Helmut Denzau/Naturepl.com. Reproduced by permission.)

ally close to the talus-meadow interface. Their behavior when feeding contrasts sharply with that of when they are gathering hay. Feeding pikas pluck individual small stems, generally of grass, which they eat while maintaining an alert posture; they appear to be extremely wary of predators while feeding. Pikas gather vegetation for their haypiles at far greater distances from the talus and, in contrast to their alert posture while feeding, appear foolhardy and unaware of predators while gathering hay. They try to get the largest mouthful of vegetation that they can, often diving at the base of a forb to clip it off.

Reproductive biology

Rock-dwelling pikas produce few young each year, whereas burrowing forms produce many large litters each season.

Most pikas originate from first litters as there is strong selection pressure for young to become active as early in the short summer season as possible. Juvenile pikas must grow up fast, claim a vacant territory (if one exists), and construct a haypile before the next winter's snow descends on the talus. Young normally remain close to their site of birth, and dispersal to a territory far away on their home talus, or movement to another talus patch, is rare.

Young become independent approximately three weeks after parturition, and they remain on their family burrow system territory throughout the summer and the following winter. Thus, as litter after litter appear on the meadow, the number of animals in each family grows and the overall population density skyrockets. Some populations reach densities of more than 120 animals per acre (300 per ha). Mortality is high during the harsh Tibetan winters and most animals perish; it is rare for any pika to live into its second year. The breeding season begins in early spring, and this is also the time that the composition of families is determined. There is a modest reshuffling of pikas before mating occurs. Nearly all pikas born the preceding summer remain on their home territory, but some, in particular males, disperse short distances and join neighboring families. The most common movements are to an immediately adjoining neighbor, but some pikas move as far as five territories away. The result of most of these movements is an equalizing of density across the meadow. Males do not move to families with more females. Instead, they move to families with more males.

The mating system expressed by plateau pikas results from the combination of the random nature of over-winter mortality and the few dispersal movements of animals alive just before the mating season. Most family burrow systems are occupied by a single adult male and female, which results in monogamy. However, when the number of surviving males and females is higher than can be accommodated on the restricted number of territories by only pairs, more complex situations arise. Some families are composed of one male and many females (polygyny), others with multiple males and one or more females (polyandry). These three different mating systems can occur in neighboring family burrow systems, a

An American pika (*Ochotona princeps*) in Colorado, USA. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by permission.)

An American pika (*Ochotona princeps*) gathering vegetation. (Photo by Goerge D. Lepp/Photo Researchers, Inc. Reproduced by permission.)

situation unique in mammals. In addition, the formation of these mating systems does not appear to result from variance in habitat quality on the meadow; there is no correlation between the type of mating system on a burrow system in one year with what will appear there the following year.

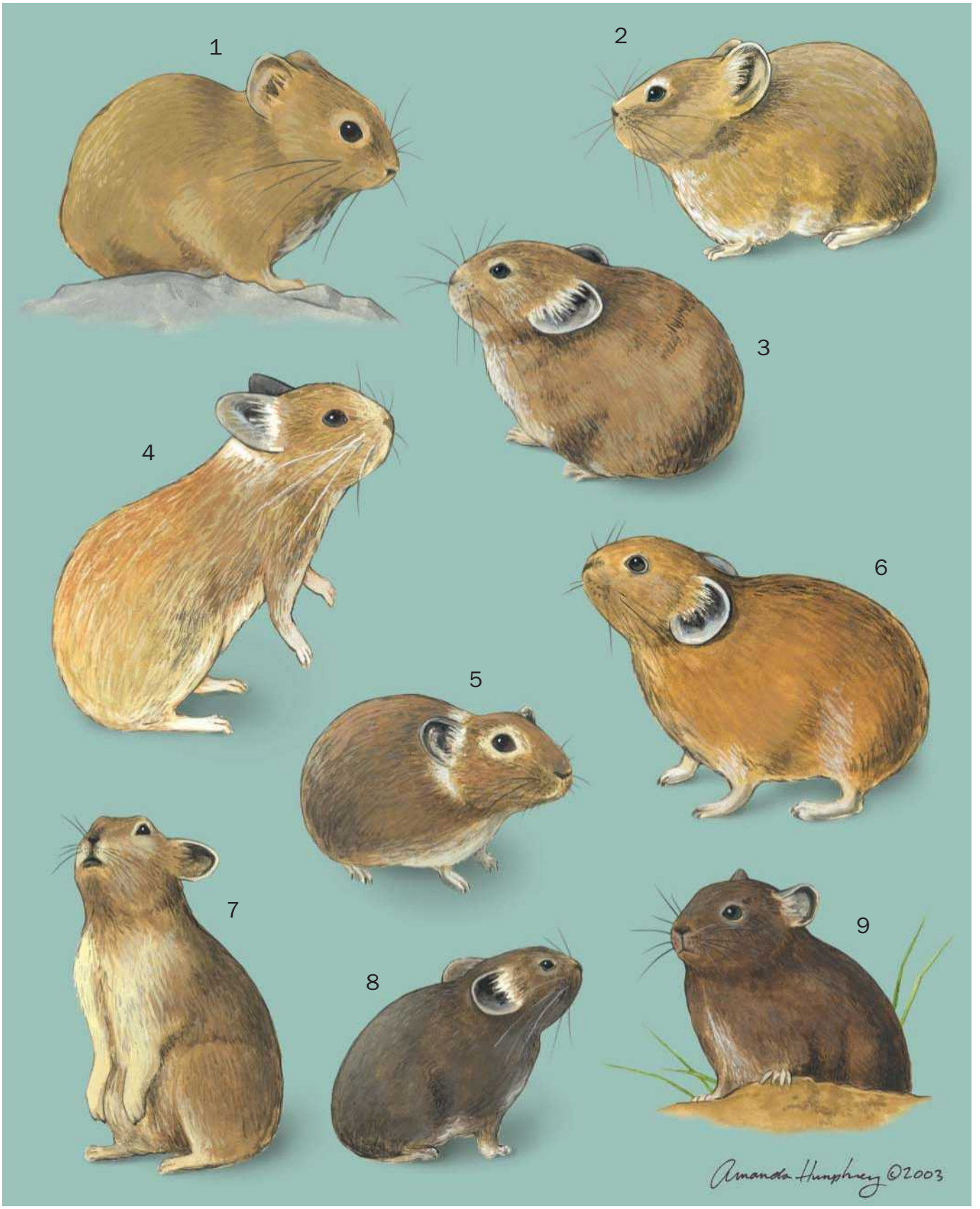
Conservation status

Twenty-six of the 30 pika species have been fully assessed for their IUCN Red List conservation status, and of these, six (23%) have been classified as Threatened (*O. argentata*, *O. hoffmanni*, *O. huangensis*, *O. iliensis*, *O. koslowi*, and *O. pusilla*). The first five on this list live in remote areas and are poorly known. The steppe pika (*O. pusilla*) has retreated as its habitat has been plowed under. An additional four species have one or more threatened subspecies. In nearly all cases, these forms are threatened because of habitat loss or inadvertent poisoning (control efforts directed at other, more common, pika species).

Significance to humans

Direct economic benefits from pikas are few; they are too small to serve as a source of country food. In central Asia, their pelts were once used to make felt. A distillate of the soft feces of pikas ("mumio") is used as a folk medicine in central Asia to speed up the healing of broken bones or to remedy rheumatism. Some species are believed to be agricultural pests or to damage rangelands and are subject to widespread poisoning efforts. A contrasting view is that these species are important in their respective ecosystems and should be preserved to maintain local biodiversity rather than to be subject to control.

A collared pika (*Ochotona collaris*) surveying for predators on tallas slope. (Photo by John Hyde. Bruce Coleman, Inc. Reproduced by permission.)



1. Pallas's pika (*Ochotona pallasi*); 2. Large-eared pika (*Ochotona macrotis*); 3. American pika (*Ochotona princeps*); 4. Turkestan red pika (*Ochotona rutila*); 5. Afghan pika (*Ochotona rufescens*); 6. Northern pika (*Ochotona hyperborea*); 7. Plateau pika (*Ochotona curzoniae*); 8. Steppe pika (*Ochotona pusilla*); 9. Gansu pika (*Ochotona cansus*). (Illustration by Amanda Humphrey)

Species accounts

American pika
Ochotona princeps

TAXONOMY
Ochotona princeps (Richardson, 1828), Rocky Mountains, Canada. Thirty-six subspecies.

OTHER COMMON NAMES
English: Cony, whistling hare, rock rabbit.

PHYSICAL CHARACTERISTICS
Moderate sized, with short ears and egg shaped body. Body is 6 to 8.5 in (162–216 mm). Buffy pelage; it lacks the grayish collar and the white ventral pelage found on the only other North American pika (the collared pika).

DISTRIBUTION
Found primarily at high elevations throughout the intermontane west of North America. Many of the 36 subspecies correspond to populations from isolated mountain ranges.

HABITAT
A characteristic rock-dwelling species.

BEHAVIOR
Males and females defend individual territories of approximately equal size. These territories are relatively large, and normally only about six animals will occupy 1 acre (15 per ha).

FEEDING ECOLOGY AND DIET
Generalized herbivores.

REPRODUCTIVE BIOLOGY
Rock-dwelling pikas produce few young each year (normally only two or three offspring), but normally only two are weaned successfully. They mate early in the spring. All adult females initiate two small litters during each short summer season. If the first litter is successful, then the second litter is abandoned. If the first is claimed by a weasel or lost because the female was in poor physiological condition coming out of the long winter, then the second litter as a back up is produced. Gestation is approximately 30 days, and young normally become surface active about a month after parturition.

CONSERVATION STATUS
Several isolated subspecies are considered Vulnerable to extinction.

SIGNIFICANCE TO HUMANS
None known. ◆

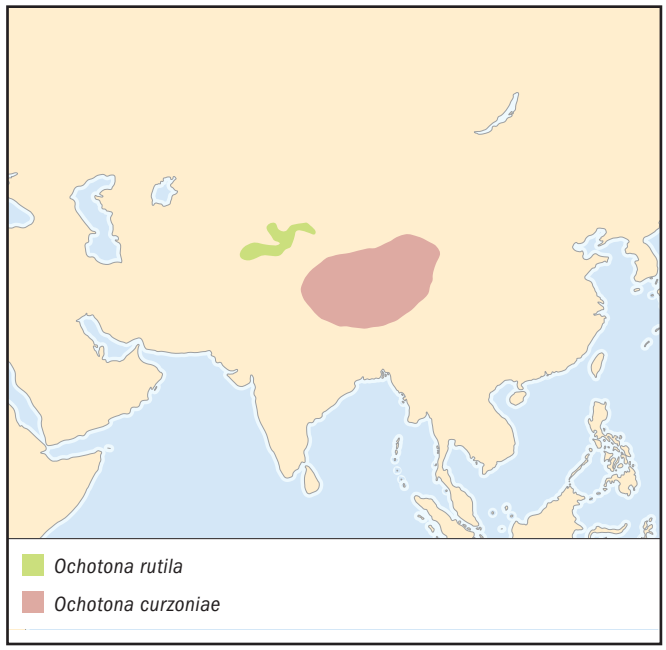
Plateau pika
Ochotona curzoniae

TAXONOMY
Ochotona curzoniae (Hodgson, 1858), Chumbi Valley, Tibet, China. No subspecies.

OTHER COMMON NAMES
English: Black-lipped pika.

PHYSICAL CHARACTERISTICS
Body length 4.7–9.8 in (12–25 cm); weight 0.4 lb (200 g). Brownish fur. The nose has a blackish tip and the lips form an indistinct black ring.

DISTRIBUTION
Confined to the high alpine meadows of the Qinghai-Xizang (Tibetan) plateau.



HABITAT
Alpine meadow habitat across the Tibetan plateau.

BEHAVIOR
The basic unit of social organization is the family unit that occupies a communal burrow system on alpine meadow habitat. These territories form a matrix of adjoining families, and the average spacing between the centers of activity of these territories is approximately 75 ft (25 m). Location of family burrow system territories is relatively stable on the meadow from year to year, however their composition may vary dramatically. Extremely social: as the density builds within a family burrow system during summer, the frequency of affiliative behavior soars. Rates of behavior may be as high as one social encounter per minute. These behaviors are complemented by a rich vocal repertoire (whines, trills, muffle calls) that appears to initiate many of these social encounters. In contrast to these social behaviors seen within families, most behaviors between individuals from different families are aggressive, long chases and fights.

FEEDING ECOLOGY AND DIET
Generalized herbivores that eat a wide variety of grasses, sedges, and forbs that grow on the high alpine meadows of the Tibetan plateau. The lack of a snowpack on the plateau allows them to forage year-round, and thus they are one of the few pika species that does not build a conspicuous haypile.

REPRODUCTIVE BIOLOGY
Different mating systems exist yearly, relating to current populations of local territories. Have a high rate of reproduction. During the spring to summer breeding season mothers initiate many sequential litters at three-week intervals. Most mothers wean three large litters (up to eight young), while others may produce up to five litters in a year.

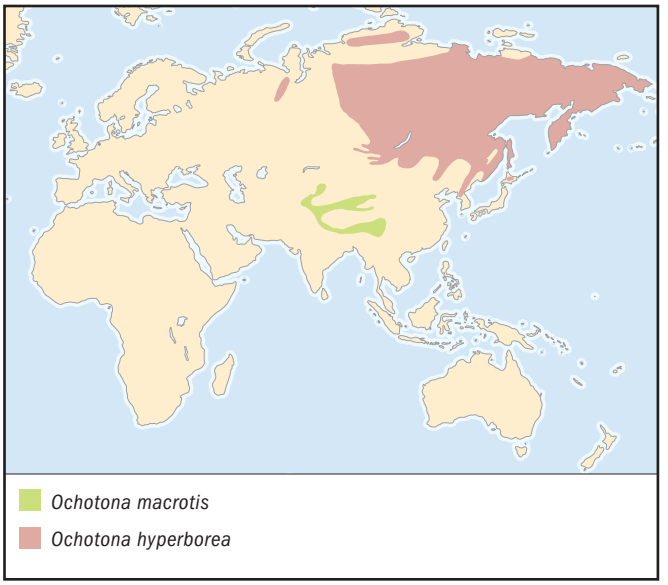
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Treated as a pest species for nearly four decades, it is believed that they cause rangeland degradation and eat vegetative resources that could better be utilized by local livestock (primarily yak and sheep). As a result, this species has been poisoned extensively. In Qinghai Province alone, pikas have been poisoned over 80,000 mi^2 (200,000 km^2), and the onslaught continues. Unfortunately, loss of the plateau pika over vast expanses of the Tibetan Plateau has resulted in a loss of many native species that rely on the pika. Most endemic native birds nest only in pika burrows, and when these collapse following poisoning, the birds disappear. Most predators on the plateau (weasels, ferrets, Pallas's cat, Tibetan fox, wolf, brown bear, upland buzzard, saker falcon, and black-eared kite) rely almost exclusively on pikas in their diet. When the pikas are poisoned, these animals also disappear. Thus, it appears that the plateau pika is a keystone species for biodiversity on the plateau and should be managed accordingly. Fortunately, as of 2002, the tide has been turning toward a policy that embraces the pika rather than one bent on destruction of the species. ◆

Large-eared pika
Ochotona macrotis

TAXONOMY
Ochotona macrotis (Günther, 1875), Tibet, China. Four subspecies.

OTHER COMMON NAMES
None known.



PHYSICAL CHARACTERISTICS
Body length 5.9–7.9 in (15–20 cm). A generalized ochotonid, but with large thin ears. Brown coat with gray undercoat.

DISTRIBUTION
High mountains of central Asia; has been recorded as high as 20,100 ft (6,130 m).

HABITAT
A typical rock-dwelling pika; it lives in high mountains.

BEHAVIOR
Adults live in pairs.

FEEDING ECOLOGY AND DIET
A generalized herbivore, some do not cache vegetation in haypiles, a characteristic of most pika species; it is felt that the lack of snow in parts of their range allowing for year-round foraging may be responsible.

REPRODUCTIVE BIOLOGY
Monogamous. Typical of most talus-dwelling pikas, they produce few (generally two) small litters (three to five young) per year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Northern pika
Ochotona hyperborea

TAXONOMY
Ochotona hyperborea (Pallas, 1811), Chukotsk Peninsula, Russia. Seven subspecies.

OTHER COMMON NAMES
English: Siberian pika.

PHYSICAL CHARACTERISTICS
A generalized ochotonid with no obvious external discriminating characteristics. Medium brown with orange to buffy under parts.

DISTRIBUTION
Largest distribution of any pika species; found across most of eastern Siberia to Sakhalin and Hokkaido islands.

HABITAT
A typical rock-dwelling pika, although throughout much of its range it also is known to inhabit tree-falls, stumps, and mossy banks.

BEHAVIOR
Adults live in pairs, although they rarely interact.

FEEDING ECOLOGY AND DIET
Forages on grasses and other vegetable matter; constructs large haypiles for winter feeding.

REPRODUCTIVE BIOLOGY
Assumed monogamous. Most females initiate two litters per summer reproductive season, and most litters range in size from one to five young.

CONSERVATION STATUS
Common. However, subspecies on Hokkaido Island, Japan (*O. h. yesoensis*), are locally considered to be endangered.

SIGNIFICANCE TO HUMANS
On Hokkaido Island, it is an important animal for ecotourism. ◆

Turkestan red pika
Ochotona rutila

TAXONOMY
Ochotona rutila (Severtzov, 1873), Kazakhstan. No subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Known primarily for its rich rust-reddish dorsal pelage in summer. Size and weight not available.

DISTRIBUTION
Primarily found in the Parmir, Kirgiz, Gissar, and Tien Shan mountains of central Asia.

HABITAT
A typical rock-dwelling pika in the central Asian mountains.

BEHAVIOR
It is unusual among rock-dwelling pikas by having a significantly larger territory on which it forages, and its tendency for juveniles to over-winter on the territory with their parents. Sometimes this is called the "silent" pika, as it has no song or typical alarm call.

FEEDING ECOLOGY AND DIET
Construct large haypiles. They appear more reticent to forage on open meadows than most pikas, confining most of their foraging to patches of vegetation among the rocks on its large territory.

REPRODUCTIVE BIOLOGY
Normally two litters are initiated, and litter size is small (two to six young/litter). Mating system may vary yearly depending on populations of local territories.

CONSERVATION STATUS
Common, not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Pallas's pika
Ochotona pallasi

TAXONOMY
Ochotona pallasi (Gray, 1876), Kazakhstan. Three subspecies.

OTHER COMMON NAMES
English: Mongolian pika.

PHYSICAL CHARACTERISTICS
A generalized ochotonid, no strong external discriminating characteristics. Size and weight not available.

DISTRIBUTION
Primarily mountains of western Mongolia and isolated subspecies in Mongolia and northern China.

HABITAT
Habitat utilization varies across the species. The subspecies *O. p. pricei* usually occupies arid steppe environments and may construct burrows, whereas the other subspecies are more likely to live in rocky habitats.

BEHAVIOR
Just as the habitats occupied by Pallas's pika vary, so does the ecology of the species. The marked differences in reproduction, habitat, behavior, and vocalizations may indicate that *O. p. pricei* will ultimately be treated as a different species. Pallas's pika appears to be an intermediate species (with habitat characteristics between those of the obligate rock-dwellers and the meadow-dwelling burrowing pikas). In these intermediate species, and certainly true for Pallas's pika, the life history features more closely resemble those of the burrowing forms than those of rock-dwelling pikas.

FEEDING ECOLOGY AND DIET
Known to make large haypiles, although some populations store most of their winter cache under rocks.

REPRODUCTIVE BIOLOGY
Has a high reproductive rate; several litters may be born per reproductive season, and litter sizes may be large (one to 13 young per litter). Mating system may vary yearly depending on populations of local territories.

CONSERVATION STATUS
Common, species-wide. However, two subspecies are threatened with extinction: *O. p. hamica* (IUCN status: Critically Endangered) and *O. p. sunidica* (IUCN status: Endangered).

SIGNIFICANCE TO HUMANS
O. p. pricei has been considered a focus for plague and subjected to control efforts. This activity is no longer being pursued. ◆

Afghan pika
Ochotona rufescens

TAXONOMY
Ochotona rufescens (Gray, 1842), Kabul, Afghanistan. Two subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
During summer, it possesses a cream-colored collar that is outlined with russet pelage. Size and weight not available.

DISTRIBUTION
Patchily distributed in the mountains of Iran, Afghanistan, and Pakistan.

HABITAT
Another intermediate species one that has a tendency to live in rocks, but also constructs burrows. Unlike most alpine pikas, the Afghan pika may occupy landscapes that are significantly more xeric (dry).

BEHAVIOR
Its life history characteristics mimic those of the true burrowing forms. It lives in family groups at medium-high densities (up to 30 animals per acre [70/ha]), but it does not have a well-developed vocal repertoire.

FEEDING ECOLOGY AND DIET
Known to eat thistles and other xeric plants. They make large hay piles, but normally collect these stores twice per year (in spring before the vegetation dries up and again in fall when the vegetation is revived by seasonal rains).

REPRODUCTIVE BIOLOGY
Have a high rate of reproduction; females may produce up to five litters in an extended breeding season, and litter sizes may contain as many as 11 young. Mating system may vary yearly depending on populations of local territories.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Considered a threat to agricultural crops and orchards throughout much of its range, and as a consequence has been subject to control programs. ◆

Gansu pika
Ochotona cansus

TAXONOMY
Ochotona cansus Lyon, 1907, Gansu, China. Three subspecies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Very small, with adults weighing only about 3 oz (80 g). Otherwise, it is typical of most ochotonids. Brownish fur is lighter below.

DISTRIBUTION
Distributed throughout the north-central Tibetan Plateau.

HABITAT
Lives in shrubby habitats, largely dominated by *Potentilla fruticosa* and *Caragana* spp., under which it constructs burrows.

BEHAVIOR
The ecology and behavior of the Gansu pika closely resembles that of the plateau pika; it has a vocal repertoire of four calls.

FEEDING ECOLOGY AND DIET
A generalized herbivore.

REPRODUCTIVE BIOLOGY
Two or three litters are produced during a breeding season that extends from early April until late August. Litter sizes range from one to six young. Mating system may vary yearly depending on populations of local territories.

CONSERVATION STATUS
Common, species-wide. However, one subspecies is threatened with extinction (*O. c. sorella*; Endangered); and another is Data Deficient (*O. c. morose*).

SIGNIFICANCE TO HUMANS
None known. ◆

Steppe pika
Ochotona pusilla

TAXONOMY
Ochotona pusilla (Pallas, 1769), Orenburgsk Obl, Russia.

OTHER COMMON NAMES
English: Little pika.

PHYSICAL CHARACTERISTICS
Body length is 5.9 in (15 cm). Color is darker grayish brown above, lighter below. A small generalized ochotonid.

DISTRIBUTION
Found from the Ural Mountains east across southern Russia and northern Kazakhstan.

HABITAT
Occupies flat meadow and steppe country where it utilizes burrows.

BEHAVIOR
The ecology and behavior of the steppe pika closely resemble that of the plateau pika. The steppe pika is the only truly nocturnal pika. One of its key characteristics is the loudness of its short call, which can be heard over very long distances.

FEEDING ECOLOGY AND DIET
A generalized herbivore that constructs haypiles.

REPRODUCTIVE BIOLOGY
Have a high reproductive rate; three to five litters are produced per year and litter sizes may contain as many as 13 young. Mating system may vary yearly depending on populations of local territories.

CONSERVATION STATUS
Vulnerable.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Alpine pika *Ochotona alpina*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Northwestern Kazakhstan, southern Russia, northwestern Mongolia, and northwestern China.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Collared pika *Ochotona collaris*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	West-central Mackenzie, southern Yukon, and northwestern British Columbia, Canada; and southeastern Alaska, United States.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Chinese red pika *Ochotona erythrotis*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	West-central China.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Gaoligong pika *Ochotona gaoligongensis*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Northwest Yunnan, China.	Shrubs, grasses, sedges, herbs, and lichens.	Data Deficient
Himalayan pika *Ochotona himalayana*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Mt. Jolmolunga (Everest) area, southern Tibet, China; probably adjacent Nepal.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN

[continued]

Common name / Scientific name	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Ili pika *Ochotona iliensis*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Xinjiang, China.	Shrubs, grasses, sedges, herbs, and lichens.	Vulnerable
Ladakh pika *Ochotona ladacensis*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Southwestern Xinjiang, Qinghai, and eastern Tibet, China; Kashmir, India; and Pakistan.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Nubra pika *Ochotona nubrica*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Southern edge of Tibetan Plateau from Ladakh, India, through Nepal to eastern Tibet, China.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Moupin pika *Ochotona thibetana*	Their long, soft, fine fur is usually gray to brown, typically darker above. Short legs and tails. Body length 4.9–11.8 in (12.5–30 cm); weight 3.5–7.1 oz (100–200 g).	Open, rocky areas, including grasslands, northern tundra, and mountain slopes to elevations over 19,000 ft (5,790 m). Diurnal; they do not appear to hibernate. Females produce two or more litters per year.	Shanxi, Shaanxi, W Hubei, Yunnan, Sichuan, and southern Tibet, China; northern Myanmar; Sikkim, India; and perhaps adjacent Bhutan and India.	Shrubs, grasses, sedges, herbs, and lichens.	Not listed by IUCN
Sardinian pika *Prolagus sardus*	Extinct, but likely similar to others in the family.	Open, rocky areas, including grasslands, and mountain slopes to elevations over 19,000 ft (5,790 m). Details of this extinct animal's behavior not known.	Mediterranean Islands of Corsica and Sardinia, and adjacent small islands.	Likely shrubs, grasses, sedges, herbs, and lichens.	Extinct

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Organizations

IUCN Species Survival Commission, Lagomorph Specialist Group. Department of Biology, Box 871501, Arizona State University, Tempe, AZ 85287-1501 USA. E-mail: a.smith@asu.edu Web site: <http://www.ualberta.ca/dhik/lsg>

Other

IUCN—The World Conservation Union, Species Survival Commission, Red List Programme Office. *Official IUCN Red List of Threatened Species*. <http://www.redlist.org>.

Andrew T. Smith, PhD

Hares and rabbits

(Leporidae)

Class Mammalia
Order Lagomorpha
Family Leporidae

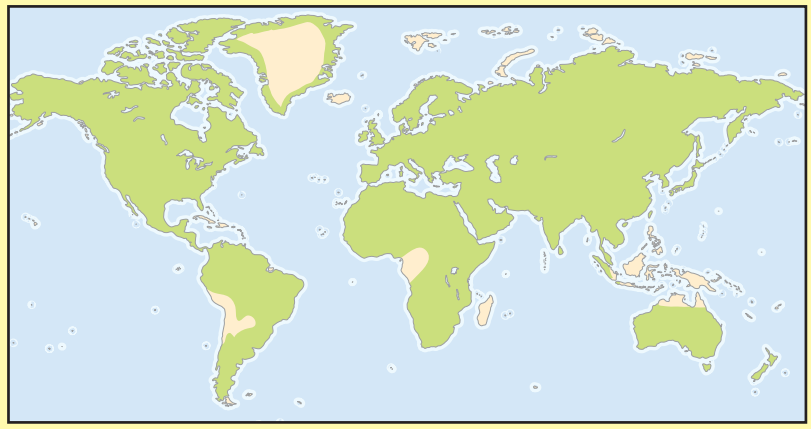
Thumbnail description
Small- to medium-sized mammals with long ears, short tails, and long hind legs

Size
10–30 in (25–75 cm); 14 oz–13.2 lb (400–6,000 g); females usually larger than males

Number of genera, species
11 genera; 61 species

Habitat
Forest, woodland, savanna, scrub, and tundra

Conservation status
Critically Endangered: 2; Endangered: 7; Vulnerable: 3; Data Deficient: 9



Distribution
Africa, Asia, Europe, North America, South America, and introduced to Australia, New Zealand, Java, and other islands

Evolution and systematics

The Leporidae is sometimes divided into subfamilies Paleolaginae (*Pentalagus*, *Pronolagus*, and *Romerolagus*) and Leporinae (remaining genera). There are 11 genera: 32 *Lepus*, true hares; 1 *Oryctolagus*, European rabbit; 17 *Sylvilagus*, cottontails; 1 *Brachylagus*, pygmy rabbit; 3 *Pronolagus*, red rock-hares; 1 *Bunolagus*, riverine rabbit; 1 *Pentalagus*, Amami rabbit; 1 *Caprolagus*, hispid hare; 1 *Poelagus*, Bunyoro rabbit; 2 *Nesolagus*, striped rabbits; and 1 *Romerolagus*, volcano rabbit.

Early leporids were found in both the Old and New World before *Lepus* evolved, but had a probable origin in Asia. The Leporidae arose in the Pliocene and *Lepus* in the early Middle Pleistocene. Whereas *Pentalagus*, *Pronolagus*, and *Romerolagus* are ancient forms, *Lepus* is a young expanding genus.

The monotypical genera in Leporidae are taxonomically distinct with the exception of *Brachylagus*, which sometimes is included in *Sylvilagus*. However, the *Lepus* genus is in a state of confusion regarding both phylogeny and number of species.

Physical characteristics

All species in the family Leporidae have basic brown or gray soft fur with relatively long legs, feet, and ears. The tail is short and bushy. Some northern forms turn white for winter, and two are striped. The family can be split into two groups, hares and rabbits, based on morphology and ecology. The hare group includes all hares and jackrabbits in the genus *Lepus*, hereafter called hares. The rabbit group consists of the remaining genera in the family, despite that they are sometimes also known as hares (for example, hispid hares) hereafter called rabbits. Hares have long legs and can reach considerable running speed. They also have longer ears, usually with black tips, and are, overall, larger than rabbits. The body length of hares is 15–30 in (40–75 cm), with a weight of 3–13.2 lb (1,350–6,000 g). Rabbits, on the other hand, have shorter legs and are generally smaller: 10–20 in (25–50 cm); 14 oz–6.6 lb (400–3,000 g).

Distribution

Altogether, hares and rabbits are distributed over most areas of the world: Africa, the Americas, Asia, and Europe, and have also been introduced into southern South America, Australia, New Zealand, Java, and other islands.

The natural habitat of European hares is open terrain ranging from forest steppes to arid steppes. They therefore benefit from cultivation of fields. In connection to agriculture, they spread rapidly to the east and northeast during the nineteenth and twentieth centuries. They were also successfully introduced in agricultural areas in Argentina, Ireland, Scandinavia, New Zealand, Australia, and southern Siberia.

The European rabbit has a similar increase in distribution due to many introductions in suitable habitats. Before the Ice Age, it inhabited parts of Western Europe, as indicated by fossils. However, its natural post-Ice Age distribution includes only Spain and northwest Africa. But already the Romans had introduced rabbits to different parts of Europe. There were several introductions in Australia, but the successful ones came from 24 rabbits in 1859 in Victoria and in 1864 to New Zealand. Both Australia and New Zealand suffered tremendously from a gigantic rabbit population explosion. In spite

A young Arctic hare (*Lepus arcticus*) eating willow in Northwest Territory, Canada. (Photo by Animals Animals ©Brian Milne. Reproduced by permission.)

An antelope jackrabbit (*Lepus alleni*) checking for predators in Arizona, USA. (Photo by Animals Animals ©Paul Berquist. Reproduced by permission.)

of the disastrous consequences, wild rabbits were later introduced into Chile and became a plague there as well.

Habitat

Since hares and rabbits are found almost all over the world, they are also both found in a variety of habitats, from deep forests to open deserts. But hares have different basic habitat requirements than rabbits.

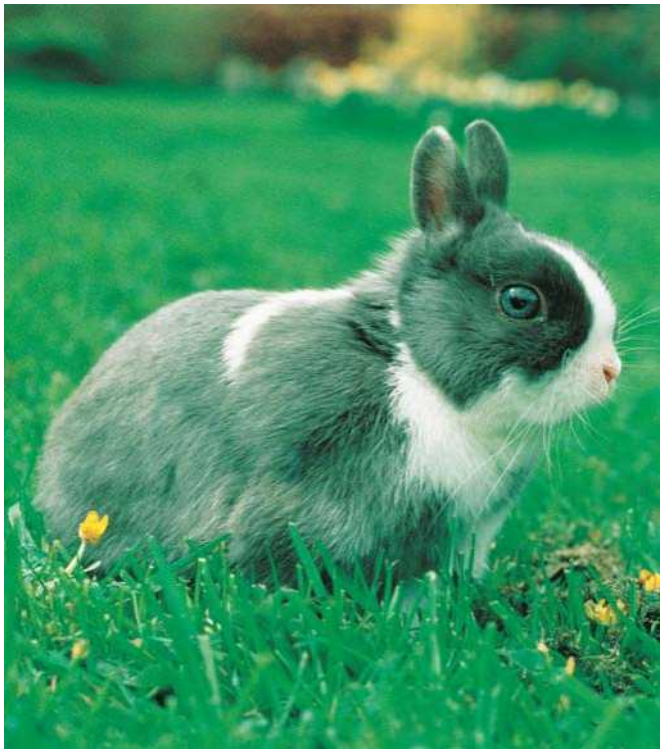
Hares are mostly found in open areas where their running speed is a good adaptation to escape predators. They can thus be found from arctic tundra to productive grasslands or deserts. In these open areas, they take advantage of shrubs and rocks to hide, and rely on their well-camouflaged fur. But snowshoe hares and partly mountain hares and Manchurian hares prefer coniferous or mixed forests.

However, rabbits are confined to forests and shrubs where they can hide in the vegetation or in burrows. Some rabbits are found in deep tropical forests, such as the striped rabbits, and others use specific habitats like riverine shrubs, as do the riverine rabbit and hispid hare. Cottontails inhabit a large variety of habitats, including swamps, forests, parks, agricultural field, shrubs, and deserts.

Behavior

Predation is an important aspect in the life of hares and rabbits. Hares escape predators by running away and try to confuse predators by backtracking themselves. Rabbits try to escape predators by running into burrows or holes. Therefore, hares can travel considerable distances and have large home ranges, while rabbits mostly stay in the vicinity of safe hiding places in small home ranges or territories. Many species use distress calls or thump their hind feet on the ground to warn for predators. They also use a soft sound produced by grinding their teeth.

A marsh rabbit (*Sylvilagus palustris*) eating vegetation in Everglades National Park, Florida, USA. (Photo by Animals Animals ©Joe McDonald. Reproduced by permission.)



A dwarf domestic rabbit in a field in Oxon, United Kingdom. (Photo by Animals Animals ©A. Ramage, OSF. Reproduced by permission.)

A snowshoe hare (*Lepus americanus*) changing from winter white coat to summer brown. (Photo by L. L. Rue. Bruce Coleman, Inc. Reproduced by permission.)

A desert cottontail (*Sylvilagus audubonii*) burrowing in South Dakota, USA. (Photo by John Shaw. Bruce Coleman, Inc. Reproduced by pernssion.)

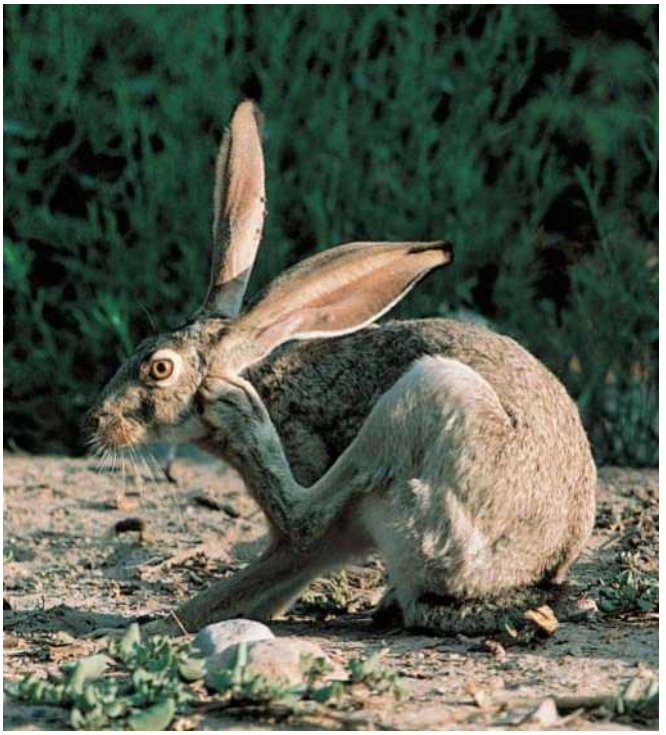
Hearing is the most important sense for leporids, but scent marking is also an central way to communicate. They have scent glands on their nose, chin, and around the anus. This is important in sexual situations, especially for the social European rabbit.

Feeding ecology and diet

All hares and rabbits are strictly herbivores. Their diets include green plant parts, especially grasses, clover, and, to a lesser extent, cruciferous and composite plants (e.g., dandelions). In winter, the diet also includes dry twigs, buds, young tree bark, roots, and seeds. In steppe regions, the winter diet consists of dry weeds and seeds. Most like cultivated plants such as winter grains, rapeseed, cabbage, parsley, and carnations. Both hares and rabbits may damage cereals, brassica crops, fruit trees, and tree plantations, especially in winter. Hares rarely drink when there are enough moist plants around, but sometimes eat snow in the winter.

Reproductive biology

Most hares and rabbits are solitary, although they can be seen in groups around mating season when males fight each other to build social hierarchies and try to get access to females in estrous. But the European rabbit forms highly social groups with one to four males and one to nine females. They can dig complex burrows that they defend against other social groups. Both males and females are promiscuous. Like many leporids, they mate again soon after giving birth. Since



A black-tailed jackrabbit (*Lepus californicus*) scratching. (Photo by Gary Zahm. Bruce Coleman, Inc. Reproduced by permission.)

gestation length for the European rabbit is about 30 days, they give birth to five to seven litters a year. European hares increase reproductive output by fertilizing a second litter before the first one is born (superfetation).

A snowshoe hare (*Lepus americanus*) in winter. (Photo by Animals Animals ©Peter Weimann. Reproduced by permission.)

A European hare (*Lepus europaeus*) running through a poppy field. (Photo by Animals Animals ©Robert Maier. Reproduced by permission.)

Hares give birth, after a long gestation period, to well-developed fur-covered leverets that have open eyes and that can already move around at birth. Rabbits have a shorter gestation period and build nests with fur in burrows or hollows underground or in dense cover. The newborn rabbit kittens are poorly developed with eyes closed and no fur. After birth,

An Arctic hare (*Lepus arcticus*) feeding in Newfoundland, Canada. (Photo by Animals Animals ©Ted Levin. Reproduced by permission.)

both hare and rabbit mothers suckle their leverets only once a day with highly nutritious milk. This lack of social contact makes it difficult for predators to find juvenile hares and rabbits. Litter size of both hares and rabbits vary with geography and climate.

Conservation status

Typically, the ancient rabbit species are threatened with extinction because of low population sizes and restricted distributions, including the riverine rabbit, volcano rabbit, hispid hare, and the two striped rabbits. Some species on islands are also Endangered, such as the Hainan hare, Tres Marias cottontail, and Amami rabbit.

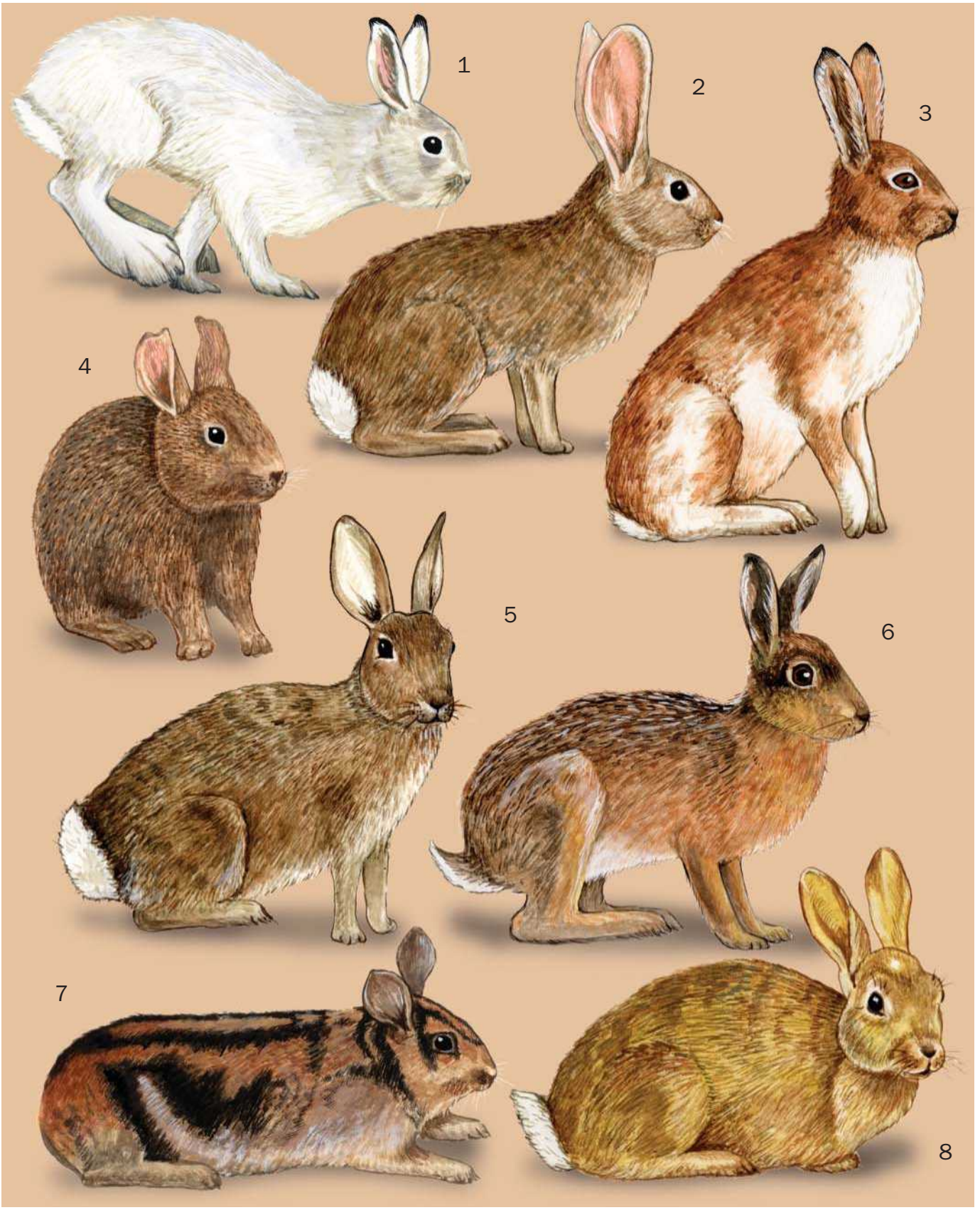
Many species have not been evaluated by IUCN and some of those will undoubtedly be listed as threatened such as the newly described Annamite striped rabbit. Another problem is the taxonomy where relationships between taxa are not well described.

Significance to humans

Many hares and rabbits are economically important for humans. They are hunted for meat, skin, and for sport. Cottontails and some of the hares are hunted in millions every year. However, they may also damage agricultural crops and forestry plantations. When introduced into new areas, they can also threaten native species.

Hares and rabbits are known from tales dating back centuries, mostly as tricksters and fertility symbols. The hare was, for example, important in the Germanic heathen mythology as the fertility goddess Ostara, and was transformed by Christians into the Easter celebration.

The domestic European rabbit is well known all over the world and used extensively in laboratory research and as pet animals. The first descriptions of domestic breeds of European rabbits come from France in the sixteenth century.



1. Snowshoe hare (*Lepus americanus*); 2. Desert cottontail (*Sylvilagus audubonii*); 3. Mountain hare (*Lepus timidus*); 4. Volcano rabbit (*Romerolagus diazi*); 5. Eastern cottontail (*Sylvilagus floridanus*); 6. European hare (*Lepus europaeus*); 7. Annamite striped rabbit (*Nesolagus limminsi*); 8. European rabbit (*Oryctolagus cuniculus*). (Illustration by Amanda Smith)

Species accounts

Snowshoe hare
Lepus americanus

TAXONOMY
Lepus americanus Erxleben, 1777, Fort Severn, Ontario, Canada. Fifteen subspecies.

OTHER COMMON NAMES
French: Lièvre d'Amérique; German: Schneeschuhhase; Spanish: Liebre nival.

PHYSICAL CHARACTERISTICS
The smallest of the hares with large hind feet that turn white during the winter.

DISTRIBUTION
From Alaska to Newfoundland and south through the coastal range; the Rockies and the Appalachians to northern California, northern New Mexico, and Tennessee.

HABITAT
From conifer forests to mixed forests, with a preference for transition zones.

BEHAVIOR
Populations show large synchronized fluctuations with a peak every eight to 11 years (10-year cycles). They use forms for cover during the day and make regular trails to feeding areas.

FEEDING ECOLOGY AND DIET
Summer diet is grasses, sedges, and various herbs, but changes to birch, aspen, willow, spruce, and pine during the winter.

REPRODUCTIVE BIOLOGY
Promiscuous. Most reproductive characters are related to the 10-year population cycle. Normally gives birth to two litters per year, but this can increase to four, dependent on geography and population phase. Litter sizes vary from one to 10.

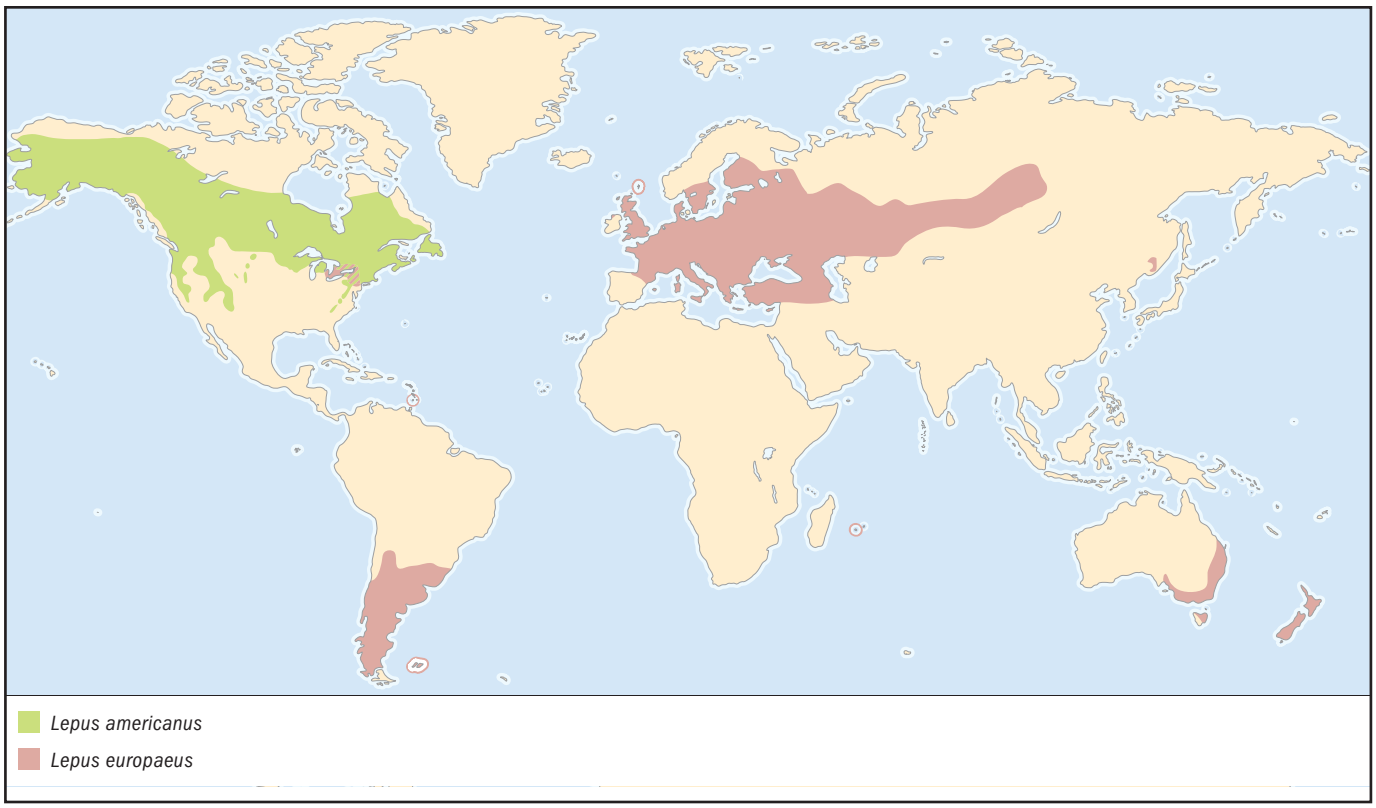
CONSERVATION STATUS
Common; not threatened.

SIGNIFICANCE TO HUMANS
Important game species; may damage tree plantations. ◆

European hare
Lepus europaeus

TAXONOMY
Lepus europaeus Pallas, 1778, southwest Poland. Thirty subspecies.

OTHER COMMON NAMES
English: Brown hare; French: Lièvre brun; German: Feldhase; Spanish: Liebre común.



PHYSICAL CHARACTERISTICS
Body length 20–27 in (52–68 cm), tail 3–5 in (8–12 cm), body weight 5.5–14 lb (2,500–6,000 g). A large hare that is brown throughout the year with long ears, relatively long tail, and long limbs.

DISTRIBUTION
Most of Europe, south to Iran, and into western Siberia. Introduced in eastern North America, southern South America, southeastern Australia, New Zealand, and several islands.

HABITAT
Open country as mixed farmland, moorland, steppe, but also open woodland. In introduced areas habitats can be variable, including pampas, sand dunes, marshes, and alpine grassland.

BEHAVIOR
Solitary, but may aggregate in groups when feeding; males fight around females in estrous.

FEEDING ECOLOGY AND DIET
Diet varies with mostly grass in the summer and can include shrubs in the winter, but on agricultural land crops dominates.

REPRODUCTIVE BIOLOGY
Males and females are promiscuous. Females give birth to two to four litters per year with a mean litter size of one to four.

CONSERVATION STATUS
Common; not threatened.

SIGNIFICANCE TO HUMANS
Important game species that may damage crops. ◆

Mountain hare
Lepus timidus

TAXONOMY
Lepus timidus Linnaeus, 1758, Uppsala, Sweden.

OTHER COMMON NAMES
English: Blue hare, varying hare; French: Lièvre variable; German: Schneehase; Spanish: Liebre variable.

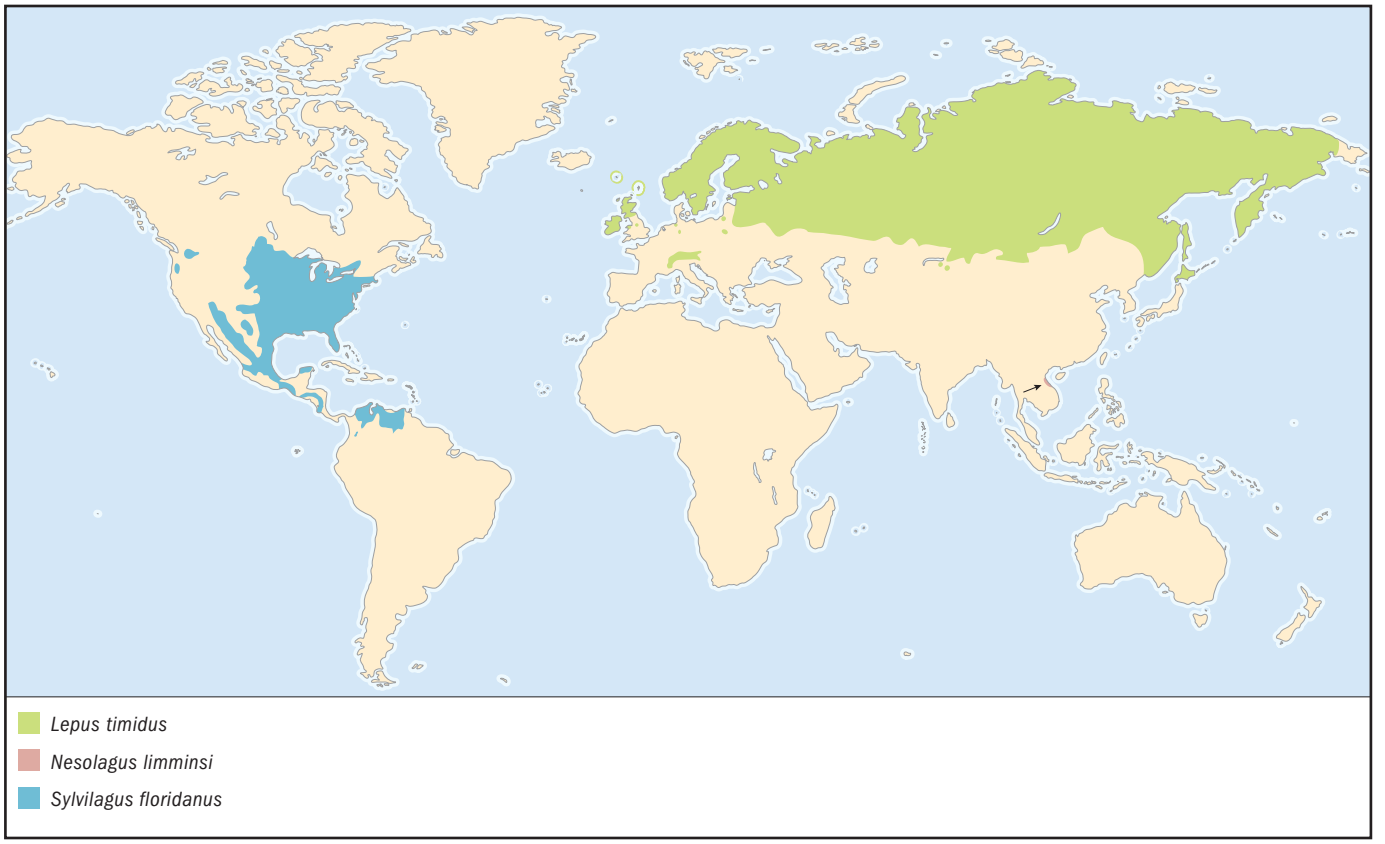
PHYSICAL CHARACTERISTICS
Body length 18–24 in (46–61 cm); weight 4.4–10.4 lb (2,000–4,700 g). A medium-sized hare with long hind feet and short ears; summer fur is brown and turns mostly white in winter.

DISTRIBUTION
Circumpolar in tundra and taiga habitats from Britain to Japan.

HABITAT
Common in tundra, taiga habitats, and mixed forests. Prefer transition zones with open clearings, and in swamps and river valleys. In Scotland found on heather moorland, and in Ireland and Hokkaido, Japan also on agricultural land.

BEHAVIOR
A solitary animal. During mating season, it can be seen in groups, sometimes fights upright on its hind legs.

FEEDING ECOLOGY AND DIET
Leaves and twigs of willow, rowan, birch, juniper, aspen, and heather; in tundra, alpine plants, especially dwarf willow, and blueberry are important. Palatable grasses and herbs are eaten in the summer when available: grasses, sedge, and dicotyledons.



REPRODUCTIVE BIOLOGY
Promiscuous. In tundra areas, only one litter per year with a mean litter size of five to six young, but up to four litters per year depending on the length of the vegetation season with a mean litter size of two to four. At birth, the young are fully furred, their eyes are open, and they start suckling at once.

CONSERVATION STATUS
Very widespread and abundant over most of its range; not threatened.

SIGNIFICANCE TO HUMANS
Important game species; may damage crops and tree plantations. ◆

Annamite striped rabbit
Nesolagus limminsi

TAXONOMY
Nesolagus limminsi Averianov, Abramov, and Tikhonov, 2000, Huong Son District, Ha Tinh Province, Vietnam.

OTHER COMMON NAMES
French: Lapin Annamite; German: Annamitekaninchen; Spanish: Conejo de Annamite.

PHYSICAL CHARACTERISTICS
Body length 13.5–15.8 in (35240 cm). Coat buffy gray with brown stripes. Under parts are white.

DISTRIBUTION
Known only from the vicinity of the type locality in Vietnam.

HABITAT
Forest with thick undergrowth.

BEHAVIOR
Probably nocturnal.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Presumed rare and potentially endangered.

SIGNIFICANCE TO HUMANS
Unknown, but used as food. ◆

European rabbit
Oryctolagus cuniculus

TAXONOMY
Oryctolagus cuniculus (Linneaus, 1758), Germany.

OTHER COMMON NAMES
French: Lapin de garenne; German: Wildkaninchen; Spanish: Conejo europeo.

PHYSICAL CHARACTERISTICS
Body length 14–20 in (35–50 cm), weight 3.3–6.6 lb (1,500–3,000 g). The fur is brown with light and black tips, tail white below.

DISTRIBUTION
Original distribution in the Iberian Peninsula and northwest Africa, but introduced 2,000 years ago to the rest of Europe. Later introductions also to Australia, New Zealand, South America, and several islands all over the world.

HABITAT
In Europe, found in well-drained areas where it is easy to dig dens such as riverbanks. But in introduced areas, it shows great adaptability and inhabits anything from deserts to sub-alpine valleys, including gardens and parks.

BEHAVIOR
It digs complex burrows for protection against predators and for reproduction. Scent marking is common in social communication, with dominant males being most active.

FEEDING ECOLOGY AND DIET
Grass, herbs, roots, bark, and cultivated plants.

REPRODUCTIVE BIOLOGY
Gestation length is about 30 days and they produce five to seven litters per year with a mean size of five to six. It forms highly social groups with one to four males and one to nine females; promiscuous mating.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Many introduced populations have reached pest proportions. Important game animal in many areas, and domestic breeds are used in laboratory research and as pet animals. ◆

Volcano rabbit
Romerolagus diazi

TAXONOMY
Romerolagus diazi (Ferrari-Pérez, 1893), San Martin Texmelusán, Mexico.

OTHER COMMON NAMES
English: Zacatuche; French: Lapin des volcans; German: Vulkankaninchen; Spanish: Conejo zacatuche, teporingo.

PHYSICAL CHARACTERISTICS
One of the smallest leporids; body length 10–14 in (27–36 cm), weight 14–18 oz (400–500 g). The ears are short and the hair is dark brown, and it lacks a visible external tail.

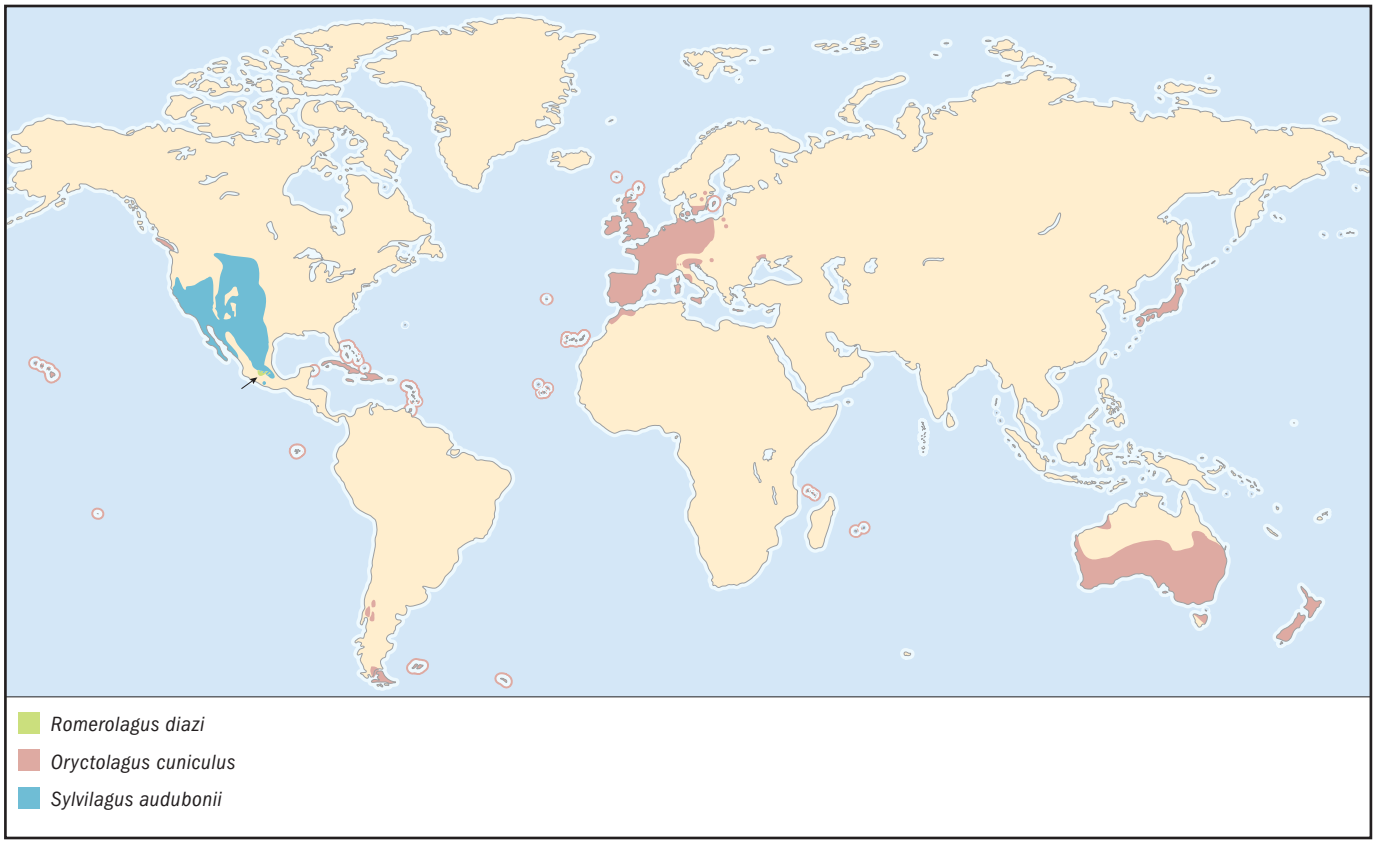
DISTRIBUTION
They occur only on the slopes of the Mexican volcanoes, Ajusco and Ixtacihuatl; Popocateptl at 9,190–13,120 ft (2,800–4,000 m).

HABITAT
Open pine forests with a unique grass habitat, *zacaton*.

BEHAVIOR
Vocalizations resemble those of pikas. Mainly active during the days.

FEEDING ECOLOGY AND DIET
Feeding on the typical *zacaton* grasses.

REPRODUCTIVE BIOLOGY
Assumed promiscuous. Average litters size one to three. Breeding season December–July.



CONSERVATION STATUS
Listed as Endangered by the IUCN an U.S. Endangered Species Act. Also listed on CITES Appendix I. A very restricted distribution close to Mexico City.

SIGNIFICANCE TO HUMANS
Threatened by habitat destruction, forest fires, agriculture, and property developments. Hunting is now illegal. ◆

Desert cottontail
Sylvilagus audubonii

TAXONOMY
Sylvilagus audubonii (Baird, 1858), San Francisco Co., California, United States. Twelve subspecies.

OTHER COMMON NAMES
English: Audubon's cottontail; French: Lapin Audubon; German: Audubonkaninchen; Spanish: Conejo del desierto.

PHYSICAL CHARACTERISTICS
Body length 14–15 in (37–40 cm); tail 1.6–2.4 in (4–6 cm); weight 26.5–44 oz (750–1,250 g). A relatively large cottontail with large ears.

DISTRIBUTION
From Montana south to central Mexico and west to the Californian coast.

HABITAT
Typically arid areas, but also at higher altitudes.

BEHAVIOR
Not social, but with overlapping home ranges of up to 15 acres (6 ha).

FEEDING ECOLOGY AND DIET
Diet mostly grasses, but also some wood species such as *Rosa* and *Rubus*.

REPRODUCTIVE BIOLOGY
Males and females promiscuous. Mean litter size two to three; breeding season from January to August; sexual maturity reached as early as 80 days after birth.

CONSERVATION STATUS
Common; not threatened.

SIGNIFICANCE TO HUMANS
Important game species. ◆

Eastern cottontail
Sylvilagus floridanus

TAXONOMY
Sylvilagus floridanus (J. A. Allen, 1890), Florida, United States. Thirty-five recognized subspecies.

OTHER COMMON NAMES
French: Lapin à queue blanche; German: Florida-Waldkaninchen; Spanish: Conejo castellano.

PHYSICAL CHARACTERISTICS
Body length 15–19 in (40–48 cm); tail 1–2.4 in (2.5–6 cm); weight 1.8–3.3 lb (800–1,500 g). A large cottontail with brown or grayish fur.

DISTRIBUTION
From southern Canada through central and eastern United States, Central America, and northern South America.

HABITAT
Widely distributed in many habitats such as woodlands, prairies, farmlands, deserts, and rainforests.

BEHAVIOR
Do not dig burrows, but females dig nests in holes where the young are reared. Males fight one another to establish dominance hierarchies at mating.

FEEDING ECOLOGY AND DIET
Herbs and grasses are preferred during growing season, and woody species during winter.

REPRODUCTIVE BIOLOGY
Promiscuous. Normally three to five litters per year, but could be up to seven. Mean litter size vary geographically from, typically, two to six. Up to 50% of juveniles breed their first year.

CONSERVATION STATUS
Common; not threatened.

SIGNIFICANCE TO HUMANS
Important game species, but could sometimes damage crops and forest plantations. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Pygmy rabbit *Brachylagus id*	Slate-gray tipped with brown. Belly is white, legs, chest, and short, rounded ears are brown. Small; head and body length 11.5 in (29.2 cm).	Dense sage brush habitat. Breeding season is from February to May. Shy, active only at night, distinct alarm call, make burrows and nests of their own hair.	Southwestern Oregon to east-central California, southwestern Utah, north to southwestern Montana, United States.	Mainly sage brush.	Lower Risk/Near Threatened
Riverine rabbit *Bunolagus monticularis*	Black stripe runs from corner of mouth over cheek. Tail is brown and woolly, belly and throat are cream-colored. Tail is pale brown with black tip. Coat is soft and silky, limbs are short and very furry. Head and body length 13–18.5 in (33.7–47 cm), weight of average male 3.3 lb (1.5 kg).	Dense riverine scrub along the seasonal rivers in the central Karoo Desert in the Cape Province of South Africa. Breeding season is from August to May. Nocturnal, solitary, and territorial.	South Africa.	Salty plants, leaves, and flowers.	Endangered
Hispid hare *Caprolagus hispidus* English: Assam rabbit; French: Lapin de l'assam; German: Borstenkaninchen; Spanish: Conejo de Assam	Ears are short and broad, eyes are small, hind legs are short and stout. Pelage is coarse and bristly on outer surface, while being short and fine on undersurface. Color is dark brown above, brownish white underparts. Head and body length 15–20 in (38–50 cm), tail length 0.9–1.5 in (2.5–3.8 cm), weight 5.5 lb (2,500 g).	Tall grass-scrub savanna, in flat, well-drained and thinly forested country. Breeding season is from January to March. Not gregarious, but sometimes lives in pairs.	India, Nepal, and Bangladesh.	Bark, shoots, and roots of grasses.	Endangered
Antelope jackrabbit *Lepus alleni*	Color is pale, sandy. Ears are tipped in black. Head and body length 19–25 in (48.3–63.5 cm), ear length 5.4–6.8 in (13.8–17.3 cm), average weight 6–11 lb (2,720–4,990 g).	Prefer grassy slopes at moderate elevation, cactus belt, creosote bush desert and valley bottoms. Litter size varies from one to five. Nocturnal.	South-central Arizona, United States, to northern Nayarit and Tiburon Island, Mexico.	Fresh grass, mesquite, and cacti.	Not threatened
Arctic hare *Lepus arcticus* German: Eishase	White in color, ears tipped in black. Summer pelage coloration varies geographically. Underfur is dense and gray. Adult weight 7–12 lb (3,175–4,990 g).	Mountainous and lowland areas. Nocturnal, generally solitary, but groups may range from 100 to 300 individuals. Breeding season from mid-April to September.	Tundra of Canada from Newfoundland and Labrador to the Mackenzie Delta of the Northwest Territories, Arctic Islands, and in Greenland from sea level to 2,950 ft (900 m).	Woody plants, including mosses, lichens, buds, berries, blooms, leaves, saxifrages, cinquefoils, campoins, sedges, seaweed, bark, willow twigs and roots, and crowberry.	Not threatened
Black-tailed jackrabbit *Lepus californicus*	Black stripe runs down back of this large animal, black rump patch is present, tail is dorsally black. Head and body length 119–160 in (47–63 cm), ear length 3.9–5.1 in (10–13 cm), weight 2.2–6.6 lb (1–3 kg).	Desert scrubland, prairies, farmlands, dunes, and moors. Do not dig burrows, but lie in shallow dug-outs. Breeding season from December through September. Mainly nocturnal.	Hidalgo and southern Queretaro to northern Sonora and Baja California, Mexico, north to southwestern Oregon and central Washington, southern Idaho, eastern Colorado, southern South Dakota, western Missouri, and northwestern Arkansas, United States.	Grasses, herbaceous matter, and young bark of woody plants.	Not threatened

[continued]

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
White-sided jackrabbit *Lepus callotis*	Pelage is short, coarse, pale ochraceous-cinnamon in color, mixed heavily with black. Underparts, rump, and thighs are white and lined with a few black hairs. Head is cream buff color mixed with black, whitish areas around eyes. Ears are tipped in white. Winter pelage is mostly gray with underparts being dark gray-buff and white. Head and body length 17–23.5 in (43.2–59.8 cm), tail length 1.8–3.6 in (4.7–;9.2 cm), weight 4.4–6.6 lb (2–3 kg).	High plateaus at high elevations, including the grassy plains. Breeding season from mid-April to mid-August. Usually occurs in pairs and at night.	Southern New Mexico to northwestern and central Mexico.	Mainly grasses.	Lower Risk/Near Threatened
Sumatran rabbit *Nesolagus netscheri* French: Lapin de Sumatra; Spanish: Conejo de Sumatra	Base color of buffy gray, striking brown stripes, mid-dorsal stripe from shoulders to rump. Rump and tail are bright red, underparts are white. Head and body length 13.5–15.8 in (35–40 cm), tail length 0.6 in (1.5 cm).	Forests at 1,950–4,600 ft (600–1,400 m). Nocturnal. Nothing known of reproductive patterns.	Highlands of the Barisan range in southwestern Sumatra.	Stalks and leaves of understory plants.	Critically Endangered
Amami rabbit *Pentalagus furnessi* English: Ryukyu rabbit	Fur is woolly, dense, dark brown on back in color, reddish brown on the sides. Underparts are light reddish brown. Head and body length 16–20 in (43–51 cm), tail length 0.6 in (1.5 cm), weight 4.4–6.6 lb (2–3 kg).	Dense old-growth forests on the two islands. Mate in November or December, two or three young per litter. Nocturnal, digs burrows.	Amami Oshima and Tokuno-shima: small islands in Ryukyu Archipelgo, southern Japan.	A variety of different plants and fruits.	Endangered
Swamp or water rabbit *Sylvilagus aquaticus*	Pelage is brown on top with some white underneath. Ears are medium in size, females and males are about the same size. Hair is short and thin. Ear length 2.6 in (6.6 cm), weight 2.2–4.4 lb (1–2 kg).	Swamp and lowland areas close to water. Solitary. Year-round breeding season.	South-central United States.	Marsh and swamp plants.	Not threatened
Mountain cottontail *Sylvilagus nuttallii*	Grayish brown, underbelly is white. Hind legs are reddish brown. Ears are short, rounded, and tipped in black. Head and body length 13.7–15 in (35–39 cm), weight 1.5–2.6 lb (0.7–1.2 kg).	Brushy or wooded areas on slopes or riverbanks that are often covered with grasses, willows, and most importantly, sagebrush. Breeding season from March to July. Solitary. Active all year long.	Western part of the United States.	Mainly grasses.	Not threatened

Resources

Books

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Organizations

IUCN—The World Conservation Union, Species Survival Commission, Lagomorph Specialist Group. Web site: <http://www.ualberta.ca/dhik/lsg/>

Anders Angerbjörn, PhD

Macroscelidea
Sengis
(Macroscelididae)

Class Mammalia
Order Macroscelidea
Family Macroscelididae
Number of families 1

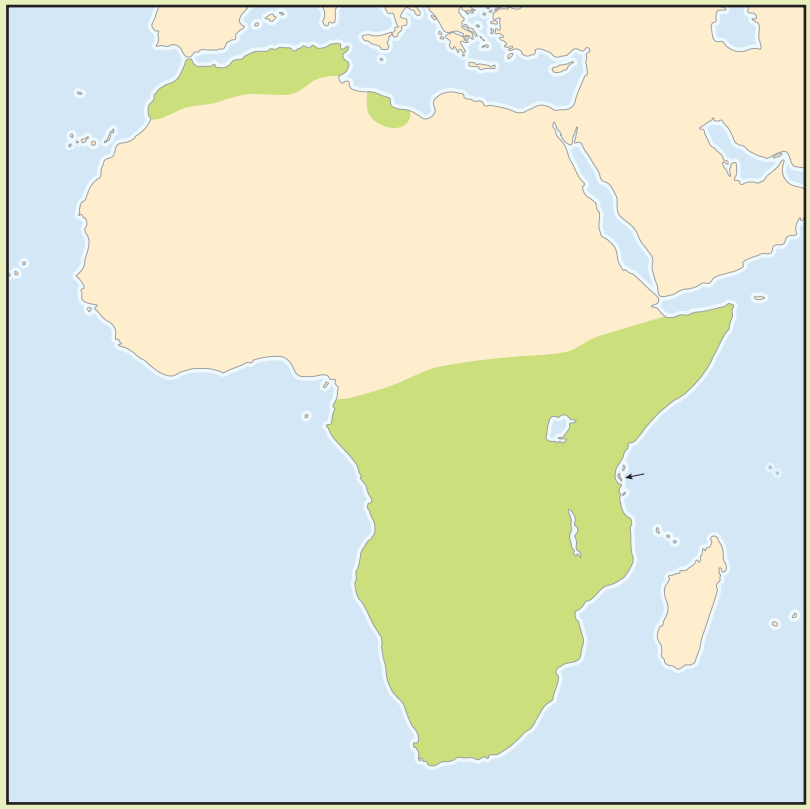
Thumbnail description
Small, mouse-like or shrew-like mammals with long legs and elongated, mobile snouts

Size
Species range from mouse-sized to rabbit-sized, adult body weights ranging 1–160 oz (25–550 g), head-and-body lengths 3.5–12.5 in (90–315 mm), tail lengths 3–11 in (80–263 mm)

Number of genera, species
4 genera; 15 species

Habitat
Varied, from tropical lowland and montane forests, to dry savannas, scrub forest and brush, rocky outcrops, and deserts

Conservation status
Endangered: 3 species; Vulnerable: 4 species



Distribution
Central, southern and eastern Africa, and a separate region in northwestern Africa

Evolution and systematics

Elephant shrews, or "sengis," are not shrews at all, despite their long inclusion by taxonomists within the order Insectivora, which does include shrews (family Soricidae). As of 2001, extensive genetic comparison studies, along with morphological studies, strongly support placing sengis in their own order, Macroscelidae, and family, Macroscelididae. Scientific and popular literature are now using the new common name "sengi," from Swahili so as to disassociate the species from the Soricidae shrews.

The same and related genetic and morphological comparison studies support the inclusion of several African mammal orders into the superorder Afrotheria: the sengis (order Macroscelidea); elephants (Proboscidea); manatees and dugongs (order Sirenia); hyraxes (order Hyracoidea); aardvarks (order Tubulidentata); and Afrosoricida (or Tenrecomorpha), including golden-moles (family Chrysochloridae) and tenrecs and otter-shrews (family Tenrecidae).

Although still a widespread, vigorous family of mammals, the glory days of the Macroscelididae were in the past, when there were many more species, including an additional four families. The 15 species that remain are but leftovers of an extensive pan-African radiation of sengis that began as far back as the Eocene Epoch, then peaked during the Miocene and Pliocene Epochs (24 to 2 million years ago [mya]). By 2 mya, all but the present living sengi species had become extinct.

Studies of the teeth of fossil and modern sengis indicate that the earliest ancestral sengis were primarily or exclusively consumers of plant material, some forms gradually changing over the ages to a more insectivorous diet. Present-day sengis eat only animal food, mostly invertebrates, or a combination of that and plant food.

The earliest known fossils in the sengi line are *Chambius kasserinensis* from the early Eocene of Tunisia and *Herodotius pattersoni* from the Late Eocene of Egypt (Eocene Epoch: 55 to 34 mya). The dental anatomy of these and other sengi fossils support (but do not confirm) a common ancestry of sengis with *condylarths*, primitive, extinct ungulate animals that gave rise to numerous lines of more recent and modern ungulates.

A bushveld sengi (*Elephantulus intufi*) at Kalahari Gemsbok National Park, South Africa. (Photo by Nigel J. Dennis/Photo Researchers, Inc. Reproduced by permission.)

There are two subfamilies within the single surviving family of Macroscelididae: Rhynchocyoninae, the giant sengis, with the single genus *Rhynchocyon*; and Macroscelidinae, the soft-furred sengis, with the genus *Elephantulus* and the monotypic genera *Petrodromus* and *Macroscelides*.

Physical characteristics

Sengis can charm the viewer with their rather humorous and endearing appearance and behavior. The sight of a sengi calls to mind a mouse with long, spindly legs and a mobile, slightly downturned snout varying in length among species. The long legs enable a sengi to walk, trot, run, or hop like a large, long-legged mammal, rather than with the scampering motions common among other small mammals. The body is compact, the head large in proportion. The coat is soft and full. The eyes are large, dark, and limpid, and the long proboscis moves continually in hesitant, circular twitchings. The effect is cute and slightly cartoonish.

The different sengi species share similar body proportions, ranging from mouse-sized to rabbit-sized. The *Rhynchocyon* species are the largest, with an adult head and body length of 9–12.5 in (235–315 mm), the tail adding another 7.5–10 in (190–263 mm). Adult weights can reach 14.5–15.5 oz (408–550 g). An example of a smaller sengi species is the four-toed sengi (*Petrodromus tetradactylus*), with an adult head and body length of 7–8.5 in (185–220 mm), tail length of 5–7 in (130–180 mm), and weight of 5–9 oz (150–280 g), but still large in comparison to the round-eared sengi (*Macroscelides proboscideus*) and other *Elephantulus* species, that are smaller and more mouselike in appearance, with adult head-and-body lengths of 3.5–6 in (90–145 mm), tail lengths of 3–6.5 in (80–165 mm), and weights of 1–2.5 oz (25–70 g).

Larger sengi species tend toward bright colors and patterns, while smaller species display more camouflaging browns and grays, often closely matching the soil color of a particular area. There is little sexual dimorphism throughout the family.

Sengi limbs feature long bones, the hindlimbs longer than the forelimbs, for cursorial (running) and ricochetal (hopping weith the hind legs) locomotion. The tibia and fibula (lower bones of the hindlimbs) are long and fused, the metatarsals are lengthened, and the ulna and radius (lower bones of the forelimbs) are also long, thus lengthening the stride and contributing to high-speed running and jumping.

Numbers and arrangements of digits vary throughout the family, from the traditional 10 fingers-10 toes arrangement to various reductions and modifications, described below in the species accounts.

The long tail is furless or sprouts bristles that vary in density and texture among species.

A sengi's mobile, somewhat flexible snout, which inspired the "elephant" word in the old common name, is both sense organ and tool. When not foraging, a sengi continually moves its snout in a subdued, circular motion from the base, seeking scents. When foraging, a sengi pokes its snout into

An eastern rock sengi (*Elephantulus myurus*) checking for predators. (Photo by Animals Animals ©Ingrid Van Den Berg. Reproduced by permission.)

A checkered sengi (*Rhynchocyon cirnei*) in its den in Democratic Republic of the Congo (Zaire). Photo by Animals Animals ©Bruce Davidson. Reproduced by permission.)

crevices or leaf litter, sniffing for food. The nostrils are located at the forward end of the snout. Long sensory vibrissae, or whiskers, arise from the base of the snout.

The senses of smell, vision and hearing are well-developed and highly tuned. The eyes are conspicuously large, dark, and limpid. Most species have a pale ring around each eye. The ears are large in proportion to the head, and in the *Elephantulus* species, the auditory bulla is almost grotesquely enlarged, to enhance the animal's already acute hearing abilities. The braincase is relatively large, and more complex than that of similarly-sized insectivores.

Sengi bodies are riddled with scent glands, at the base of the tail, soles of the feet, chest, behind the ears, at the corners of the mouth and in the genital and anal regions, with which they mark territory.

Metabolic rates among sengi species are like those in similarly small mammals, not lower or fluctuating, as in shrews. A few sengi species, such as the North African sengi (*Elephantulus rozeti*), can adjust metabolism and activity to changes in their environments, going into torpor when temperatures or food availability go low.

A sengi lives from one to five years in the wild. The record longevity, held by a captive Bushveld sengi (*E. intufi*), is eight years and nine months.

Distribution

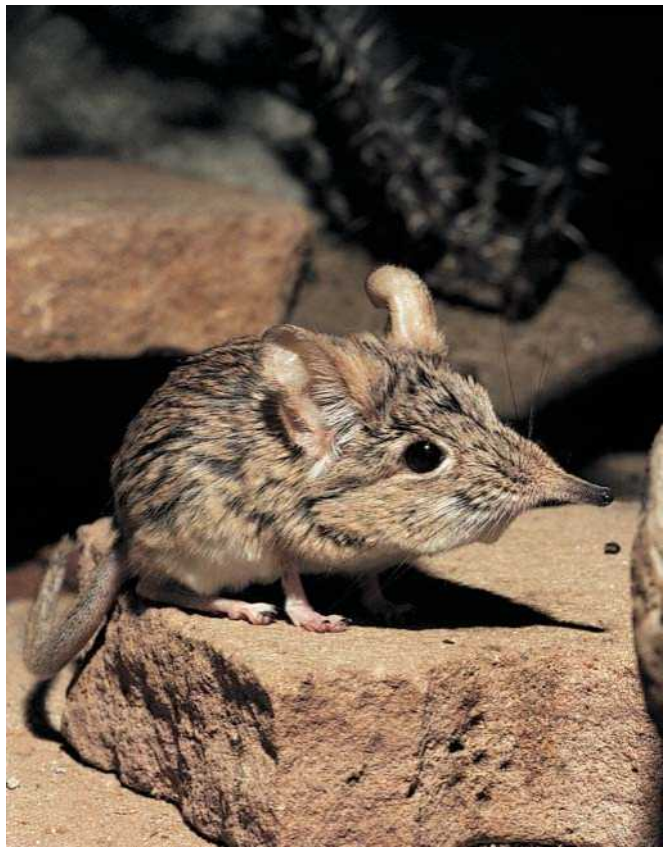
All sengi species are confined to the African continent, including, for a few species, the island of Zanzibar (but not including Madagascar). The three Rhynchocyon species live in central and eastern Africa. The four-toed sengi (*Petrodromus tetradactylus*) is widespread through eastern and southern Africa. The round-eared sengi (*Macroscelides proboscideus*) is found only in southern Africa. A majority of the ten Elephantulus species occur in southern Africa, followed by eastern Africa, excepting the North African sengi (*Elephantulus rozeti*), found only in Morocco, Algeria, Tunisia, and Libya, separated by the Sahara Desert from all the other sengi species.

Habitat

Genus *Rhynchocyon* is mostly confined to tropical lowland and montane forests, while all other sengi species live in dry savannas, scrub forest and brush, rocky outcrops, and deserts.

Behavior

Sengis are alert, high-strung creatures with hair-trigger senses and reactions, always primed for escape, fleeing into hiding at the least threat. The enemies of sengis are legion. Snakes, birds of prey, and carnivorous mammals are known predators of sengis. Accordingly, the sengi lifestyle balances the vulnerability of small size, short life-span and low reproductive rate with keen senses, lightning-swift reflexes, and alterations that the sengi makes in its territory to ensure maximum safety.



The North African sengi (*Elephantulus rozeti*) ranges from southwestern Morocco to western Libya. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

The round-eared sengi (*Macroscelides proboscideus*) has smaller, rounder ears than are typical of the genus. (Photo by S. R. Maglione/Photo Researchers, Inc. Reproduced by permission.)

Sengis sleep or hide in tucked-away shelters, such as rock crevices, burrows, nests and depressions of their own making, or burrows abandoned by other small mammals. Sengi-made burrows often include an inconspicuous emergency exit.

Individuals may live alone (except during mating), or as monogamous, pair-bonded male and female, or in small groups. Whether a loner, or one of a pair or group, a sengi patrols its territory constantly. A male-female bonded pair defends its territory "sex-specifically" against other members of its species, i.e., males confront and chase off intruding males, females do likewise to trespassing females.

Active times of day and night vary among species. The *Rhynchocyon* species are diurnal, while other species tend toward crepuscular (twilight) or nocturnal activity. Some diurnal species switch to nocturnal foraging in exceptionally hot weather, on adequately moonlit nights, or if overly harassed by daytime predators.

Many of the soft-furred sengi species make and maintain elaborate trail systems through leaf litter or grass, with strategically located hiding spots along the way for quick cover from threats. Males and females scent-mark stones and twigs along the trail systems and deposit identifying little heaps of excrement where their path crosses a path in an abutting territory. The animals fastidiously maintain the trails, booting off intruding pebbles, twigs, and leaves with their forelimbs. This behavior keeps the trails open and ready for the sengi to flee along toward shelter in response to threats.

A trail-making sengi marks its trails with little heaps of excrement wherever its path crosses the path of an abutting, same-species territory. If individuals of abutting territories meet at the crossroads, they interract with elaborate threat rituals, ending in a stalemate and truce, or a fight.

Unlike the soft-furred sengi species, the giant sengi species seldom maintain trail systems, but an individual or pair will build a network of leaf nests throughout their territory. The giant species scent-mark their territories but never resort to excremental signatures. There are no elaborate rituals if individuals of abutting territories meet. One simply and pointedly chases off the other, finishing with a nip by incisors to the fleeing hindquarters.

Sengi limbs are built for walking, trotting, and high-velocity running and hopping. Most species go to hopping mode only occasionally, while all are quadrupedal walkers and runners. Sengis walk and run in digitigrade fashion, i.e., on the tips of their fore-digits and hind-digits. When threatened, they prefer to run for a hiding spot, but will go into hopping mode with their hind limbs, tail extended, in extreme danger.

The short-snouted sengi's (*Elephantulus brachyrhynchus*) nose tapers at the end. (Photo by Jane Burton. Bruce Coleman, Inc. Reproduced by permission.)

The rufous sengi (*Elephantulus rufescens*) eats termites, ants, worms, roots, berries, and fruits. (Photo by Kenneth W. Fink. Bruce Coleman, Inc. Reproduced by permission.)

In open country, soft-furred sengis often sunbathe just outside their home shelters, sitting on their haunches, their senses always alert for the least inkling of a threat, at which point they instantly rouse and flee into hiding.

Some sengi species also "sand-bathe," wallowing in dry sand, a behavior noted in other rodent species. Sand-bathing both scent-marks the immediate territory and serves to clean the fur of accumulated oil, dandruff, and dirt. Established sand-bathing spots are scattered throughout a sengi trail system. Soft-furred sengis also clean their fur with their tongues and scratch with their hind legs, able thereby to reach all parts of their bodies.

Sengis are not particularly vocal creatures. *Elephantulus* and *Rhynchocyon* species make squeaking sounds, and drum the leaf litter with their hind feet. The four-toed sengi (*Petrodromus tetradactylus*) makes a cricketlike call. The golden-rumped sengi (*Rhynchocyon chrysopygus*), the four-toed sengi, and *Elephantulus* species all rap the ground with their hind feet to sound alarms or for other reasons, doing so in species-specific patterns that vary in regular or irregular rhythms, intervals between each rap, number of raps in a set, and number of sets in a series. *Rhynchocyon* species and *Petrodromus tetradactylus* make similar warning noises by rapping their tails against the ground.

Feeding ecology and diet

Digestion in sengis is similar to that of small insectivorous mammals, although ancestral sengis were herbivorous. All sengis prey on invertebrates, mostly insects, while most supplement this fare with fruits, seeds, and green plant material, the one exception being *Rhynchocyon chrysopygus*, the golden-rumped sengi, which eats only animals, mostly invertebrates. Smaller species of sengis feed mainly on ants and termites.

The sengi digestive tract includes a caecum (analogous to the appendix in humans). This organ has been little studied in the Macroscelidae, and may not be functional in all species. In species in which it does function, the caecum is full of bacteria that break down cellulose in ingested plant matter. The functional caecum is another legacy from the purely herbivorous diets of sengi ancestors. The caecum of some sengi species may also be used to store water for hot, dry months.

Reproductive biology

Mating behavior varies according to whether the male and female of a sengi species are monogamous (for life) or solitary. Males of solitary species, or young males of monogamous species on their first mating run, go in search of rutting females of their particular species by sensing olfactory cues left in scent markings left by females in strategic spots. When a male and female of a solitary species have found each other, they stay together for several days, mate, then go their separate ways. Pair-bonded couples remain together as long as both are alive. They may be strictly monogamous or they may mate with other individuals while always reassuming the original pair relationship. Males take little or no part in direct care of the young.

A female sengi carries four or six mammae, depending on species.

The reproductive systems of female sengis, during mating, show *polyovulation*, in which anywhere from a dozen to 100 egg cells are released during ovulation, most of which become

The checkered sengi (*Rhynchocyon cirnei*) foraging in southeast Africa. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

fertilized by male sperm and begin cell division, but only one, two, or three fertilized eggs will implant in the uterus, while the rest are expelled. This may be a holdover from past ages when sengi ancestors bore larger litters, as do most mammal species in their size range.

After a gestation period of about 50 days, sengis are born in small litters of one, two, or rarely, three or four young, which enter the world precocial, i.e., with their eyes open, full coats of fur, and able to move about and explore within a few days, often a few hours, of birth. The mother leaves the infants alone most of the time, in a shelter separate from the parents' shelter, coming by only to nurse at fixed intervals, a behavior known as absentee parental care. After five days the mother starts feeding the young mashed insects that she stuffs in her cheek pouches, in addition to her milk.

In about two weeks, the young emerge from their shelter, effectively weaned and able to forage, although they will remain with the mother for three or four weeks, accompanying her as she forages. Eventually, within a month to two months after weaning, the young strike off on their own, or are driven from the territory by the parents, to establish territory of their own, reaching sexual maturity by 40–50 days. A female sengi may produce several litters per year.

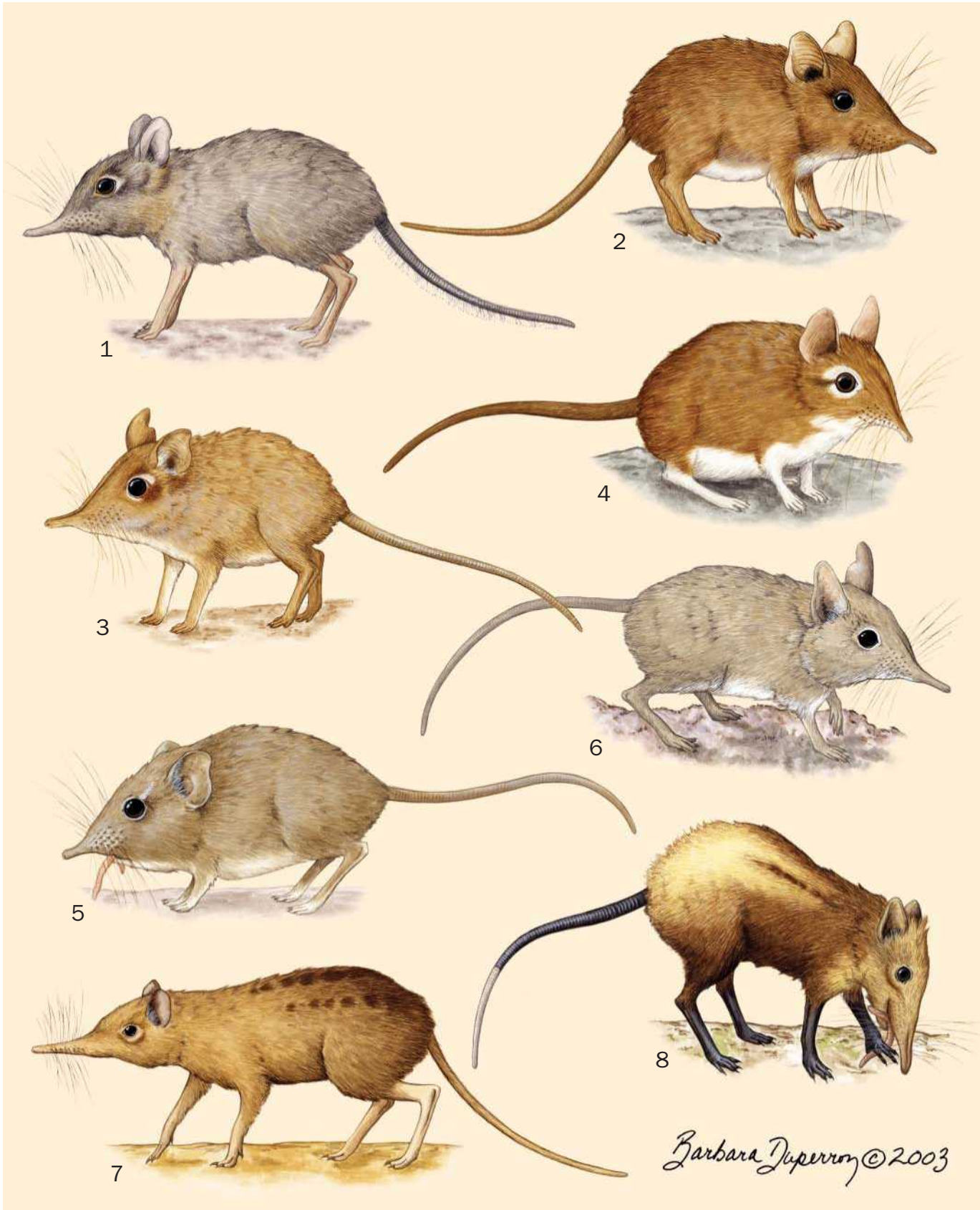
Conservation status

The 2002 IUCN Red List of Threatened Species includes seven species of sengis. Vulnerable: *Rhynchocyon cirnei*, *Macroscelides proboscideus*, *Elephantulus edwardii*, and *Elephantulus rupestris*; Endangered: *Rhynchocyon chrysopygus*, *Rhynchocyon petersi*, and *Elephantulus revoili*.

The main problems besetting sengi species are, for some species, a limited area of distribution, e.g., the golden-rumped sengi, *R. chrysopygus*, for others, fragmentation of their habitats. Both conditions are caused or exacerbated by humans clearing land for agriculture. Sengis are only occasionally hunted and trapped for food.

Significance to humans

With their mainly insectivorous diets, sengis are significant natural checks on insect abundance that might otherwise negatively affect human health and agriculture. In some areas, people hunt, trap, and eat sengis, although most people find sengi meat distasteful. In Kenya, the golden-rumped sengi, *R. chrysopygus*, has become a rallying symbol for conservation.



1. Four-toed sengi (*Petrodromus tetradactylus*); 2. North African sengi (*Elephantulus rozeti*); 3. Short-snouted sengi (*Elephantulus brachyrhynchus*); 4. Rufous sengi (*Elephantulus rufescens*); 5. Round-eared sengi (*Macroscelides proboscideus*); 6. Eastern rock sengi (*Elephantulus myurus*); 7. Checkered sengi (*Rhynchocyon cirnei*); 8. Golden-rumped sengi (*Rhynchocyon chrysopygus*). (Illustration by Barbara Duperron)

Species accounts

Golden-rumped sengi
Rhynchocyon chrysopygus

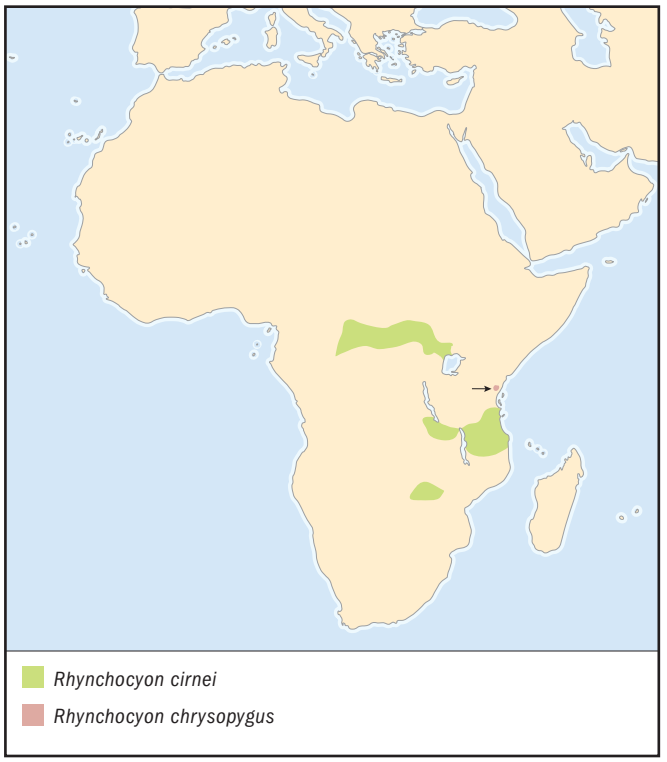
SUBFAMILY
Rhynchocyoninae

TAXONOMY
Rhynchocyon chrysopygus Günther, 1881, Mombasa, Kenya.

OTHER COMMON NAMES
French: Rat à trompe à croupe dorée; German: Goldrücken-Rüsselhündchen; Spanish: Musaraña elefante de trompa dorada.

PHYSICAL CHARACTERISTICS
Rhynchocyon chrysopygus, the golden-rumped sengi, and the two other species within the genus, *R. cirnei*, the checkered sengi, and *R. petersi*, the black-and-rufous sengi, are the largest species in the family, and about equal in size. The head and body length of an adult golden-rumped sengi runs 9–12.5 in (235–315 mm), the tail adding another 7–10 in (190–263 mm). Adult weight reaches 14.5–15.5 oz (408–550 g).

The fur is fine, yet stiff in texture, and glossy. The ears are hairless and the tail is less furred than the body. The signature characteristic is a large, bright yellow rump patch. Feet, ears, and legs are black, likewise the tail, exept its lower third, which is white with a black tip. The upper body is deep red-brown and black, the undersides paler. There is a scarcely visible vestige of a checkered pattern on the body similar to that of *R. cirnei*, more obvious in the young.



Both sexes carry a patch of thickened skin, called a dermal shield, under the yellow rump patch, the shield being thicker in the males. The dermal shield may protect individuals when being bitten on that vulnerable spot by same-species rivals. Complementing the dermal shields are the sexually dimorphic canines, 0.26 in (6.6 mm) long in males, 0.18 in (4.6 mm) in females, and probably seeing service during attacks on rivals.

The snout is reinforced within by a row of 30 rings of cartilage similar to those in a human larynx.

Golden-rumped sengis, like the other species in this genus, have only four toes on front and hind feet, missing the pollex ("thumb") and hallux ("big toe").

DISTRIBUTION
R. chrysopygus is found with certainty only in the Arabuko-Sokoke Forest Reserve on the coast near Mombasa, Kenya.

HABITAT
The Arabuko-Sokoke Forest is a 155 mi^2 (400 km^2) block of moist and dry coastal tropical forest, the largest surviving fragment of an indigenous forest type that once extended along the east coast of Africa from northern Mozambique to southern Somalia. The forest reserve encompasses 109 acres (44 ha) of the Gedi Historical Monument, while a 2.3 mi^2 (6 km^2) bloc has been set aside as Arabuko-Sokoke National Park. The forest is under consideration as a World Heritage Site. An estimated 20,000 individuals of *R. chrysopygus* inhabit the entire forest.

BEHAVIOR
Golden-rumped sengis are diurnally active. Monogamous pairs hold territories sex-specifically, one pair per average territory of 4.2 (1.7 ha), the neighboring territories contiguous, or abutting on one another. Individuals exude a pungent odor from a gland behind the anus, with which the animals mark territory. Both sexes scent-mark territory.

Individuals sleep in shelters made up of small pits lined and covered with leaves. The animals build new shelters every few days, digging out a hollow in the soil, upholstering it with litter leaves and roofing it with more litter leaves into a blanket 3 ft (0.9 m) across. A finished shelter is almost unnoticeable. The monogamous pair builds shelters in the early morning, when leaf litter is moist from dew and less likely to make rustling sounds as the sengis move leaves into place. There may be 10 such shelters in a territory. Individuals of a monogamous pair stay in separate shelters. An individual sleeps in a crouching position, head tucked under forequarters, ready to instantly awake at the sounds of a predator trodding on the edge of the leaf blanket, dashing up through the blanket of leaves and away.

The garishly bright, golden rump may seem a liability in such a vulnerable creature, but it does have a defensive function: its brilliance and motion are likely to catch the attention of a possible predator and tempt it to close in, too early and from too far. The predator, on the hunt, spotting the bright rump patch from a distance, reacts and moves, thus producing slight sounds that the sengi's alert ears can pick up as early warning to facilitate its escape. On sensing the predator in this way, a golden-rumped sengi will slap its tail loudly against the leaf litter, communicating to the approaching predator that the

sengi is aware of its presence, is ready to flee, and is too far away to be worth the predator's efforts. If the predator decides otherwise and the sengi chooses to flee, its noisy boundings over the leaf litter warns its mate and young that a predator is in their territory. A golden-rumped sengi in full flight is a memorable sight. The gait has been compared to the stotting, or running in a series of high leaps, of gazelles.

FEEDING ECOLOGY AND DIET
The golden-rumped sengi is the only sengi species that eats exclusively animal food, mostly invertebrates of many sorts, including earthworms, millipedes, insects, and spiders, using its long, flexible snout to poke through leaf litter in search of edibles.

Golden-rumped sengis share a commensal relationship with the red-capped robin-chat (*Cossypha natalensis*). A red-capped robin-chat will follow a foraging golden-rumped sengi or pair through the forest, feeding on scraps of invertebrates left behind by the sengi.

REPRODUCTIVE BIOLOGY
Golden-rumped sengi sexes mate for life, yet take opportunities to mate with lone individuals. The species breeds throughout the year. Females give birth to a single young after a gestation period of 42 days. The youngster remains in the nest for two weeks, then emerges as a fully weaned individual. It follows the mother while she forages, but is able to fend for itself after five days, although it stays in the parents' territory until establishing its own, anywhere from five to 10 weeks after weaning. Having secured a territory with a mate, an individual can live up to five years.

CONSERVATION STATUS
Rhynchocyon chrysopygus is listed as Endangered in the 2002 IUCN Red List of Threatened Species. That status is due to its limited range and restriction to the forest floor (it cannot climb and does not burrow), the latter condition rendering it vulnerable to wild predators and domestic or feral dogs. People living in areas adjacent to the forest hunt and trap sengis for food, while clearing forested land along its edges.

A support group, "Friends of the Arabuko-Sokoke Forest," made up of Kenyan and foreign individuals and institutions, works actively to protect the forest. The group publicizes, encourages ecotourism, and involves local people in conservation and in using forest products in sustainable ways.

SIGNIFICANCE TO HUMANS
Golden-rumped sengis are hunted for food by locals. From the viewpoint of conservation, they are symbols of a unique and vanishing ecosystem and of the wisdom of protecting it. ◆

Checkered sengi
Rhynchocyon cirnei

SUBFAMILY
Rhynchocyoninae

TAXONOMY
Rhynchocyon cirnei Peters, 1847, Quelimane, Bororo District, Mozambique.

OTHER COMMON NAMES
English: Giant sengi; French: Rat à trompe à damier; German: Geflecktes Rüsselhündchen; Swahili: Njule madoa.

PHYSICAL CHARACTERISTICS
The checkered sengi is similar to the golden-rumped sengi in size specifics (adult head and body length 9–12.5 in (235–315 mm), tail adding another 7–10 in (190–263 mm). Adult weight 14.5–15.5 oz (408–550 g). The animal can justly be proud of its unique pelt design: several dark stripes, on each side, running the length of the body, broken into squarish spots of alternate chestnut and off-white, or whitish and dark brown. The main coat color is yellowish to dark brown. In some populations, the distal portion of the tail is white.

DISTRIBUTION
R. cirnei lives in northern and eastern Democratic Republic of the Congo, Uganda, southern Tanzania, northeastern Zambia, Malawi, and northern Mozambique.

HABITAT
Checkered sengis prefer dense, lowland and montane tropical rainforest.

BEHAVIOR
Individuals may live alone, in pairs or in small groups, are active during daytime but are occasionally nocturnal. Pairs or groups vocalize constantly to keep in touch with one another, and tail-rap the ground when alarmed.

FEEDING ECOLOGY AND DIET
Checkered sengis forage for invertebrates on the forest floor in the daytime, alone or in small groups, maintaining group cohesion by continually uttering squeals and squeaks. They make little conical depressions in the soil during their grubbings, offering a sign diagnostic of their presence. The diet is mainly insectivorous, with some emphasis on ants, but they may help themselves to small mammals, birds, bird eggs, mollusks, and other animal foods on occasion. While rooting, the sengis ingest a good deal of dirt, which apparently passes through them with little harm.

REPRODUCTIVE BIOLOGY
Specifics of reproduction are similar to that of the closely related golden-rumped sengi. The litter nest is an inconspicuous heap of leaves in a shallow ground depression. The female bears a single, precocial young.

CONSERVATION STATUS
The 2002 IUCN Red List of Threatened Species lists *R. cirnei* as Vulnerable. The main problem facing the species is deforestation.

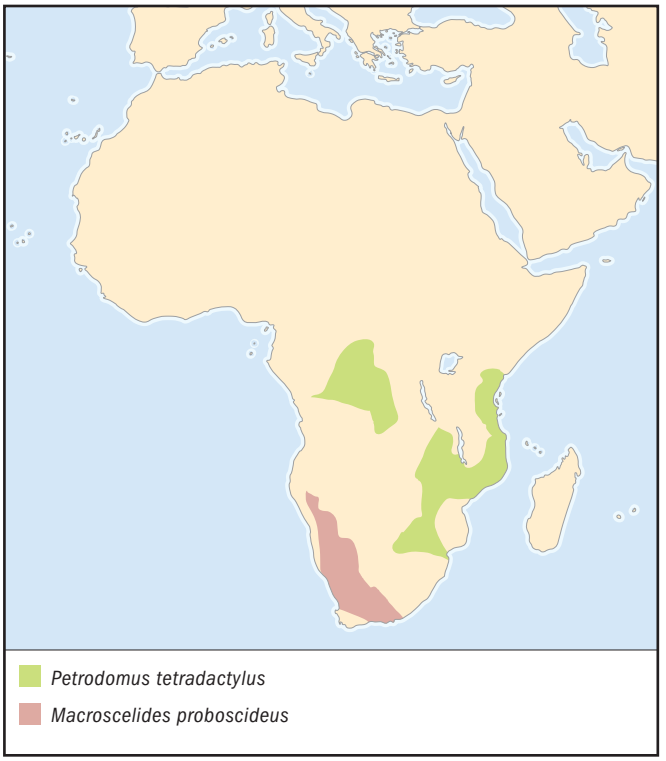
SIGNIFICANCE TO HUMANS
None known. ◆

Round-eared sengi
Macroscelides proboscideus

SUBFAMILY
Macroscelidinae

TAXONOMY
Macroscelides proboscideus (Shaw, 1800), Roodeval, Oudtshoorn Division, Cape Province, South Africa.

OTHER COMMON NAMES
English: Short-eared sengi, jumping shrew; French: Macroscelide d'Afrique du sud, rat à trompe d'Afrique du sud; German: Kurzohr-rüsselspringer; Afrikaans: Ronde-oorklaasneus.



PHYSICAL CHARACTERISTICS

The round-eared sengi is among the smallest of the living sengi species. The adult head and body length runs 3.5–4.5 in (95–115 mm), the long tail adding another 4–5.5 in (97–135 mm). Adult weight is 1–2 oz (30–50 g). The body fur of the animals is long, dense and soft, hued orange, brown, or gray on the upper body or dorsal area and whitish on the underparts or ventral area. The tail bears coarse, black fur. The skin at the base of the tail is pink or dark. The limbs bear short, white fur. The body fur is two-colored throughout, the tips of hairs colored and the bases dark. Fur colors vary widely throughout the range of the species.

All four feet have five toes each, and on the hindlimbs, the hallux, or equivalent of the big toe, is set off from the others. All the digits have small, dark claws.

The head bears large, limpid, dark eyes that lack the pale, surrounding ring seen in other sengi species. The characteristic long, mobile snout is covered with short, white fur. The nostrils, at the nether tip of the snout, are set in dark, wet, furless skin. The ears are rounder and shorter than in other sengi species, and are backed and bordered by fur, providing signs diagnostic of the species. The skull has almost grotesquely inflated auditory bullae, or inner ear chambers of bone, indicating the importance of hearing in the species. The female has six mammae.

DISTRIBUTION

Round-eared sengis live throughout Namibia, Cape Province in South Africa, and southern Botswana. In Great Namaqualand, South Africa, the ranges of the round-eared sengis and *Elephantulus rupestris*, the Western rock sengi, overlap.

HABITAT

The preferred habitat for *Macroscelides proboscideus* is desert, semidesert, and scrub forest.

BEHAVIOR

Despite also being called "jumping shrews," round-eared sengis rarely jump, preferring to walk or run, carrying their tails horizontally. They can run with speeds up to 12.4 mph (20 km/h), quite impressive for such a small creature. Individuals hide in sparse grass cover or bushes, and can quickly burrow into the sand for protection.

Individuals live solitarily in home ranges that may reach 2.5 acres (1 ha) and include foraging areas and way-shelters. The shelters are short burrows located under stones, roots, or bush. Sengis can and will enlarge their refuge rapidly by digging. The burrows have a main entrance/exit and an emergency exit, the latter inconspicuous. Round-eared sengis also take refuge in deserted shelters of suricates (Viverridae) or gerbils (Gerbillidae), fastidiously cleaning their new homes of sand, gravel, and other detritus.

During the day, round-eared sengis may nap in the sun, sitting on their haunches, still alert for the slightest hint of danger. They also sand-bathe, wallowing in pre-established patches of dry sand, to scent-mark and to clean their coats.

FEEDING ECOLOGY AND DIET

Round-eared sengis are primarily crepuscular (twilight) and nocturnal foragers. They start foraging at twilight, then continue through most of the night, sniffing with their mobile snouts in crevices between stones, under roots, and in carpets of fallen leaves. Although mainly insectivorous, with a preference for ants and termites, they also eat other small invertebrates and plant material, including roots, shoots, and berries. The round-eared sengi can be considered a functional omnivore, since at least half of its food intake is often plant material, balanced by invertebrate food.

REPRODUCTIVE BIOLOGY

Although solitary most of the time, individual males and females pair up in the mating season and stay together for several days, defending their territory sex-specifically. There is a distinct breeding season, in August and September, which are warm, wet months in southern Africa.

The one or two young are born precocial, able to run a few hours after birth. The female bears and keeps her young in a hideaway separate from the parents' burrow, stopping by once a day to nurse them. The young are weaned at 16–25 days and reach sexual maturity at about 43 days.

CONSERVATION STATUS

Due to destruction of its habitat, *Macroscelides proboscideus* is listed as Vulnerable by the the 2002 IUCN Red List of Endangered Species.

SIGNIFICANCE TO HUMANS

There is no known significance to humans. ◆

Four-toed sengi

Petrodromus tetradactylus

SUBFAMILY

Macroscelidinae

TAXONOMY

Petrodromus tetradactylus Peters, 1846, Tette, Mozambique.

OTHER COMMON NAMES
French: Petrodrome, Rat à trompe tétradactyle; German: Vierzehen-Rüsselratte; Spanish: Petrodromo; Afrikaans: Bosklaasneus; Swahili: Isange.

PHYSICAL CHARACTERISTICS
The four-toed sengi is one of the larger sengi species, with a head and body length of 7–8.5 in (185–220 mm) and a tail length of 5–7 in (130–180 mm). Adult body weight runs 5–9.5 oz (150–280 g). The fur is long and soft. The coloration above is buffy with an orange or yellow tinge, or brown with a reddish tinge, with a grayish or brownish streak on the sides and flanks. White and reddish brown markings are usually present about the eyes. The underparts are white or red-brown. There are four toes on each hind foot (hence the common name), the first digit (hallux) missing. Females have four mammae.

DISTRIBUTION
Four-toed sengis are widespread, from central Democratic Republic of the Congo and southeastern Kenya through Tanzania, Zambia, Malawi, and Mozambique to the northern Transvaal (South Africa).

HABITAT
Although sometimes found in semi-arid, rocky habitats, four-toed sengis prefer thickets and undergrowth of dense, equatorial forests.

BEHAVIOR
The species makes and maintains runways through brush and grass. It has a gait between walking and running, the tail pointed upward, but if alarmed it will break into long jumps with the hind legs. Individuals sleep outside under brush rather than in nests.

Four-toed sengis ground-rap or foot-drum with their hind feet, to sound warnings, invite the opposite sex during mating, and apparently to excite underground ants, which respond with sounds of their own that the sengi can hear and use to locate, uncover, and eat the ants. Individual four-toed sengis vocalize with shrill, cricketlike calls. They do not make nests, but shelter beneath dense vegetation or in random depressions.

FEEDING ECOLOGY AND DIET
The four-toed sengi is mostly crepuscular, major activity peaking just before dawn and just after nightfall. Their diet consists mainly of insects, particularly termites and ants, but they may add some plant matter to the menu.

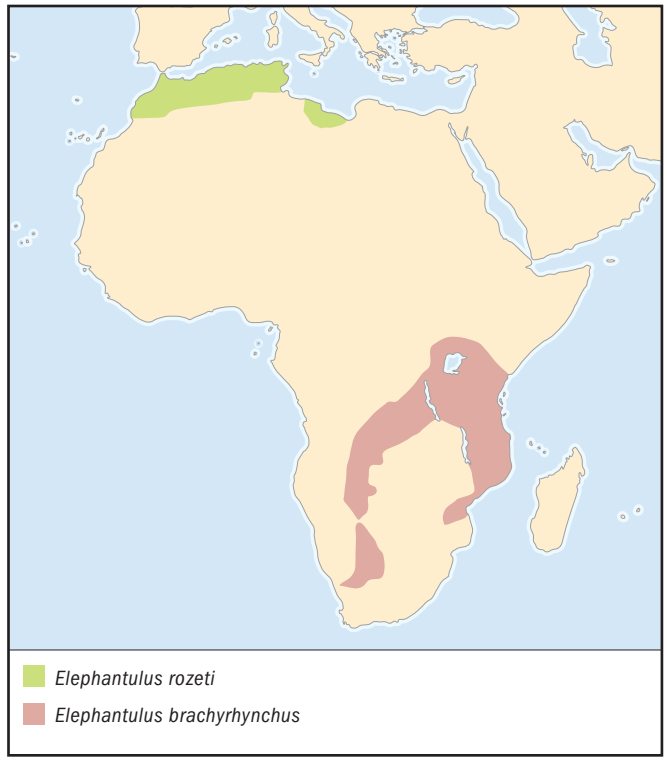
REPRODUCTIVE BIOLOGY
Monogamous pairs defend territories sex-specifically. Breeding occurs throughout the year. The female gives birth to one or two young, each weighing about 1 oz (32 g). The precocial young can run as fast as their parents a day or two after birth.

CONSERVATION STATUS
Not listed by the IUCN.The species is so widespread that it seems in little danger of decline.

SIGNIFICANCE TO HUMANS
Some humans hunt four-toed sengis for food. ◆

Short-snouted sengi
Elephantulus brachyrhynchus

SUBFAMILY
Macroscelidinae (Soft-furred sengis)



TAXONOMY
Elephantulus brachyrhynchus (A. Smith, 1836), Kuruman, north Cape Province, South Africa.

OTHER COMMON NAMES
French: Rat à trompe à museau court; German: Kurznasen-Elefantenspritzmaus, Kurznasenrüsselspringer; Spanish: Musaraña elefante hocicorta; Afrikaans: Kortneus klaasneus.

PHYSICAL CHARACTERISTICS
The weight of an adult short-snouted sengi runs 1.5–2 oz (40–60 g). Average body length is 8 in (210 mm), the tail length about the same. Short-snouted sengis have the mobile snout characteristic of all sengi species, but it is conspicuously shorter and more tapered. The soft fur varies in color, depending on geography and habitat, ranging from reddish yellow to yellowish brown to gray, rendering the animal cryptic in its various habitats. There is a faint white ring around each eye.

DISTRIBUTION
Elephantulus brachyrhynchus lives from northern South Africa and northeastern Namibia through Angola, southern Democratic Republic of the Congo, Mozambique, Kenya, and Uganda.

HABITAT
Short-snouted sengis inhabit arid and semi-arid environments with wooded bushlands, dense grasslands, and scrub.

BEHAVIOR
Short-snouted sengis are diurnal and most active during the morning. They are primarily solitary but will occasionally live as monogamous pairs. They run frantically throughout their territory, avoiding areas without ground cover. Short-snouted sengis may dig their own burrows or move into abandoned rodent burrows. They foot-drum, in a regular and irregular pattern, as a warning or to facilitate mating.

FEEDING ECOLOGY AND DIET
The short-snouted sengi is primarily insectivorous, eating mostly ants and termites, nevertheless taking small amounts of green plant material, fruits, and seeds.

REPRODUCTIVE BIOLOGY
Some short-snouted sengis live as monogamous pairs. Reproduction occurs throughout the year, decreasing during cool months. The gestation period lasts between 57 and 65 days. The young weigh approximately 0.4 oz (10 g) at birth and reach adult size by 50 days. Usually one young is born, though occasionally litters of two or even three are born.

CONSERVATION STATUS
Not listed by the IUCN. Short-snouted sengis, since they live in more or less marginal habitats, need fear little from humans.

SIGNIFICANCE TO HUMANS
None known. ◆

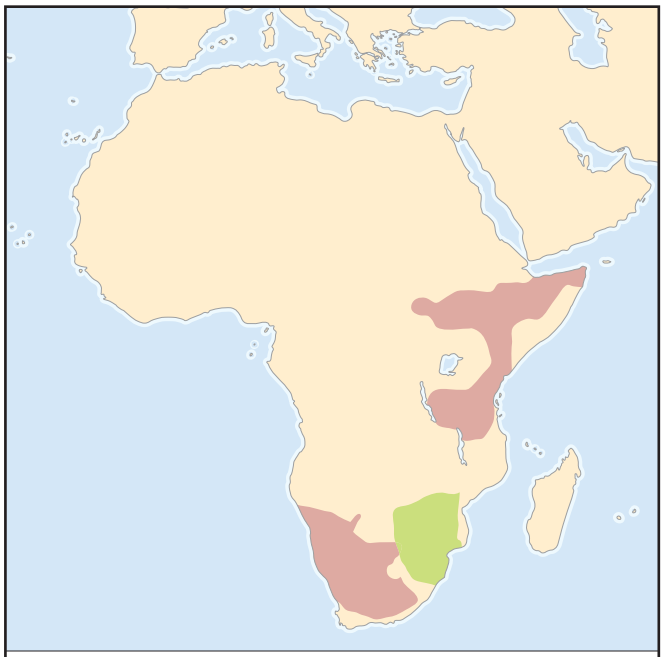
Eastern rock sengi
Elephantulus myurus

SUBFAMILY
Macroscelidinae

TAXONOMY
Elephantulus myurus Thomas and Schwann, 1906, Woodbush, Transvaal, South Africa.

OTHER COMMON NAMES
German: Langschwanz-Rüsselspringer.

PHYSICAL CHARACTERISTICS
The head and body length range 8–11.5 in (202–290 mm), the tail slightly longer. Adult body weight runs 1.5–3 oz (41–98 g).



Eastern rock sengis may hop with the hindlimbs, but most of the time they walk or run about on all fours. There are five digits on each foot with small claws, while the digits of the hind feet, are equipped with digital pads to give them purchase on rocky surfaces. The first digit of the forefoot (as in all species within genus *Elephantulus*) is set off from the other digits.

The dorsal coat of the animal is brownish gray and soft, while the ventral side is pale gray. The ears and eyes are dark brown, each eye framed by a white ring. Limbs and tail are white on the dorsal sides and devoid of hair on the ventral sides. Black limbs and tail distiguish *E. myurus* from other *Elephantulus* species.

DISTRIBUTION
Elephantulus myurus is distributed across southern Africa from western Mozambique in the north to Orange Free State in the south, and in southern Zimbabwe, eastern Botswana, and throughout the Transvaal.

HABITAT
Eastern rock sengis live in the semi-arid, temperate savannas of southern Africa, most often within heaps of boulders (koppies). The climate is semi-arid and nearly rainless for eight months of the year, interrupted by four months of rains. Temperatures can rise to 95–104°F (35–40°C) in hot summer months, descending to subzero temperatures in winter.

Another sengi species, *E. brachyrhynchus*, the short-snouted sengi, shares general territory with *E. myurus*, but *E. brachyrhynchus* prefers a separate habitat, the sandy, flat terrain surrounding the koppies; the habitats of the two species rarely overlap.

BEHAVIOR
The eastern rock sengi is primarily diurnal, but shows a good deal of activity at sunrise and sunset. The species avoids activity during the afternoon, the hottest time of day. During the winter months, the animals are less active. Eastern rock sengis do not make nests or burrows, but hide in rock crannies, so that they take up residence only in koppies with generous complements of cracks and crevices. Eastern rock sengi vocalizations and footdrumming may be alarm calls or feints to throw off pursuers. They can run fast and hop if needed, and usually stay near or uunder rocky overhangs.

Although not confirmed, eastern rock sengis probably live as monogamous pairs, sex-specifically defending their territory. The animals forage in areas within or near their koppies, close to vegetation or overhanging ledges, for cover from predators.

FEEDING ECOLOGY AND DIET
The Eastern rock sengi is primarily insectivorous, but varies its diet with plant material. Ants and termites are the major insect food, making up about 42% of its diet, but it nevertheless helps itself to a broad variety of invertebrate food. The diet remains constant even through changes of season. Individuals snag ants and termites with their snouts in tandem with their fore-claws. Glands within the snout produce secretions that collect on the bare nether tip, which may counterract the chemical defenses of the ants and termites.

The eastern rock sengi has a functioning caecum which may also store water. While the weights of individual *E. myurus* remain constant throughout all seasons, the digestive tract significantly shortens during the rainy winter, when the animals slow their activities. As the tract shortens, its ability to resorb water decreases. This physiology and behavior restricts needless activity during the cool, non-mating months of winter. The digestive tract lengthens in the spring, and its water resorbtion

increases, as the sengis step up their activities for the mating season, their need for more food energy increases to fill the energy demands for reproduction, and their bodies begin hoarding water for the approaching hot, dry summer.

Kidney function aids and abets water retention in *E. myurus*, the kidney design being similar to that of other mammals adapted to dry ecosystems, allowing increased urine concentration in order to retain water.

REPRODUCTIVE BIOLOGY
Eastern rock sengis mate between July and January, during which time they use foot-drumming and scent-marking to announce intentions and attract mates. The male reproductive organs increase in size during the breeding season, and decrease size and sperm production somewhat during the nonbreeding months.

The young are born anytime from September to March. Newborns are highly precocial, able to run several hours after birth. Average weight of the young at birth is 0.28 oz (8.1 g). The young remain hidden until they reach about one-third adult size. The parents drive the young away when the latter become sexually mature.

CONSERVATION STATUS
No Special Status. The rocky habitat of *E. myurus* is useless to humans and therefore little disturbed by people.

SIGNIFICANCE TO HUMANS
The eastern rock sengi is home to a variety of parasites, particularly ticks, the specific tick species varying in abundance with seasons. Some of these parasites are vectors for a variety of human and domestic animal diseases. The tick species *Ixodes rubicundus* and *R. punctatus* can cause paralysis in domestic livestock, *H. leachi* is a vector for biliary fever in dogs and Q-fever in humans, and *Rhipicentor nuttalli* causes paralysis in dogs.

Studies of a related sengi species, *E. edwardii*, the cape sengi, report on a form of malaria carried by that species that is not normally found in humans, thus rendering the species valuable in malarial research.

Rufous sengi
Elephantulus rufescens

SUBFAMILY
Macroscelidinae

TAXONOMY
Elephantulus rufescens (Peters, 1878), Ndi, Taita, Kenya.

OTHER COMMON NAMES
English: East African long-nosed sengi; French: Rat à trompe rouge; German: Rotbraune Elefantenspitzmaus.

PHYSICAL CHARACTERISTICS
Adult rufous sengis weigh 1.5–3.5 oz (41–98 g). The head and body length runs 8–11.5 in (202–290 mm), the tail about the same length. The fur is long and soft, the upper coat colored sandy brown, light gray or light orange, while the underparts are white or grayish. A patchwork of white spots and black streaks on the face render the large, dark eyes less obvious.

DISTRIBUTION
A widespread species, the rufous sengi is found in Namibia, the Cape Province of South Africa, and extreme southern Botswana, and from southeastern Sudan, southern and eastern Ethiopia and northeastern Somalia to north and southeast Kenya to central and western Tanzania.

HABITAT
Elephantulus rufescens lives in open plains, arid lowlands, savannas, deserts, thornbush, and tropical forests. Most individuals, pairs, or groups will take over abandoned rodent burrows for habitation.

BEHAVIOR
Elephantulus rufescens individuals live singly, in monogamous pairs, or in small colonies. They are usually diurnal, occasionally nocturnal. An individual, pair, or group occupies a territory about 0.84 acres (0.34 ha).

FEEDING ECOLOGY AND DIET
The diet consists mainly of termites and ants, but also includes other invertebrates, shoots, berries, and roots.

REPRODUCTIVE BIOLOGY
Rufous sengis form monogamous pairs when mating, defending territory sex-specifically. Before mating, individuals leave scent markings along trails by means of their sternal (chest) and other scent glands. Mating takes place throughout the year. The young are precocial, as with other sengi species, and weigh about 0.4 oz (10.6 g) at birth. The mating pair spends minimum time together, the females usually dominant to the males.

CONSERVATION STATUS
According to the 2002 IUCN Red List of Threatened Species, *E. rufescens* is classified as Vulnerable. The most important causes for its decline are habitat loss and fragmentation.

SIGNIFICANCE TO HUMANS
Elephantulus rufescens carries a type of malaria to which humans are immune. The species has thus proven valuable in malaria research. ◆

North African sengi
Elephantulus rozeti

SUBFAMILY
Macroscelidinae

TAXONOMY
Elephantulus rozeti (Duvernoy, 1833), near Oran, Algeria.

OTHER COMMON NAMES
French: Macroscélide de l'Afrique du nord; German: Nordafrikanische Elefantenspitzmaus; Spanish: Musaraña elefante norteafricana.

PHYSICAL CHARACTERISTICS
The adult head and body length averages about 5 in (125 mm), tail length is about the same, and adult weight is around 1.5 oz (45 g). The fur is soft and often closely and remarkably simulates the local color of the soil, usually some shade of yellowish brown.

DISTRIBUTION
North African sengis live in northwestern Africa, separated from the other species of sengi by the Sahara Desert. This discontinuous distribution of species is probably an outcome of the Macroscelididae having been more widespread throughout

Africa in past ages, and in the Sahara region when it was rainier and more congenial. There are two distinct populations of the North African sengi, the main group in Algeria, Morocco, and Tunisia, and a second, small, isolated population in western Libya.

HABITAT
Open, arid, or semi-arid savanna shrubland, and woodland.

BEHAVIOR
Little is known about this understudied species. Individuals construct burrows under rocks. They are active during the day, but retire to their burrows during the hottest daylight hours. Experiments have shown that North African sengis will fall into torpor as a response to changes in temperature, cycles of light and darkness, and to lower supplies of food.

FEEDING ECOLOGY AND DIET
North African sengis are primarily insectivorous.

REPRODUCTIVE BIOLOGY
Knowledge of reproduction specifics for *Elephantulus rozeti* is incomplete, but what is known is unusual. The gestation period is at least 75 days, and up to four young may be born in a litter, the most common number being two, but fairly often, three. Females only give birth to two litters per year. In the colder climate of the highlands of Algeria and Morocco, the year's first litters are born starting toward the end of April, but in lowland, warmer Tunisia and parts of Morocco, births begin in March. In other respects, reproductive biology likely accords with the general sengi scheme.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Common name / Scientific name/ Other common names	Physical characteristics	Habitat and behavior	Distribution	Diet	Conservation status
Black and rufous sengi *Rhynchocyon petersi* English: Zanj sengi; French: Rat à trompe de Peters; German: Rotschulterruesselhuendchen; Spanish: Musaraña elefante de Petrs; Swahili: Njule kinguja	Smallish, shrew-like mammal with long legs and long, mobile snout. Rump and center of the back are black, rest of the body except tail is orange-reddish or maroon, tail is pale orange-brown. Head and body length to 12.4 in (31.5 cm), tail length to 11 in (28 cm); maximum adult weight 18.3 oz (520 g).	Coastal and montane tropical forests. Diurnal, monogamous pairs defend territory sex-specifically.	Coastal zone of south-eastern Kenya and northeastern Tanzania, including Zanzibar and Mafia Islands.	Insects, other invertebrates.	Endangered
Cape sengi *Elephantulus edwardii* English: Cape rock sengi; French: Macroscelide du cap, Rat à trompe du cap; German: Kap-Rüsselspringer; Afrikaans: Kaapse klipklaasneus	Small, mouse-like mammal with mobile snout. Tan to light-brown pelt. Head and body length 3.7 in (9.5 cm), tail 3.5 in (9 cm); adult weight 1.8 oz (50 g).	Shrubland, succulent thickets, and grassland. Live solitarily or as mated pairs; latter defend territory sex-specifically; maintain trail system.	South Africa in coastal southwestern and central Cape Province.	Insects, mostly ants and termites.	Vulnerable
Dusky-footed sengi *Elephantulus fuscipes* German: Schwarzfüßige Elefantenspitzmaus	Small, mouse-like mammal with mobile snout. Tan to light-brown pelt, with dark brown feet. Head and body length 3.1 in (8 cm), tail length 3.1 in (8 cm); adult weight 1.8 oz (50 g).	Bushy and scrubby habitats, open woodlands. Solitary or monogamous pairs, pairs defend territory sexual-specifically; maintain trail system.	A small area of eastern-central Africa covering parts of Sudan, Uganda, Democratic Republic of the Congo (Zaire), and Central African Republic.	Insects, mostly ants and termites.	Not listed by IUCN
Dusky sengi *Elephantulus fuscus* German: Dunkle Elefantenspitzmaus; Afrikaans: Peters se kortneus klaasneus	Small, mouse-like mammal with mobile snout. Medium-brown to dark-brown pelt. Head and body length 3.5 in (9 cm), tail length 3.3 in (8.5 cm); adult weight 2.1 oz (60 g).	Grassland with scattered trees and bushes and in savanna. Solitary or monogamous pairs, pairs defend territory sexual-specifically; maintain trail system.	Malawi, Mozambique, and Zambia, marginally to Zimbabwe.	Insects, mostly ants and termites.	Not listed by IUCN
Bushveld sengi *Elephantulus intufi* French: Rat à trompe jaune; German: Trockenland-Elefantenspitzmaus; Spanish: Musaraña elefante de bushveld; Afrikaans: Bosveldklaasneus	Small, mouse-like mammal with mobile snout. Tan to medium-brown pelt. Head and body length 3.3 in (8.5 cm), tail length 3.3 in (8.5 cm); adult weight 1.4 oz (40 g).	Scrub bush with a light grass cover. Solitary or monogamous pairs, pairs defend territory sexual-specifically; maintain trail system.	Angola to South Africa.	Insects, mostly ants and termites.	Not listed by IUCN
Somali sengi *Elephantulus revoili* French: Macroscélide de Somalie, Rat à trompe de Revoil; German: Somali-Rüsselspringer; Spanish: Musaraña elefante de Somalia	Small, mouse-like mammal with mobile snout. Tan to light-brown pelt. Head and body length 3.7 in (9.5 cm), tail length 3.5 in (9 cm); adult weight 1.8 oz (50 g).	Arid bushy and scrubby habitats. Solitary or monogamous pairs, pairs defend territory sexual-specifically; maintain trail system.	Northern Somalia to the Ethiopian border.	Insects, mostly ants and termites.	Endangered
Western rock sengi *Elephantulus rupestris* English: Smith's rock sengi; French: Macroscélide des rochers, rat à trompe des roches de l'ouest; German: Klippen-Elefantenspitzmaus; Afrikaans: Smith se klipklaasneus	Small, mouse-like mammal with mobile snout. Tan to light-brown pelt. Head and body length 3.9 in (10 cm), tail length 3.7 in (9.5 cm); adult weight 1.8–2.1 oz (50–60 g).	Arid and semi-arid vegetation. Solitary or monogamous pairs, pairs defend territory sexual-specifically; maintain trail system.	Central South Africa through central Namibia.	Insects, mostly ants and termites.	Vulnerable

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Glossary

Adaptive radiation—Diversification of a species or single ancestral type into several forms that are each adaptively specialized to a specific niche.

Agonistic—Behavioral patterns that are aggressive in context.

Allopatric—Occurring in separate, nonoverlapping geographic areas.

Alpha breeder—The reproductively dominant member of a social unit.

Altricial—An adjective referring to a mammal that is born with little, if any, hair, is unable to feed itself, and initially has poor sensory and thermoregulatory abilities.

Amphibious—Refers to the ability of an animal to move both through water and on land.

Austral—May refer to "southern regions," typically meaning Southern Hemisphere. May also refer to the geographical region included within the Transition, Upper Austral, and Lower Austral Life Zones as defined by C. Hart Merriam in 1892–1898. These zones are often characterized by specific plant and animal communities and were originally defined by temperature gradients especially in the mountains of southwestern North America.

Bergmann's rule—Within a species or among closely related species of mammals, those individuals in colder environments often are larger in body size. Bergmann's rule is a generalization that reflects the ability of endothermic animals to more easily retain body heat (in cold climates) if they have a high body surface to body volume ratio, and to more easily dissipate excess body heat (in hot environments) if they have a low body surface to body volume ratio.

Bioacoustics—The study of biological sounds such as the sounds produced by bats or other mammals.

Biogeographic region—One of several major divisions of the earth defined by a distinctive assemblage of animals and plants. Sometimes referred to as "zoogeographic regions or realms" (for animals) or "phytogeographic regions or realms" (for plants). Such terminology dates from the late nineteenth century and varies considerably. Major biogeographic regions each have a somewhat distinctive flora and fauna. Those generally recognized include Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian.

Blow—Cloud of vapor and sea water exhaled by cetaceans.

Boreal—Often used as an adjective meaning "northern"; also may refer to the northern climatic zone immediately south of the Arctic; may also include the Arctic, Hudsonian, and Canadian Life Zones described by C. Hart Merriam.

Brachiating ancestor—Ancestor that swung around by the arms.

Breaching—A whale behavior—leaping above the water's surface, then falling back into the water, landing on its back or side.

Cephalopod—Member of the group of mollusks such as squid and octopus.

Cladistic—Evolutionary relationships suggested as "tree" branches to indicate lines of common ancestry.

Cline—A gradient in a measurable characteristic, such as size and color, showing geographic differentiation. Various patterns of geographic variation are reflected as clines or clinal variation, and have been described as "ecogeographic rules."

Cloaca—A common opening for the digestive, urinary, and reproductive tracts found in monotreme mammals.

Colony—A group of mammals living in close proximity, interacting, and usually aiding in early warning of the presence of predators and in group defense.

Commensal—A relationship between species in which one benefits and the other is neither benefited nor harmed.

Congeneric—Descriptive of two or more species that belong to the same genus.

Conspecific—Descriptive of two or more individuals or populations that belong to the same species.

Contact call—Simple vocalization used to maintain communication or physical proximity among members of a social unit.

Convergent evolution—When two evolutionarily unrelated groups of organisms develop similar characteristics due to adaptation to similar aspects of their environment or niche.

Coprophagy—Reingestion of feces to obtain nutrients that were not ingested the first time through the digestive system.

Cosmopolitan—Adjective describing the distribution pattern of an animal found around the world in suitable habitats.

Crepuscular—Active at dawn and at dusk.

Critically Endangered—A technical category used by IUCN for a species that is at an extremely high risk of extinction in the wild in the immediate future.

Cryptic—Hidden or concealed; i.e., well-camouflaged patterning.

Dental formula—A method for describing the number of each type of tooth found in an animal's mouth: incisors (I), canines (C), premolars (P), and molars (M). The formula gives the number of each tooth found in an upper and lower quadrant of the mouth, and the total is multiplied by two for the total number of teeth. For example, the formula for humans is: I2/2 C1/1 P2/2 M3/3 (total, 16, times two is 32 teeth).

Dimorphic—Occurring in two distinct forms (e.g., in reference to the differences in size between males and females of a species).

Disjunct—A distribution pattern characterized by populations that are geographically separated from one another.

Diurnal—Active during the day.

DNA-DNA hybridization—A technique whereby the genetic similarity of different animal groups is determined based on the extent to which short stretches of their DNA, when mixed together in solution in the laboratory, are able to join with each other.

Dominance hierarchy—The social status of individuals in a group; each animal can usually dominate those animals below it in a hierarchy.

Dorso-ventrally—From back to front.

Duetting—Male and female singing and integrating their songs together.

Echolocation—A method of navigation used by some mammals (e.g., bats and marine mammals) to locate objects and investigate surroundings. The animals emit audible "clicks" and determine pathways by using the echo of the sound from structures in the area.

Ecotourism—Travel for the primary purpose of viewing nature. Ecotourism is now "big business" and is used as a non-consumptive but financially rewarding way to protect important areas for conservation.

Ectothermic—Using external energy and behavior to regulate body temperature. "Cold-blooded."

Endangered—A term used by IUCN and also under the Endangered Species Act of 1973 in the United States in reference to a species that is threatened with imminent extinction or extirpation over all or a significant portion of its range.

Endemic—Native to only one specific area.

Endothermic—Maintaining a constant body-temperature using metabolic energy. "Warm-blooded."

Eocene—Geological time period; subdivision of the Tertiary, from about 55.5 to 33.7 million years ago.

Ethology—The study of animal behavior.

Exotic—Not native.

Extant—Still in existence; not destroyed, lost, or extinct.

Extinct—Refers to a species that no longer survives anywhere.

Extirpated—Referring to a local extinction of a species that can still be found elsewhere.

Feral—A population of domesticated animal that lives in the wild.

Flehmen—Lip curling and head raising after sniffing a female's urine.

Forb—Any herb that is not a grass or grass-like.

Fossorial—Adapted for digging.

Frugivorous—Feeds on fruit.

Granivorous—Feeding on seeds.

Gravid—Pregnant.

Gregarious—Occuring in large groups.

Hibernation—A deep state of reduced metabolic activity and lowered body temperature that may last for weeks or months.

Holarctic—The Palearctic and Nearctic bigeographic regions combined.

Hybrid—The offspring resulting from a cross between two different species (or sometimes between distinctive subspecies).

Innate—An inherited characteristic.

Insectivorous—Technically refers to animals that eat insects; generally refers to animals that feed primarily on insects and other arthropods.

Introduced species—An animal or plant that has been introduced to an area where it normally does not occur.

Iteroparous—Breeds in multiple years.

Jacobson's organ—Olfactory organ found in the upper palate that first appeared in amphibians and is most developed in these and in reptiles, but is also found in some birds and mammals.

Kiva—A large chamber wholly or partly underground, and often used for religious ceremonies in Pueblo Indian villages.

Mandible—Technically an animal's lower jaw. The plural, mandibles, is used to refer to both the upper and lower jaw. The upper jaw is technically the maxilla, but often called the "upper mandible."

Marsupial—A mammal whose young complete their embryonic development outside of the mother's body, within a maternal pouch.

Matrilineal—Describing a social unit in which group members are descended from a single female.

Melon—The fat-filled forehead of aquatic mammals of the order Cetacea.

Metabolic rate—The rate of chemical processes in living organisms, resulting in energy expenditure and growth. Metabolic rate decreases when an animal is resting and increases during activity.

Migration—A two-way movement in some mammals, often dramatically seasonal. Typically latitudinal, though in some species is altitudinal or longitudinal. May be short-distance or long-distance.

Miocene—The geological time period that lasted from about 23.8 to 5.6 million years ago.

Molecular phylogenetics—The use of molecular (usually genetic) techniques to study evolutionary relationships between or among different groups of organisms.

Monestrous—Experiencing estrus just once each year or breeding season.

Monogamous—A breeding system in which a male and female mate only with one another.

Monophyletic—A group (or clade) that shares a common ancestor.

Monotypic—A taxonomic category that includes only one form (e.g., a genus that includes only one species; a species that includes no subspecies).

Montane—Of or inhabiting the biogeographic zone of relatively moist, cool upland slopes below timberline dominated by large coniferous trees.

Morphology—The form and structure of animals and plants.

Mutualism—Ecological relationship between two species in which both gain benefit.

Near Threatened—A category defined by the IUCN suggesting possible risk of extinction in the medium term (as opposed to long or short term) future.

Nearctic—The biogeographic region that includes temperate North America. faunal region.

Neotropical—The biogeographic region that includes South and Central America, the West Indies, and tropical Mexico.

New World—A general descriptive term encompassing the Nearctic and Neotropical biogeographic regions.

Niche—The role of an organism in its environment; multidimensional, with habitat and behavioral components.

Nocturnal—Active at night.

Old World—A general term that usually describes a species or group as being from Eurasia or Africa.

Oligocene—The geologic time period occurring from about 33.7 to 23.8 million years ago.

Omnivorous—Feeding on a broad range of foods, both plant and animal matter.

Palearctic—A biogeographic region that includes temperate Eurasia and Africa north of the Sahara.

Paleocene—Geological period, subdivision of the Tertiary, from 65 to 55.5 million years ago.

Pelage—Coat, skin, and hair.

Pelagic—An adjective used to indicate a relationship to the open sea.

Pestiferous—Troublesome or annoying; nuisance.

Phylogeny—A grouping of taxa based on evolutionary history.

Piscivorous—Fish-eating.

Placental—A mammal whose young complete their embryonic development within the mother's uterus, joined to her by a placenta.

Pleistocene—In general, the time of the great ice ages; geological period variously considered to include the last 1 to 1.8 million years.

Pliocene—The geological period preceding the Pleistocence; the last subdivision of what is known as the Tertiary; lasted from 5.5 to 1.8 million years ago.

Polyandry—A breeding system in which one female mates with two or more males.

Polygamy—A breeding system in which either or both male and female may have two or more mates.

Polygyny—A breeding system in which one male mates with two or more females.

Polyphyletic—A taxonomic group that is believed to have originated from more than one group of ancestors.

Post-gastric digestion—Refers to the type of fermentative digestion of vegetative matter found in tapirs and other animals by which microorganisms decompose food in a caecum. This is not as thorough a decomposition as occurs in ruminant digesters.

Precocial—An adjective used to describe animals that are born in an advanced state of development such that they generally can leave their birth area quickly and obtain their own food, although they are often led to food and guarded by a parent.

Proboscis—The prehensile trunk (a muscular hydrostat) found in tapirs, elephants, etc.

Quaternary—The geological period, from 1.8 million years ago to the present, usually including two subdivisions: the Pleistocene, and the Holocene.

Refugium (pl. refugia) —An area relatively unaltered during a time of climatic change, from which dispersion and speciation may occur after the climate readjusts.

Reproductive longevity—The length of an animal's life over which it is capable of reproduction.

Ruminant—An even-toed, hoofed mammal with a four-chambered stomach that eats rapidly to regurgitate its food and chew the cud later.

Scansorial—Specialized for climbing.

Seed dispersal—Refers to how tapirs and other animals transport viable seeds from their source to near or distant, suitable habitats where they can successfully germinate. Such dispersal may occur through the feces, through sputum, or as the seeds are attached and later released from fur, etc.

Semelparity—A short life span, in which a single instance of breeding is followed by death in the first year of life.

Sexual dimorphism—Male and female differ in morphology, such as size, feather size or shape, or bill size or shape.

Sibling species—Two or more species that are very closely related, presumably having differentiated from a common ancestor in the recent past; often difficult to distinguish, often interspecifically territorial.

Sonagram—A graphic representation of sound.

Speciation—The evolution of new species.

Spy-hopping—Positioning the body vertically in the water, with the head raised above the sea surface, sometimes while turning slowly.

Steppe—Arid land with vegetation that can thrive with very little moisture; found usually in regions of extreme temperature range.

Suspensory—Moving around or hanging by the arms.

Sympatric—Inhabiting the same range.

Systematist—A specialist in the classification of organisms; systematists strive to classify organisms on the basis of their evolutionary relationships.

Taxon (pl. taxa) —Any unit of scientific classification (e.g., species, genus, family, order).

Taxonomist—A specialist in the naming and classification of organisms. (See also Systematist. Taxonomy is the older science of naming things; identification of evolutionary relationships has not always been the goal of taxonomists. The modern science of systematics generally incorporates taxonomy with the search for evolutionary relationships.)

Taxonomy—The science of identifying, naming, and classifying organisms into groups.

Territoriality—Refers to an animal's defense of a certain portion of its habitat against other conspecifics. This is often undertaken by males in relation to one another and as a lure to females.

Territory—Any defended area. Territorial defense is typically male against male, female against female, and within a species or between sibling species. Area defended varies greatly among taxa, seasons, and habitats. A territory may include the entire home range, only the area immediately around a nest, or only a feeding area.

Tertiary—The geological period including most of the Cenozoic; from about 65 to 1.8 million years ago.

Thermoregulation—The ability to regulate body temperature; can be either behavioral or physiological.

Tribe—A unit of classification below the subfamily and above the genus.

Truncal erectness—Sitting, hanging, arm-swinging (brachiating), walking bipedally with the backbone held vertical.

Ungulate—A hoofed mammal.

Upper cone—The circle in which the arm can rotate when raised above the head.

Viable population—A population that is capable of maintaining itself over a period of time. One of the major conservation issues of the twenty-first century is determining what is a minimum viable population size. Population geneticists have generally come up with estimates of about 500 breeding pairs.

Vulnerable—A category defined by IUCN as a species that is not Critically Endangered or Endangered, but is still facing a threat of extinction.

Mammals species list

Monotremata [Order]

Tachyglossidae [Family]
Tachyglossus [Genus]
T. aculeatus [Species]
Zaglossus [Genus]
Z. bruijni [Species]

Ornithorhynchidae [Family]
Ornithorhynchus [Genus]
O. anatinus [Species]

Didelphimorphia [Order]

Didelphidae [Family]
Caluromys [Genus]
C. derbianus [Species]
C. lanatus
C. philander
Caluromysiops [Genus]
C. irrupta [Species]
Chironectes [Genus]
C. minimus [Species]
Didelphis [Genus]
D. albiventris [Species]
D. aurita
D. marsupialis
D. virginiana
Glironia [Genus]
G. venusta [Species]
Gracilinanus [Genus]
G. aceramarcae [Species]
G. agilis
G. dryas
G. emiliae
G. marica
G. microtarsus
Lestodelphys [Genus]
L. halli [Species]
Lutreolina [Genus]
L. crassicaudata [Species]
Marmosa [Genus]
M. andersoni [Species]
M. canescens
M. lepida
M. mexicana
M. murina
M. robinsoni
M. rubra
M. tyleriana
M. xerophila
Marmosops [Genus]
M. cracens [Species]
M. dorothea
M. fuscatus
M. handleyi
M. impavidus
M. incanus
M. invictus
M. noctivagus
M. parvidens
Metachirus [Genus]
M. nudicaudatus [Species]
Micoureus [Genus]
M. alstoni [Species]
M. constantiae
M. demerarae
M. regina
Monodelphis [Genus]
M. adusta [Species]
M. americana
M. brevicaudata
M. dimidiata
M. domestica
M. emiliae
M. iheringi
M. kunsi
M. maraxina
M. osgoodi
M. rubida
M. scalops
M. sorex
M. theresa
M. unistriata
Philander [Genus]
P. andersoni [Species]
P. opossum
Thylamys [Genus]
T. elegans [Species]
T. macrura
T. pallidior
T. pusilla
T. velutinus

Paucituberculata [Order]

Caenolestidae [Family]
Caenolestes [Genus]
C. caniventer [Species]
C. convelatus
C. fuliginosus
Lestoros [Genus]
L. inca [Species]
Rhyncholestes [Genus]
R. raphanurus [Species]

Microbiotheria [Order]

Microbiotheriidae [Family]
Dromiciops [Genus]
D. gliroides [Species]

Dasyuromorphia [Order]

Dasyuridae [Family]
Antechinus [Genus]
A. bellus [Species]
A. flavipes
A. godmani
A. leo
A. melanurus
A. minimus
A. naso
A. stuartii
A. swainsonii
A. wilhelmina
Dasycercus [Genus]
D. byrnei [Species]
D. cristicauda
Dasykaluta [Genus]
D. rosamondae [Species]
Dasyurus [Genus]
D. albopunctatus [Species]
D. geoffroii
D. hallucatus

D. maculatus
D. spartacus
D. viverrinus
Murexia [Genus]
M. longicaudata [Species]
M. rothschildi
Myoictis [Genus]
M. melas [Species]
Neophascogale [Genus]
N. lorentzi [Species]
Ningaui [Genus]
N. ridei [Species]
N. timealeyi
N. yvonnae
Parantechinus [Genus]
P. apicalis [Species]
P. bilarni
Phascogale [Genus]
P. calura [Species]
P. tapoatafa
Phascolosorex [Genus]
P. doriae [Species]
P. dorsalis
Planigale [Genus]
P. gilesi [Species]
P. ingrami
P. maculata
P. novaeguineae
P. tenuirostris
Pseudantechinus [Genus]
P. macdonnellensis [Species]
P. ningbing
P. woolleyae
Sarcophilus [Genus]
S. laniarius [Species]
Sminthopsis [Genus]
S. aitkeni [Species]
S. archeri
S. butleri
S. crassicaudata
S. dolichura
S. douglasi
S. fuliginosus
S. gilberti
S. granulipes
S. griseoventer
S. hirtipes
S. laniger
S. leucopus
S. longicaudata
S. macroura
S. murina
S. ooldea
S. psammophila
S. virginiae
S. youngsoni

Myrmecobiidae [Family]
Myrmecobius [Genus]
M. fasciatus [Species]

Thylacinidae [Family]
Thylacinus [Genus]
T. cynocephalus [Species]

Peramelemorphia [Order]

Peramelidae [Family]
Chaeropus [Genus]
C. ecaudatus [Species]
Isoodon [Genus]
I. auratus [Species]
I. macrourus
I. obesulus
Macrotis [Genus]
M. lagotis [Species]
M. leucura
Perameles [Genus]
P. bougainville [Species]
P. eremiana
P. gunnii
P. nasuta

Peroryctidae [Family]
Echymipera [Genus]
E. clara [Species]
E. davidi
E. echinista
E. kalubu
E. rufescens
Microperoryctes [Genus]
M. longicauda [Species]
M. murina
M. papuensis
Peroryctes [Genus]
P. broadbenti [Species]
P. raffrayana
Rhynchomeles [Genus]
R. prattorum [Species]

Notoryctemorphia [Order]

Notoryctidae [Family]
Notoryctes [Genus]
N. caurinus [Species]
N. typhlops

Diprotodontia [Order]

Phascolarctidae [Family]
Phascolarctos [Genus]
P. cinereus [Species]

Vombatidae [Family]
Lasiorhinus [Genus]
L. krefftii [Species]
L. latifrons
Vombatus [Genus]
V. ursinus [Species]

Phalangeridae [Family]
Ailurops [Genus]
A. ursinus [Species]
Phalanger [Genus]
P. carmelitae [Species]
P. lullulae
P. matanim
P. orientalis
P. ornatus
P. pelengensis
P. rothschildi
P. sericeus
P. vestitus
Spilocuscus [Genus]
S. maculatus [Species]
S. rufoniger
Strigocuscus [Genus]
S. celebensis [Species]
S. gymnotis
Trichosurus [Genus]
T. arnhemensis [Species]
T. caninus
T. vulpecula
Wyulda [Genus]
W. squamicaudata [Species]

Hypsiprymnodontidae [Family]
Hypsiprymnodon [Genus]
H. moschatus [Species]

Potoroidae [Family]
Aepyprymnus [Genus]
A. rufescens [Species]
Bettongia [Genus]
B. gaimardi [Species]
B. lesueur
B. penicillata
Caloprymnus [Genus]
C. campestris [Species]
Potorous [Genus]
P. longipes [Species]
P. platyops
P. tridactylus

Macropodidae [Family]
Dendrolagus [Genus]
D. bennettianus [Species]
D. dorianus
D. goodfellowi
D. inustus
D. lumholtzi
D. matschiei
D. scottae
D. spadix
D. ursinus
Dorcopsis [Genus]
D. atrata [Species]
D. hageni
D. luctuosa
D. muelleri
Dorcopsulus [Genus]
D. macleayi [Species]
D. vanheurni
Lagorchestes [Genus]

L. asomatus [Species]
L. conspicillatus
L. hirsutus
L. leporides
Lagostrophus [Genus]
L. fasciatus [Species]
Macropus [Genus]
M. agilis [Species]
M. antilopinus
M. bernardus
M. dorsalis
M. eugenii
M. fuliginosus
M. giganteus
M. greyi
M. irma
M. parma
M. parryi
M. robustus
M. rufogriseus
M. rufus
Onychogalea [Genus]
O. fraenata [Species]
O. lunata
O. unguifera
Petrogale [Genus]
P. assimilis [Species]
P. brachyotis
P. burbidgei
P. concinna
P. godmani
P. inornata
P. lateralis
P. penicillata
P. persephone
P. rothschildi
P. xanthopus
Setonix [Genus]
S. brachyurus [Species]
Thylogale [Genus]
T. billardierii [Species]
T. brunii
T. stigmatica
T. thetis
Wallabia [Genus]
W. bicolor [Species]

Burramyidae [Family]
Burramys [Genus]
B. parvus [Species]
Cercartetus [Genus]
C. caudatus [Species]
C. concinnus
C. lepidus
C. nanus

Pseudocheiridae [Family]
Hemibelideus [Genus]
H. lemuroides [Species]
Petauroides [Genus]
P. volans [Species]
Petropseudes [Genus]
P. dahli [Species]
Pseudocheirus [Genus]
P. canescens [Species]
P. caroli
P. forbesi
P. herbertensis
P. mayeri
P. peregrinus
P. schlegeli
Pseudochirops [Genus]
P. albertisii [Species]
P. archeri
P. corinnae
P. cupreus

Petauridae [Family]
Dactylopsila [Genus]
D. megalura [Species]
D. palpator
D. tatei
D. trivirgata
Gymnobelideus [Genus]
G. leadbeateri [Species]
Petaurus [Genus]
P. abidi [Species]
P. australis
P. breviceps
P. gracilis
P. norfolcensis

Tarsipedidae [Family]
Tarsipes [Genus]
T. rostratus [Species]

Acrobatidae [Family]
Acrobates [Genus]
A. pygmaeus [Species]
Distoechurus [Genus]
D. pennatus [Species]

Xenarthra [Order]

Megalonychidae [Family]
Choloepus [Genus]
C. didactylus [Species]
C. hoffmanni

Bradypodidae [Family]
Bradypus [Genus]
B. torquatus [Species]
B. tridactylus
B. variegatus

Myrmecophagidae [Family]
Cyclopes [Genus]
C. didactylus [Species]
Myrmecophaga [Genus]
M. tridactyla [Species]
Tamandua [Genus]
T. mexicana [Species]
T. tetradactyla

Dasypodidae [Family]
Chlamyphorus [Genus]
C. retusus [Species]
C. truncatus
Cabassous [Genus]
C. centralis [Species]
C. chacoensis
C. tatouay
C. unicinctus
Chaetophractus [Genus]
C. nationi [Species]
C. vellerosus
C. villosus
Dasypus [Genus]
D. hybridus [Species]
D. kappleri
D. novemcinctus
D. pilosus
D. sabanicola
D. septemcinctus
Euphractus [Genus]
E. sexcinctus [Species]
Priodontes [Genus]
P. maximus [Species]
Tolypeutes [Genus]
T. matacus [Species]
T. tricinctus
Zaedyus [Genus]
Z. pichiy [Species]

Insectivora [Order]

Erinaceidae [Family]
Atelerix [Genus]
A. albiventris [Species]
A. algirus
A. frontalis
A. sclateri
Erinaceus [Genus]
E. amurensis [Species]
E. concolor
E. europaeus
Hemiechinus [Genus]
H. aethiopicus [Species]
H. auritus
H. collaris
H. hypomelas
H. micropus
H. nudiventris
Mesechinus [Genus]
M. dauuricus [Species]
M. hughi
Echinosorex [Genus]
E. gymnura [Species]
Hylomys [Genus]
H. hainanensis [Species]
H. sinensis
H. suillus
Podogymnura [Genus]
P. aureospinula [Species]
P. truei

Chrysochloridae [Family]
Amblysomus [Genus]
A. gunningi [Species]
A. hottentotus
A. iris
A. julianae
Calcochloris [Genus]
C. obtusirostris [Species]
Chlorotalpa [Genus]
C. arendsi [Species]
C. duthieae
C. leucorhina
C. sclateri
C. tytonis
Chrysochloris [Genus]
C. asiatica [Species]
C. stuhlmanni
C. visagiei
Chrysospalax [Genus]
C. trevelyani [Species]
C. villosus
Cryptochloris [Genus]
C. wintoni [Species]
C. zyli
Eremitalpa [Genus]
E. granti [Species]

Tenrecidae [Family]
Echinops [Genus]
E. telfairi [Species]
Geogale [Genus]
G. aurita [Species]
Hemicentetes [Genus]
H. semispinosus [Species]
Limnogale [Genus]
L. mergulus [Species]
Microgale [Genus]
M. brevicaudata [Species]
M. cowani
M. dobsoni
M. dryas
M. gracilis
M. longicaudata
M. parvula
M. principula
M. pulla
M. pusilla
M. talazaci
M. thomasi
Micropotamogale [Genus]
M. lamottei [Species]
M. ruwenzorii
Oryzorictes [Genus]
O. hova [Species]
O. talpoides
O. tetradactylus
Potamogale [Genus]
P. velox [Species]
Setifer [Genus]
S. setosus [Species]
Tenrec [Genus]
T. ecaudatus [Species]

Solenodontidae [Family]
Solenodon [Genus]
S. cubanus [Species]
S. marcanoi
S. paradoxus

Nesophontidae [Family]
Nesophontes [Genus]
N. edithae [Species]
N. hypomicrus
N. longirostris
N. major
N. micrus
N. paramicrus
N. submicrus
N. zamicrus

Soricidae [Family]
Anourosorex [Genus]
A. squamipes [Species]
Blarina [Genus]
B. brevicauda [Species]
B. carolinensis
B. hylophaga
Blarinella [Genus]
B. quadraticauda [Species]
B. wardi
Chimarrogale [Genus]
C. hantu [Species]
C. himalayica
C. phaeura
C. platycephala
C. styani
C. sumatrana
Congosorex [Genus]
C. polli [Species]
Crocidura [Genus]
C. aleksandrisi [Species]
C. allex
C. andamanensis
C. ansellorum
C. arabica
C. armenica
C. attenuata
C. attila
C. baileyi
C. batesi
C. beatus
C. beccarii
C. bottegi
C. bottegoides
C. buettikoferi
C. caliginea
C. canariensis
C. cinderella
C. congobelgica
C. cossyrensis
C. crenata
C. crossei
C. cyanea
C. denti
C. desperata
C. dhofarensis
C. dolichura
C. douceti
C. dsinezumi
C. eisentrauti
C. elgonius
C. elongata
C. erica
C. fischeri
C. flavescens
C. floweri
C. foxi
C. fuliginosa
C. fulvastra
C. fumosa
C. fuscomurina
C. glassi
C. goliath
C. gracilipes
C. grandiceps
C. grandis
C. grassei
C. grayi
C. greenwoodi
C. gueldenstaedtii
C. harenna
C. hildegardeae
C. hirta
C. hispida
C. horsfieldii
C. jacksoni
C. jenkinsi
C. kivuana
C. lamottei
C. lanosa
C. lasiura
C. latona
C. lea
C. leucodon
C. levicula
C. littoralis
C. longipes
C. lucina
C. ludia
C. luna
C. lusitania
C. macarthuri
C. macmillani
C. macowi
C. malayana
C. manengubae
C. maquassiensis
C. mariquensis
C. maurisca
C. maxi
C. mindorus

C. minuta
C. miya
C. monax
C. monticola
C. montis
C. muricauda
C. mutesae
C. nana
C. nanilla
C. neglecta
C. negrina
C. nicobarica
C. nigeriae
C. nigricans
C. nigripes
C. nigrofusca
C. nimbae
C. niobe
C. obscurior
C. olivieri
C. orii
C. osorio
C. palawanensis
C. paradoxura
C. parvipes
C. pasha
C. pergrisea
C. phaeura
C. picea
C. pitmani
C. planiceps
C. poensis
C. polia
C. pullata
C. raineyi
C. religiosa
C. rhoditis
C. roosevelti
C. russula
C. selina
C. serezkyensis
C. sibirica
C. sicula
C. silacea
C. smithii
C. somalica
C. stenocephala
C. suaveolens
C. susiana
C. tansaniana
C. tarella
C. tarfayensis
C. telfordi
C. tenuis
C. thalia
C. theresae
C. thomensis
C. turba
C. ultima
C. usambarae
C. viaria
C. voi
C. whitakeri
C. wimmeri
C. xantippe
C. yankariensis
C. zaphiri
C. zarudnyi
C. zimmeri
C. zimmermanni
Cryptotis [Genus]
C. avia [Species]
C. endersi
C. goldmani
C. goodwini
C. gracilis
C. hondurensis
C. magna
C. meridensis
C. mexicana
C. montivaga
C. nigrescens
C. parva
C. squamipes
C. thomasi
Diplomesodon [Genus]
D. pulchellum [Species]
Feroculus [Genus]
F. feroculus [Species]
Megasorex [Genus]
M. gigas [Species]
Myosorex [Genus]
M. babaulti [Species]
M. blarina
M. cafer
M. eisentrauti
M. geata
M. longicaudatus
M. okuensis
M. rumpii
M. schalleri
M. sclateri
M. tenuis
M. varius
Nectogale [Genus]
N. elegans [Species]
Neomys [Genus]
N. anomalus [Species]
N. fodiens
N. schelkovnikovi
Notiosorex [Genus]
N. crawfordi [Species]
Paracrocidura [Genus]
P. graueri [Species]
P. maxima
P. schoutedeni
Ruwenzorisorex [Genus]
R. suncoides [Species]
Scutisorex [Genus]
S. somereni [Species]
Solisorex [Genus]
S. pearsoni [Species]
Sorex [Genus]
S. alaskanus [Species]
S. alpinus
S. araneus
S. arcticus
S. arizonae
S. asper
S. bairdii
S. bedfordiae
S. bendirii
S. buchariensis
S. caecutiens
S. camtschatica
S. cansulus
S. cinereus
S. coronatus
S. cylindricauda
S. daphaenodon
S. dispar
S. emarginatus
S. excelsus
S. fumeus
S. gaspensis
S. gracillimus
S. granarius
S. haydeni
S. hosonoi
S. hoyi
S. hydrodromus
S. isodon
S. jacksoni
S. kozlovi
S. leucogaster
S. longirostris
S. lyelli
S. macrodon
S. merriami
S. milleri
S. minutissimus
S. minutus
S. mirabilis
S. monticolus
S. nanus
S. oreopolus
S. ornatus
S. pacificus
S. palustris
S. planiceps
S. portenkoi
S. preblei
S. raddei
S. roboratus
S. sadonis
S. samniticus
S. satunini
S. saussurei
S. sclateri
S. shinto

S. sinalis
S. sonomae
S. stizodon
S. tenellus
S. thibetanus
S. trowbridgii
S. tundrensis
S. ugyunak
S. unguiculatus
S. vagrans
S. ventralis
S. veraepacis
S. volnuchini
Soriculus [Genus]
S. caudatus [Species]
S. fumidus
S. hypsibius
S. lamula
S. leucops
S. macrurus
S. nigrescens
S. parca
S. salenskii
S. smithii
Suncus [Genus]
S. ater [Species]
S. dayi
S. etruscus
S. fellowesgordoni
S. hosei
S. infinitesimus
S. lixus
S. madagascariensis
S. malayanus
S. mertensi
S. montanus
S. murinus
S. remyi
S. stoliczkanus
S. varilla
S. zeylanicus
Surdisorex [Genus]
S. norae [Species]
S. polulus
Sylvisorex [Genus]
S. granti [Species]
S. howelli
S. isabellae
S. johnstoni
S. lunaris
S. megalura
S. morio
S. ollula
S. oriundus
S. vulcanorum

Talpidae [Family]
Desmana [Genus]
D. moschata [Species]
Galemys [Genus]
G. pyrenaicus [Species]
Condylura [Genus]
C. cristata [Species]
Euroscaptor [Genus]
E. grandis [Species]
E. klossi
E. longirostris
E. micrura
E. mizura
E. parvidens
Mogera [Genus]
M. etigo [Species]
M. insularis
M. kobeae
M. minor
M. robusta
M. tokudae
M. wogura
Nesoscaptor [Genus]
N. uchidai [Species]
Neurotrichus [Genus]
N. gibbsii [Species]
Parascalops [Genus]
P. breweri [Species]
Parascaptor [Genus]
P. leucura [Species]
Scalopus [Genus]
S. aquaticus [Species]
Scapanulus [Genus]
S. oweni [Species]
Scapanus [Genus]
S. latimanus [Species]
S. orarius
S. townsendii
Scaptochirus [Genus]
S. moschatus [Species]
Scaptonyx [Genus]
S. fusicaudus [Species]
Talpa [Genus]
T. altaica [Species]
T. caeca
T. caucasica
T. europaea
T. levantis
T. occidentalis
T. romana
T. stankovici
T. streeti
Urotrichus [Genus]
U. pilirostris [Species]
U. talpoides
Uropsilus [Genus]
U. andersoni [Species]
U. gracilis
U. investigator
U. soricipes

Scandentia [Order]

Tupaiidae [Family]
Anathana [Genus]
A. ellioti [Species]
Dendrogale [Genus]
D. melanura [Species]
D. murina
Ptilocercus [Genus]
P. lowii [Species]
Tupaia [Genus]
T. belangeri [Species]
T. chrysogaster
T. dorsalis
T. glis
T. gracilis
T. javanica
T. longipes
T. minor
T. montana
T. nicobarica
T. palawanensis
T. picta
T. splendidula
T. tana
Urogale [Genus]
U. everetti [Species]

Dermoptera [Order]

Cynocephalidae [Family]
Cynocephalus [Genus]
C. variegatus [Species]
C. volans

Chiroptera [Order]

Pteropodidae [Family]
Acerodon [Genus]
A. celebensis [Species]
A. humilis
A. jubatus
A. leucotis
A. lucifer
A. mackloti
Aethalops [Genus]
A. alecto [Species]
Alionycteris [Genus]
A. paucidentata [Species]
Aproteles [Genus]
A. bulmerae [Species]
Balionycteris [Genus]
B. maculata [Species]
Boneia [Genus]
B. bidens [Species]
Casinycteris [Genus]
C. argynnis [Species]
Chironax [Genus]
C. melanocephalus [Species]
Cynopterus [Genus]
C. brachyotis [Species]
C. horsfieldi
C. nusatenggara
C. sphinx
C. titthaecheileus
Dobsonia [Genus]

D. beauforti [Species]
D. chapmani
D. emersa
D. exoleta
D. inermis
D. minor
D. moluccensis
D. pannietensis
D. peroni
D. praedatrix
D. viridis
Dyacopterus [Genus]
D. spadiceus [Species]
Eidolon [Genus]
E. dupreanum [Species]
E. helvum
Eonycteris [Genus]
E. major [Species]
E. spelaea
Epomophorus [Genus]
E. angolensis [Species]
E. gambianus
E. grandis
E. labiatus
E. minimus
E. wahlbergi
Epomops [Genus]
E. buettikoferi [Species]
E. dobsoni
E. franqueti
Haplonycteris [Genus]
H. fischeri [Species]
Harpyionycteris [Genus]
H. celebensis [Species]
H. whiteheadi
Hypsignathus [Genus]
H. monstrosus [Species]
Latidens [Genus]
L. salimalii [Species]
Macroglossus [Genus]
M. minimus [Species]
M. sobrinus
Megaerops [Genus]
M. ecaudatus [Species]
M. kusnotoi
M. niphanae
M. wetmorei
Megaloglossus [Genus]
M. woermanni [Species]
Melonycteris [Genus]
M. aurantius [Species]
M. melanops
M. woodfordi
Micropteropus [Genus]
M. intermedius [Species]
M. pusillus
Myonycteris [Genus]
M. brachycephala [Species]
M. relicta
M. torquata
Nanonycteris [Genus]
N. veldkampi [Species]
Neopteryx [Genus]
N. frosti [Species]
Notopteris [Genus]
N. macdonaldi [Species]
Nyctimene [Genus]
N. aello [Species]
N. albiventer
N. celaeno
N. cephalotes
N. certans
N. cyclotis
N. draconilla
N. major
N. malaitensis
N. masalai
N. minutus
N. rabori
N. robinsoni
N. sanctacrucis
N. vizcaccia
Otopteropus [Genus]
O. cartilagonodus [Species]
Paranyctimene [Genus]
P. raptor [Species]
Penthetor [Genus]
P. lucasi [Species]
Plerotes [Genus]
P. anchietai [Species]
Ptenochirus [Genus]
P. jagori [Species]
P. minor
Pteralopex [Genus]
P. acrodonta [Species]
P. anceps
P. atrata
P. pulchra
Pteropus [Genus]
P. admiralitatum [Species]
P. aldabrensis
P. alecto
P. anetianus
P. argentatus
P. brunneus
P. caniceps
P. chrysoproctus
P. conspicillatus
P. dasymallus
P. faunulus
P. fundatus
P. giganteus
P. gilliardi
P. griseus
P. howensis
P. hypomelanus
P. insularis
P. leucopterus
P. livingstonei
P. lombocensis
P. lylei
P. macrotis
P. mahaganus
P. mariannus
P. mearnsi
P. melanopogon
P. melanotus
P. molossinus
P. neohibernicus
P. niger
P. nitendiensis
P. ocularis
P. ornatus
P. personatus
P. phaeocephalus
P. pilosus
P. pohlei
P. poliocephalus
P. pselaphon
P. pumilus
P. rayneri
P. rodricensis
P. rufus
P. samoensis
P. sanctacrucis
P. scapulatus
P. seychellensis
P. speciosus
P. subniger
P. temmincki
P. tokudae
P. tonganus
P. tuberculatus
P. vampyrus
P. vetulus
P. voeltzkowi
P. woodfordi
Rousettus [Genus]
R. aegyptiacus [Species]
R. amplexicaudatus
R. angolensis
R. celebensis
R. lanosus
R. leschenaulti
R. madagascariensis
R. obliviosus
R. spinalatus
Scotonycteris [Genus]
S. ophiodon [Species]
S. zenkeri
Sphaerias [Genus]
S. blanfordi [Species]
Styloctenium [Genus]
S. wallacei [Species]
Syconycteris [Genus]
S. australis [Species]
S. carolinae
S. hobbit
Thoopterus [Genus]
T. nigrescens [Species]

Rhinopomatidae [Family]
Rhinopoma [Genus]
R. hardwickei [Species]
R. microphyllum
R. muscatellum

Emballonuridae [Family]
Balantiopteryx [Genus]
B. infusca [Species]
B. io
B. plicata
Centronycteris [Genus]
C. maximiliani [Species]
Coleura [Genus]
C. afra [Species]
C. seychellensis
Cormura [Genus]
C. brevirostris [Species]
Cyttarops [Genus]
C. alecto [Species]
Diclidurus [Genus]
D. albus [Species]
D. ingens
D. isabellus
D. scutatus
Emballonura [Genus]
E. alecto [Species]
E. atrata
E. beccarii
E. dianae
E. furax
E. monticola
E. raffrayana
E. semicaudata
Mosia [Genus]
M. nigrescens [Species]
Peropteryx [Genus]
P. kappleri [Species]
P. leucoptera
P. macrotis
Rhynchonycteris [Genus]
R. naso [Species]
Saccolaimus [Genus]
S. flaviventris [Species]
S. mixtus
S. peli
S. pluto
S. saccolaimus
Saccopteryx [Genus]
S. bilineata [Species]
S. canescens
S. gymnura
S. leptura
Taphozous [Genus]
T. australis [Species]
T. georgianus
T. hamiltoni
T. hildegardeae
T. hilli
T. kapalgensis
T. longimanus
T. mauritianus
T. melanopogon
T. nudiventris
T. perforatus
T. philippinensis
T. theobaldi

Craseonycteridae [Family]
Craseonycteris [Genus]
C. thonglongyai [Species]

Nycteridae [Family]
Nycteris [Genus]
N. arge [Species]
N. gambiensis
N. grandis
N. hispida
N. intermedia
N. javanica
N. macrotis
N. major
N. nana
N. thebaica
N. tragata
N. woodi

Megadermatidae [Family]
Cardioderma [Genus]
C. cor [Species]
Lavia [Genus]
L. frons [Species]
Macroderma [Genus]
M. gigas [Species]
Megaderma [Genus]
M. lyra [Species]
M. spasma

Rhinolophidae [Family]
Rhinolophus [Genus]
R. acuminatus [Species]
R. adami
R. affinis
R. alcyone
R. anderseni
R. arcuatus
R. blasii
R. borneensis
R. canuti
R. capensis
R. celebensis
R. clivosus
R. coelophyllus
R. cognatus
R. cornutus
R. creaghi
R. darlingi
R. deckenii
R. denti
R. eloquens
R. euryale
R. euryotis
R. ferrumequinum
R. fumigatus
R. guineensis
R. hildebrandti
R. hipposideros
R. imaizumii
R. inops
R. keyensis
R. landeri
R. lepidus
R. luctus
R. maclaudi
R. macrotis
R. malayanus
R. marshalli
R. megaphyllus
R. mehelyi
R. mitratus
R. monoceros
R. nereis
R. osgoodi
R. paradoxolophus
R. pearsoni
R. philippinensis
R. pusillus
R. rex
R. robinsoni
R. rouxi
R. rufus
R. sedulus
R. shameli
R. silvestris
R. simplex
R. simulator
R. stheno
R. subbadius
R. subrufus
R. swinnyi
R. thomasi
R. trifoliatus
R. virgo
R. yunanensis

Hipposideridae [Family]
Anthops [Genus]
A. ornatus [Species]
Asellia [Genus]
A. patrizii [Species]
A. tridens
Aselliscus [Genus]
A. stoliczkanus [Species]
A. tricuspidatus
Cloeotis [Genus]
C. percivali [Species]
Coelops [Genus]
C. frithi [Species]
C. hirsutus
C. robinsoni
Hipposideros [Genus]
H. abae [Species]
H. armiger

H. ater
H. beatus
H. bicolor
H. breviceps
H. caffer
H. calcaratus
H. camerunensis
H. cervinus
H. cineraceus
H. commersoni
H. coronatus
H. corynophyllus
H. coxi
H. crumeniferus
H. curtus
H. cyclops
H. diadema
H. dinops
H. doriae
H. dyacorum
H. fuliginosus
H. fulvus
H. galeritus
H. halophyllus
H. inexpectatus
H. jonesi
H. lamottei
H. lankadiva
H. larvatus
H. lekaguli
H. lylei
H. macrobullatus
H. maggietaylorae
H. marisae
H. megalotis
H. muscinus
H. nequam
H. obscurus
H. papua
H. pomona
H. pratti
H. pygmaeus
H. ridleyi
H. ruber
H. sabanus
H. schistaceus
H. semoni
H. speoris
H. stenotis
H. turpis
H. wollastoni
Paracoelops [Genus]
P. megalotis [Species]
Rhinonicteris [Genus]
R. aurantia [Species]
Triaenops [Genus]
T. furculus [Species]
T. persicus

Phyllostomidae [Family]
Ametrida [Genus]
A. centurio [Species]
Anoura [Genus]
A. caudifer [Species]
A. cultrata
A. geoffroyi
A. latidens
Ardops [Genus]
A. nichollsi [Species]
Ariteus [Genus]
A. flavescens [Species]
Artibeus [Genus]
A. amplus [Species]
A. anderseni
A. aztecus
A. cinereus
A. concolor
A. fimbriatus
A. fraterculus
A. glaucus
A. hartii
A. hirsutus
A. inopinatus
A. jamaicensis
A. lituratus
A. obscurus
A. phaeotis
A. planirostris
A. toltecus
Brachyphylla [Genus]
B. cavernarum [Species]
B. nana
Carollia [Genus]
C. brevicauda [Species]
C. castanea
C. perspicillata
C. subrufa
Centurio [Genus]
C. senex [Species]
Chiroderma [Genus]
C. doriae [Species]
C. improvisum
C. salvini
C. trinitatum
C. villosum
Choeroniscus [Genus]
C. godmani [Species]
C. intermedius
C. minor
C. periosus
Choeronycteris [Genus]
C. mexicana [Species]
Chrotopterus [Genus]
C. auritus [Species]
Desmodus [Genus]
D. rotundus [Species]
Diaemus [Genus]
D. youngi [Species]
Diphylla [Genus]
D. ecaudata [Species]
Ectophylla [Genus]
E. alba [Species]
Erophylla [Genus]
E. sezekorni [Species]
Glossophaga [Genus]
G. commissarisi [Species]
G. leachii
G. longirostris
G. morenoi
G. soricina
Hylonycteris [Genus]
H. underwoodi [Species]
Leptonycteris [Genus]
L. curasoae [Species]
L. nivalis
Lichonycteris [Genus]
L. obscura [Species]
Lionycteris [Genus]
L. spurrelli [Species]
Lonchophylla [Genus]
L. bokermanni [Species]
L. dekeyseri
L. handleyi
L. hesperia
L. mordax
L. robusta
L. thomasi
Lonchorhina [Genus]
L. aurita [Species]
L. fernandezi
L. marinkellei
L. orinocensis
Macrophyllum [Genus]
M. macrophyllum [Species]
Macrotus [Genus]
M. californicus [Species]
M. waterhousii
Mesophylla [Genus]
M. macconnelli [Species]
Micronycteris [Genus]
M. behnii [Species]
M. brachyotis
M. daviesi
M. hirsuta
M. megalotis
M. minuta
M. nicefori
M. pusilla
M. schmidtorum
M. sylvestris
Mimon [Genus]
M. bennettii [Species]
M. crenulatum
Monophyllus [Genus]
M. plethodon [Species]
M. redmani
Musonycteris [Genus]
M. harrisoni [Species]
Phylloderma [Genus]
P. stenops [Species]
Phyllonycteris [Genus]

P. aphylla [Species]
P. poeyi
Phyllops [Genus]
P. falcatus [Species]
Phyllostomus [Genus]
P. discolor [Species]
P. elongatus
P. hastatus
P. latifolius
Platalina [Genus]
P. genovensium [Species]
Platyrrhinus [Genus]
P. aurarius [Species]
P. brachycephalus
P. chocoensis
P. dorsalis
P. helleri
P. infuscus
P. lineatus
P. recifinus
P. umbratus
P. vittatus
Pygoderma [Genus]
P. bilabiatum [Species]
Rhinophylla [Genus]
R. alethina [Species]
R. fischerae
R. pumilio
Scleronycteris [Genus]
S. ega [Species]
Sphaeronycteris [Genus]
S. toxophyllum [Species]
Stenoderma [Genus]
S. rufum [Species]
Sturnira [Genus]
S. aratathomasi [Species]
S. bidens
S. bogotensis
S. erythromos
S. lilium
S. ludovici
S. luisi
S. magna
S. mordax
S. nana
S. thomasi
S. tildae
Tonatia [Genus]
T. bidens [Species]
T. brasiliense
T. carrikeri
T. evotis
T. schulzi
T. silvicola
Trachops [Genus]
T. cirrhosus [Species]
Uroderma [Genus]
U. bilobatum [Species]
U. magnirostrum
Vampyressa [Genus]
V. bidens [Species]
V. brocki
V. melissa
V. nymphaea
V. pusilla
Vampyrodes [Genus]
V. caraccioli [Species]
Vampyrum [Genus]
V. spectrum [Species]

Mormoopidae [Family]
Mormoops [Genus]
M. blainvillii [Species]
M. megalophylla
Pteronotus [Genus]
P. davyi [Species]
P. gymnonotus
P. macleayii
P. parnellii
P. personatus
P. quadridens

Noctilionidae [Family]
Noctilio [Genus]
N. albiventris [Species]
N. leporinus

Mystacinidae [Family]
Mystacina [Genus]
M. robusta [Species]
M. tuberculata

Natalidae [Family]
Natalus [Genus]
N. lepidus [Species]
N. micropus
N. stramineus
N. tumidifrons
N. tumidirostris

Furipteridae [Family]
Amorphochilus [Genus]
A. schnablii [Species]
Furipterus [Genus]
F. horrens [Species]

Thyropteridae [Family]
Thyroptera [Genus]
T. discifera [Species]
T. tricolor

Myzopodidae [Family]
Myzopoda [Genus]
M. aurita [Species]

Molossidae [Family]
Chaerephon [Genus]
C. aloysiisabaudiae [Species]
C. ansorgei
C. bemmeleni
C. bivittata
C. chapini
C. gallagheri
C. jobensis
C. johorensis
C. major
C. nigeriae
C. plicata
C. pumila
C. russata
Cheiromeles [Genus]
C. torquatus [Species]
Eumops [Genus]
E. auripendulus [Species]
E. bonariensis
E. dabbenei
E. glaucinus
E. hansae
E. maurus
E. perotis
E. underwoodi
Molossops [Genus]
M. abrasus [Species]
M. aequatorianus
M. greenhalli
M. mattogrossensis
M. neglectus
M. planirostris
M. temminckii
Molossus [Genus]
M. ater [Species]
M. bondae
M. molossus
M. pretiosus
M. sinaloae
Mops [Genus]
M. brachypterus [Species]
M. condylurus
M. congicus
M. demonstrator
M. midas
M. mops
M. nanulus
M. niangarae
M. niveiventer
M. petersoni
M. sarasinorum
M. spurrelli
M. thersites
M. trevori
Mormopterus [Genus]
M. acetabulosus [Species]
M. beccarii
M. doriae
M. jugularis
M. kalinowskii
M. minutus
M. norfolkensis
M. petrophilus
M. phrudus
M. planiceps
M. setiger
Myopterus [Genus]

M. daubentonii [Species]
M. whitleyi
Nyctinomops [Genus]
N. aurispinosus [Species]
N. femorosaccus
N. laticaudatus
N. macrotis
Otomops [Genus]
O. formosus [Species]
O. martiensseni
O. papuensis
O. secundus
O. wroughtoni
Promops [Genus]
P. centralis [Species]
P. nasutus
Tadarida [Genus]
T. aegyptiaca [Species]
T. australis
T. brasiliensis
T. espiritosantensis
T. fulminans
T. lobata
T. teniotis
T. ventralis

Vespertilionidae [Family]
Antrozous [Genus]
A. dubiaquercus [Species]
A. pallidus
Barbastella [Genus]
B. barbastellus [Species]
B. leucomelas
Chalinolobus [Genus]
C. alboguttatus [Species]
C. argentatus
C. beatrix
C. dwyeri
C. egeria
C. gleni
C. gouldii
C. kenyacola
C. morio
C. nigrogriseus
C. picatus
C. poensis
C. superbus
C. tuberculatus
C. variegatus
Eptesicus [Genus]
E. baverstocki [Species]
E. bobrinskoi
E. bottae
E. brasiliensis
E. brunneus
E. capensis
E. demissus
E. diminutus
E. douglasorum
E. flavescens
E. floweri
E. furinalis
E. fuscus
E. guadeloupensis
E. guineensis
E. hottentotus
E. innoxius
E. kobayashii
E. melckorum
E. nasutus
E. nilssoni
E. pachyotis
E. platyops
E. pumilus
E. regulus
E. rendalli
E. sagittula
E. serotinus
E. somalicus
E. tatei
E. tenuipinnis
E. vulturnus
Euderma [Genus]
E. maculatum [Species]
Eudiscopus [Genus]
E. denticulus [Species]
Glischropus [Genus]
G. javanus [Species]
G. tylopus
Harpiocephalus [Genus]
H. harpia [Species]
Hesperoptenus [Genus]
H. blanfordi [Species]
H. doriae
H. gaskelli
H. tickelli
H. tomesi
Histiotus [Genus]
H. alienus [Species]
H. macrotus
H. montanus
H. velatus
Ia [Genus]
I. io [Species]
Idionycteris [Genus]
I. phyllotis [Species]
Kerivoula [Genus]
K. aerosa [Species]
K. africana
K. agnella
K. argentata
K. atrox
K. cuprosa
K. eriophora
K. flora
K. hardwickei
K. intermedia
K. jagori
K. lanosa
K. minuta
K. muscina
K. myrella
K. papillosa
K. papuensis
K. pellucida
K. phalaena
K. picta
K. smithi
K. whiteheadi
Laephotis [Genus]
L. angolensis [Species]
L. botswanae
L. namibensis
L. wintoni
Lasionycteris [Genus]
L. noctivagans [Species]
Lasiurus [Genus]
L. borealis [Species]
L. castaneus
L. cinereus
L. ega
L. egregius
L. intermedius
L. seminolus
Mimetillus [Genus]
M. moloneyi [Species]
Miniopterus [Genus]
M. australis [Species]
M. fraterculus
M. fuscus
M. inflatus
M. magnater
M. minor
M. pusillus
M. robustior
M. schreibersi
M. tristis
Murina [Genus]
M. aenea [Species]
M. aurata
M. cyclotis
M. florium
M. fusca
M. grisea
M. huttoni
M. leucogaster
M. puta
M. rozendaali
M. silvatica
M. suilla
M. tenebrosa
M. tubinaris
M. ussuriensis
Myotis [Genus]
M. abei [Species]
M. adversus
M. aelleni
M. albescens
M. altarium
M. annectans
M. atacamensis

M. auriculus
M. australis
M. austroriparius
M. bechsteini
M. blythii
M. bocagei
M. bombinus
M. brandti
M. californicus
M. capaccinii
M. chiloensis
M. chinensis
M. cobanensis
M. dasycneme
M. daubentoni
M. dominicensis
M. elegans
M. emarginatus
M. evotis
M. findleyi
M. formosus
M. fortidens
M. frater
M. goudoti
M. grisescens
M. hasseltii
M. horsfieldii
M. hosonoi
M. ikonnikovi
M. insularum
M. keaysi
M. keenii
M. leibii
M. lesueuri
M. levis
M. longipes
M. lucifugus
M. macrodactylus
M. macrotarsus
M. martiniquensis
M. milleri
M. montivagus
M. morrisi
M. muricola
M. myotis
M. mystacinus
M. nattereri
M. nesopolus
M. nigricans
M. oreias
M. oxyotus
M. ozensis
M. peninsularis
M. pequinius
M. planiceps
M. pruinosus
M. ricketti
M. ridleyi
M. riparius
M. rosseti
M. ruber
M. schaubi
M. scotti
M. seabrai
M. sicarius
M. siligorensis
M. simus
M. sodalis
M. stalkeri
M. thysanodes
M. tricolor
M. velifer
M. vivesi
M. volans
M. welwitschii
M. yesoensis
M. yumanensis
Nyctalus [Genus]
N. aviator [Species]
N. azoreum
N. lasiopterus
N. leisleri
N. montanus
N. noctula
Nycticeius [Genus]
N. balstoni [Species]
N. greyii
N. humeralis
N. rueppellii
N. sanborni
N. schlieffeni
Nyctophilus [Genus]
N. arnhemensis [Species]
N. geoffroyi
N. gouldi
N. heran
N. microdon
N. microtis
N. timoriensis
N. walkeri
Otonycteris [Genus]
O. hemprichi [Species]
Pharotis [Genus]
P. imogene [Species]
Philetor [Genus]
P. brachypterus [Species]
Pipistrellus [Genus]
P. aegyptius [Species]
P. aero
P. affinis
P. anchietai
P. anthonyi
P. arabicus
P. ariel
P. babu
P. bodenheimeri
P. cadornae
P. ceylonicus
P. circumdatus
P. coromandra
P. crassulus
P. cuprosus
P. dormeri
P. eisentrauti
P. endoi
P. hesperus
P. imbricatus
P. inexspectatus
P. javanicus
P. joffrei
P. kitcheneri
P. kuhlii
P. lophurus
P. macrotis
P. maderensis
P. mimus
P. minahassae
P. mordax
P. musciculus
P. nanulus
P. nanus
P. nathusii
P. paterculus
P. peguensis
P. permixtus
P. petersi
P. pipistrellus
P. pulveratus
P. rueppelli
P. rusticus
P. savii
P. societatis
P. stenopterus
P. sturdeei
P. subflavus
P. tasmaniensis
P. tenuis
Plecotus [Genus]
P. auritus [Species]
P. austriacus
P. mexicanus
P. rafinesquii
P. taivanus
P. teneriffae
P. townsendii
Rhogeessa [Genus]
R. alleni [Species]
R. genowaysi
R. gracilis
R. minutilla
R. mira
R. parvula
R. tumida
Scotoecus [Genus]
S. albofuscus [Species]
S. hirundo
S. pallidus
Scotomanes [Genus]
S. emarginatus [Species]
S. ornatus

Scotophilus [Genus]
S. borbonicus [Species]
S. celebensis
S. dinganii
S. heathi
S. kuhlii
S. leucogaster
S. nigrita
S. nux
S. robustus
S. viridis
Tomopeas [Genus]
T. ravus [Species]
Tylonycteris [Genus]
T. pachypus [Species]
T. robustula
Vespertilio [Genus]
V. murinus [Species]
V. superans

Primates [Order]

Lorisidae [Family]
Arctocebus [Genus]
A. aureus [Species]
A. calabarensis
Loris [Genus]
L. tardigradus [Species]
Nycticebus [Genus]
N. coucang [Species]
N. pygmaeus
Perodicticus [Genus]
P. potto [Species]

Galagidae [Family]
Euoticus [Genus]
E. elegantulus [Species]
E. pallidus
Galago [Genus]
G. alleni [Species]
G. gallarum
G. matschiei
G. moholi
G. senegalensis
Galagoides [Genus]
G. demidoff [Species]
G. zanzibaricus
Otolemur [Genus]
O. crassicaudatus [Species]
O. garnettii

Cheirogaleidae [Family]
Allocebus [Genus]
A. trichotis [Species]
Cheirogaleus [Genus]
C. major [Species]
C. medius
Microcebus [Genus]
Microcebus coquereli [Species]
Microcebus murinus
Microcebus rufus
Phaner [Genus]
P. furcifer [Species]

Lemuridae [Family]
Eulemur [Genus]
E. coronatus [Species]
E. fulvus
E. macaco
E. mongoz
E. rubriventer
Hapalemur [Genus]
H. aureus [Species]
H. griseus
H. simus
Lemur [Genus]
L. catta [Species]
Varecia [Genus]
V. variegata [Species]

Indriidae [Family]
Avahi [Genus]
A. laniger [Species]
Indri [Genus]
I. indri [Species]
Propithecus [Genus]
P. diadema [Species]
P. tattersalli
P. verreauxi

Lepilemuridae [Family]
Lepilemur [Genus]
L. dorsalis [Species]
L. edwardsi
L. leucopus
L. microdon
L. mustelinus
L. ruficaudatus
L. septentrionalis

Daubentoniidae [Family]
Daubentonia [Genus]
D. madagascariensis [Species]

Tarsiidae [Family]
Tarsius [Genus]
T. bancanus [Species]
T. dianae
T. pumilus
T. spectrum
T. syrichta

Cebidae [Family]
Alouatta [Genus]
A. belzebul [Species]
A. caraya
A. coibensis
A. fusca
A. palliata
A. pigra
A. sara
A. seniculus
Callicebus [Genus]
C. brunneus [Species]
C. caligatus
C. cinerascens
C. cupreus
C. donacophilus
C. dubius
C. hoffmannsi
C. modestus
C. moloch
C. oenanthe
C. olallae
C. personatus
C. torquatus
Cebus [Genus]
C. albifrons [Species]
C. apella
C. capucinus
C. olivaceus
Saimiri [Genus]
S. boliviensis [Species]
S. oerstedii
S. sciureus
S. ustus
S. vanzolinii

Callitrichidae [Family]
Callimico [Genus]
C. goeldii [Species]
Callithrix [Genus]
C. argentata [Species]
C. aurita
C. flaviceps
C. geoffroyi
C. humeralifer
C. jacchus
C. kuhlii
C. penicillata
C. pygmaea
Leontopithecus [Genus]
L. caissara [Species]
L. chrysomela
L. chrysopygus
L. rosalia
Saguinus [Genus]
S. bicolor [Species]
S. fuscicollis
S. geoffroyi
S. imperator
S. inustus
S. labiatus
S. leucopus
S. midas
S. mystax
S. nigricollis
S. oedipus
S. tripartitus

Aotidae [Family]
Aotus [Genus]
A. azarai [Species]
A. brumbacki

A. hershkovitzi
A. infulatus
A. lemurinus
A. miconax
A. nancymaae
A. nigriceps
A. trivirgatus
A. vociferans

Pitheciidae [Family]
Cacajao [Genus]
C. calvus [Species]
C. melanocephalus
Chiropotes [Genus]
C. albinasus [Species]
C. satanas
Pithecia [Genus]
P. aequatorialis [Species]
P. albicans
P. irrorata
P. monachus
P. pithecia

Atelidae [Family]
Ateles [Genus]
A. belzebuth [Species]
A. chamek
A. fusciceps
A. geoffroyi
A. marginatus
A. paniscus
Brachyteles [Genus]
B. arachnoides [Species]
Lagothrix [Genus]
L. flavicauda [Species]
L. lagotricha

Cercopithecidae [Family]
Allenopithecus [Genus]
A. nigroviridis [Species]
Cercocebus [Genus]
C. agilis [Species]
C. galeritus
C. torquatus
Cercopithecus [Genus]
C. ascanius [Species]
C. campbelli
C. cephus
C. diana
C. dryas
C. erythrogaster
C. erythrotis
C. hamlyni
C. lhoesti
C. mitis
C. mona
C. neglectus
C. nictitans
C. petaurista
C. pogonias
C. preussi
C. sclateri
C. solatus
C. wolfi
Chlorocebus [Genus]
C. aethiops [Species]
Colobus [Genus]
C. angolensis [Species]
C. guereza
C. polykomos
C. satanas
Erythrocebus [Genus]
E. patas [Species]
Lophocebus [Genus]
L. albigena [Species]
Macaca [Genus]
M. arctoides [Species]
M. assamensis
M. cyclopis
M. fascicularis
M. fuscata
M. maura
M. mulatta
M. nemestrina
M. nigra
M. ochreata
M. radiata
M. silenus
M. sinica
M. sylvanus
M. thibetana
M. tonkeana
Mandrillus [Genus]
M. leucophaeus [Species]
M. sphinx
Miopithecus
M. talapoin
Nasalis [Genus]
N. concolor [Species]
N. larvatus
Papio [Genus]
P. hamadryas [Species]
Presbytis [Genus]
P. comata [Species]
P. femoralis
P. frontata
P. hosei
P. melalophos
P. potenziani
P. rubicunda
P. thomasi
Procolobus [Genus]
P. badius [Species]
P. pennantii
P. preussi
P. rufomitratus
P. verus
Pygathrix [Genus]
P. avunculus [Species]
P. bieti
P. brelichi
P. nemaeus
P. roxellana
Semnopithecus [Genus]
S. entellus [Species]
Theropithecus [Genus]
T. gelada [Species]
Trachypithecus [Genus]
T. auratus [Species]
T. cristatus
T. francoisi
T. geei
T. johnii
T. obscurus
T. phayrei
T. pileatus
T. vetulus

Hylobatidae [Family]
Hylobates [Genus]
H. agilis [Species]
H. concolor
H. gabriellae
H. hoolock
H. klossii
H. lar
H. leucogenys
H. moloch
H. muelleri
H. pileatus
H. syndactylus

Hominidae [Family]
Gorilla [Genus]
G. gorilla [Species]
Homo [Genus]
H. sapiens [Species]
Pan [Genus]
P. paniscus [Species]
P. troglodytes
Pongo [Genus]
P. pygmaeus [Species]

Carnivora [Order]

Canidae [Family]
Alopex [Genus]
A. lagopus [Species]
Atelocynus
A. microtis
Canis [Genus]
C. adustus [Species]
C. aureus
C. latrans
C. lupus
C. mesomelas
C. rufus
C. simensis
Cerdocyon [Genus]
C. thous [Species]
Chrysocyon [Genus]
C. brachyurus [Species]
Cuon [Genus]

C. alpinus [Species]
Dusicyon [Genus]
D. australis [Species]
Lycaon [Genus]
L. pictus [Species]
Nyctereutes [Genus]
N. procyonoides [Species]
Otocyon [Genus]
O. megalotis [Species]
Pseudalopex [Genus]
P. culpaeus [Species]
P. griseus
P. gymnocercus
P. sechurae
P. vetulus
Speothos [Genus]
S. venaticus [Species]
Urocyon [Genus]
U. cinereoargenteus [Species]
U. littoralis
Vulpes [Genus]
V. bengalensis [Species]
V. cana
V. chama
V. corsac
V. ferrilata
V. pallida
V. rueppelli
V. velox
V. vulpes
V. zerda

Ursidae [Family]
Ailuropoda [Genus]
A. melanoleuca [Species]
Ailurus [Genus]
A. fulgens [Species]
Helarctos [Genus]
H. malayanus [Species]
Melursus [Genus]
M. ursinus [Species]
Tremarctos [Genus]
T. ornatus [Species]
Ursus [Genus]
U. americanus [Species]
U. arctos
U. maritimus
U. thibetanus

Procyonidae [Family]
Bassaricyon [Genus]
B. alleni [Species]
B. beddardi
B. gabbii
B. lasius
B. pauli
Potos [Genus]
P. flavus [Species]
Bassariscus [Genus]
B. astutus [Species]
B. sumichrasti
Nasua [Genus]
N. narica [Species]
N. nasua
Nasuella [Genus]
N. olivacea [Species]
Procyon [Genus]
P. cancrivorus [Species]
P. gloveralleni
P. insularis
P. lotor
P. maynardi
P. minor
P. pygmaeus

Mustelidae [Family]
Amblonyx [Genus]
A. cinereus [Species]
Aonyx [Genus]
A. capensis [Species]
A. congicus
Arctonyx [Genus]
A. collaris [Species]
Conepatus [Genus]
C. chinga [Species]
C. humboldtii
C. leuconotus
C. mesoleucus
C. semistriatus
Eira [Genus]
E. barbara [Species]
Enhydra [Genus]
E. lutris [Species]
Galictis [Genus]
G. cuja [Species]
G. vittata
Gulo [Genus]
G. gulo [Species]
Ictonyx [Genus]
I. libyca [Species]
I. striatus
Lontra [Genus]
L. canadensis [Species]
L. felina
L. longicaudis
L. provocax
Lutra [Genus]
L. lutra [Species]
L. maculicollis
L. sumatrana
Lutrogale [Genus]
L. perspicillata [Species]
Lyncodon [Genus]
L. patagonicus [Species]
Martes [Genus]
M. americana [Species]
M. flavigula
M. foina
M. gwatkinsii
M. martes
M. melampus
M. pennanti
M. zibellina
Meles [Genus]
M. meles [Species]
Mellivora [Genus]
M. capensis [Species]
Melogale [Genus]
M. everetti [Species]
M. moschata
M. orientalis
M. personata
Mephitis [Genus]
M. macroura [Species]
M. mephitis
Mustela [Genus]
M. africana [Species]
M. altaica
M. erminea
M. eversmannii
M. felipei
M. frenata
M. kathiah
M. lutreola
M. lutreolina
M. nigripes
M. nivalis
M. nudipes
M. putorius
M. sibirica
M. strigidorsa
M. vison
Mydaus [Genus]
M. javanensis [Species]
M. marchei
Poecilogale [Genus]
P. albinucha [Species]
Pteronura [Genus]
P. brasiliensis [Species]
Spilogale [Genus]
S. putorius [Species]
S. pygmaea
Taxidea [Genus]
T. taxus [Species]
Vormela [Genus]
V. peregusna [Species]

Viverridae [Family]
Arctictis [Genus]
A. binturong [Species]
Arctogalidia [Genus]
A. trivirgata [Species]
Chrotogale [Genus]
C. owstoni [Species]
Civettictis [Genus]
C. civetta [Species]
Cryptoprocta [Genus]
C. ferox [Species]
Cynogale [Genus]
C. bennettii [Species]
Diplogale [Genus]
D. hosei [Species]
Eupleres [Genus]

E. goudotii [Species]
Fossa [Genus]
F. fossana [Species]
Genetta [Genus]
G. abyssinica [Species]
G. angolensis
G. genetta
G. johnstoni
G. maculata
G. servalina
G. thierryi
G. tigrina
G. victoriae
Hemigalus [Genus]
H. derbyanus [Species]
Nandinia [Genus]
N. binotata [Species]
Macrogalidia [Genus]
M. musschenbroekii [Species]
Paguma [Genus]
P. larvata [Species]
Paradoxurus [Genus]
P. hermaphroditus [Species]
P. jerdoni
P. zeylonensis
Osbornictis [Genus]
O. piscivora [Species]
Poiana [Genus]
P. richardsonii [Species]
Prionodon [Genus]
P. linsang [Species]
P. pardicolor
Viverra [Genus]
V. civettina [Species]
V. megaspila
V. tangalunga
V. zibetha
Viverricula [Genus]
V. indica [Species]

Herpestidae [Family]
Atilax [Genus]
A. paludinosus [Species]
Bdeogale [Genus]
B. crassicauda [Species]
B. jacksoni
B. nigripes
Crossarchus [Genus]
C. alexandri [Species]
C. ansorgei
C. obscurus
Cynictis [Genus]
C. penicillata [Species]
Dologale [Genus]
D. dybowskii [Species]
Galerella [Genus]
G. flavescens [Species]
G. pulverulenta
G. sanguinea
G. swalius
Galidia [Genus]
G. elegans [Species]
Galidictis [Genus]
G. fasciata [Species]
G. grandidieri
Helogale [Genus]
H. hirtula [Species]
H. parvula
Herpestes [Genus]
H. brachyurus [Species]
H. edwardsii
H. ichneumon
H. javanicus
H. naso
H. palustris
H. semitorquatus
H. smithii
H. urva
H. vitticollis
Ichneumia [Genus]
I. albicauda [Species]
Liberiictis [Genus]
L. kuhni [Species]
Mungos [Genus]
M. gambianus [Species]
M. mungo
Mungotictis [Genus]
M. decemlineata [Species]
Paracynictis [Genus]
P. selousi [Species]
Rhynchogale [Genus]
R. melleri [Species]
Salanoia [Genus]
S. concolor [Species]
Suricata [Genus]
S. suricatta [Species]

Hyaenidae [Family]
Crocuta [Genus]
C. crocuta [Species]
Hyaena [Genus]
H. hyaena [Species]
Parahyaena [Genus]
P. brunnea [Species]
Proteles [Genus]
P. cristatus [Species]

Felidae [Family]
Acinonyx [Genus]
A. jubatus [Species]
Caracal [Genus]
C. caracal [Species]
Catopuma [Genus]
C. badia [Species]
C. temminckii
Felis [Genus]
F. bieti [Species]
F. chaus
F. margarita
F. nigripes
F. silvestris
Herpailurus [Genus]
H. yaguarondi [Species]
Leopardus [Genus]
L. pardalis [Species]
L. tigrinus
L. wiedii
Leptailurus [Genus]
L. serval [Species]
Lynx [Genus]
L. canadensis [Species]
L. lynx
L. pardinus
L. rufus
Neofelis [Genus]
N. nebulosa [Species]
Oncifelis [Genus]
O. colocolo [Species]
O. geoffroyi
O. guigna
Oreailurus [Genus]
O. jacobita [Species]
Otocolobus [Genus]
O. manul [Species]
Panthera [Genus]
P. leo [Species]
P. onca
P. pardus
P. tigris
Pardofelis
P. marmorata
Prionailurus [Genus]
P. bengalensis [Species]
P. planiceps
P. rubiginosus
P. viverrinus
Profelis [Genus]
P. aurata [Species]
Puma [Genus]
P. concolor [Species]
Uncia [Genus]
U. uncia [Species]

Otariidae [Family]
Arctocephalus [Genus]
A. australis [Species]
A. forsteri
A. galapagoensis
A. gazella
A. philippii
A. pusillus
A. townsendi
A. tropicalis
Callorhinus [Genus]
C. ursinus [Species]
Eumetopias [Genus]
E. jubatus [Species]
Neophoca [Genus]
N. cinerea [Species]
Otaria [Genus]
O. byronia [Species]

Phocarctos [Genus]
P. hookeri [Species]
Zalophus [Genus]
Z. californianus [Species]

Odobenidae [Family]
Odobenus [Genus]
O. rosmarus [Species]

Phocidae [Family]
Cystophora [Genus]
C. cristata [Species]
Erignathus [Genus]
E. barbatus [Species]
Halichoerus [Genus]
H. grypus [Species]
Hydrurga [Genus]
H. leptonyx [Species]
Leptonychotes [Genus]
L. weddellii [Species]
Lobodon [Genus]
L. carcinophagus [Species]
Mirounga [Genus]
M. angustirostris [Species]
M. leonina
Monachus [Genus]
M. monachus [Species]
M. schauinslandi
M. tropicalis
Ommatophoca [Genus]
O. rossii [Species]
Phoca [Genus]
P. caspica [Species]
P. fasciata
P. groenlandica
P. hispida
P. largha
P. sibirica
P. vitulina

Cetacea [Order]

Platanistidae [Family]
Platanista [Genus]
P. gangetica [Species]
P. minor

Lipotidae [Family]
Lipotes [Genus]
L. vexillifer [Species]

Pontoporiidae [Family]
Pontoporia [Genus]
P. blainvillei [Species]

Iniidae [Family]
Inia [Genus]
I. geoffrensis [Species]

Phocoenidae [Family]
Australophocaena [Genus]
A. dioptrica [Species]
Neophocaena [Genus]
N. phocaenoides [Species]
Phocoena [Genus]
P. phocoena [Species]
P. sinus
P. spinipinnis
Phocoenoides [Genus]
P. dalli [Species]

Delphinidae [Family]
Cephalorhynchus [Genus]
C. commersonii [Species]
C. eutropia
C. heavisidii
C. hectori
Delphinus [Genus]
D. delphis [Species]
Feresa [Genus]
F. attenuata [Species]
Globicephala [Genus]
G. macrorhynchus [Species]
G. melas
Grampus [Genus]
G. griseus [Species]
Lagenodelphis [Genus]
L. hosei [Species]
Lagenorhynchus [Genus]
L. acutus [Species]
L. albirostris
L. australis
L. cruciger
L. obliquidens
L. obscurus
Lissodelphis [Genus]
L. borealis [Species]
L. peronii
Orcaella [Genus]
O. brevirostris [Species]
Orcinus [Genus]
O. orca [Species]
Peponocephala [Genus]
P. electra [Species]
Pseudorca [Genus]
P. crassidens [Species]
Sotalia [Genus]
S. fluviatilis [Species]
Sousa [Genus]
S. chinensis [Species]
S. teuszii
Stenella [Genus]
S. attenuata [Species]
S. clymene
S. coeruleoalba
S. frontalis
S. longirostris
Steno [Genus]
S. bredanensis [Species]
Tursiops [Genus]
T. truncatus [Species]

Ziphiidae [Family]
Berardius [Genus]
B. arnuxii [Species]
B. bairdii
Hyperoodon [Genus]
H. ampullatus [Species]
H. planifrons
Indopacetus [Genus]
I. pacificus [Species]
Mesoplodon [Genus]
M. bidens [Species]
M. bowdoini
M. carlhubbsi
M. densirostris
M. europaeus
M. ginkgodens
M. grayi
M. hectori
M. layardii
M. mirus
M. peruvianus
M. stejnegeri
Tasmacetus [Genus]
T. shepherdi [Species]
Ziphius [Genus]
Z. cavirostris [Species]

Physeteridae [Family]
Kogia [Genus]
K. breviceps [Species]
K. simus
Physeter [Genus]
P. catodon [Species]

Monodontidae [Family]
Delphinapterus [Genus]
D. leucas [Species]
Monodon [Genus]
M. monoceros [Species]

Eschrichtiidae [Family]
Eschrichtius [Genus]
E. robustus [Species]

Neobalaenidae [Family]
Caperea [Genus]
C. marginata [Species]

Balaenidae [Family]
Balaena [Genus]
B. mysticetus [Species]
Eubalaena [Genus]
E. australis [Species]
E. glacialis

Balaenopteridae [Family]
Balaenoptera [Genus]
B. acutorostrata [Species]
B. borealis
B. edeni
B. musculus
B. physalus
Megaptera [Genus]
M. novaeangliae [Species]

Tubulidentata [Order]

Orycteropodidae [Family]
Orycteropus [Genus]
O. afer [Species]

Proboscidea [Order]

Elephantidae [Family]
Elephas [Genus]
E. maximus [Species]
Loxodonta [Genus]
L. africana [Species]
L. cyclotis

Hyracoidea [Order]

Procaviidae [Family]
Dendrohyrax [Genus]
D. arboreus [Species]
D. dorsalis
D. validus
Heterohyrax [Genus]
H. antineae [Species]
H. brucei
Procavia [Genus]
P. capensis [Species]

Sirenia [Order]

Dugongidae [Family]
Dugong [Genus]
D. dugon [Species]
Hydrodamalis [Genus]
H. gigas [Species]

Trichechidae [Family]
Trichechus [Genus]
T. inunguis [Species]
T. manatus
T. senegalensis

Perissodactyla [Order]

Equidae [Family]
Equus [Genus]
E. asinus [Species]
E. burchellii
E. caballus
E. grevyi
E. hemionus
E. kiang
E. onager
E. quagga
E. zebra

Tapiridae [Family]
Tapirus [Genus]
T. bairdii [Species]
T. indicus
T. pinchaque
T. terrestris

Rhinocerotidae [Family]
Ceratotherium [Genus]
C. simum [Species]
Dicerorhinus [Genus]
D. sumatrensis [Species]
Diceros [Genus]
D. bicornis [Species]
Rhinoceros [Genus]
R. sondaicus [Species]
R. unicornis

Artiodactyla [Order]

Suidae [Family]
Babyrousa [Genus]
B. babyrussa [Species]
Phacochoerus [Genus]
P. aethiopicus [Species]
P. africanus
Hylochoerus [Genus]
H. meinertzhageni [Species]
Potamochoerus [Genus]
P. larvatus [Species]
P. porcus
Sus [Genus]
S. barbatus [Species]
S. bucculentus
S. cebifrons
S. celebensis
S. heureni
S. philippensis
S. salvanius
S. scrofa
S. timoriensis
S. verrucosus

Tayassuidae [Family]
Catagonus [Genus]
C. wagneri [Species]
Pecari [Genus]
P. tajacu [Species]
Tayassu [Genus]
T. pecari [Species]

Hippopotamidae [Family]
Hexaprotodon [Genus]
H. liberiensis [Species]
H. madagascariensis
Hippopotamus [Genus]
H. amphibius [Species]
H. lemerlei

Camelidae [Family]
Camelus [Genus]
C. bactrianus [Species]
C. dromedarius
Lama [Genus]
L. glama [Species]
L. guanicoe
L. pacos
Vicugna [Genus]
V. vicugna [Species]

Tragulidae [Family]
Hyemoschus [Genus]
H. aquaticus [Species]
Moschiola [Genus]
M. meminna [Species]
Tragulus [Genus]
T. javanicus [Species]
T. napu

Cervidae [Family]
Alces [Genus]
A. alces [Species]
Axis [Genus]
A. axis [Species]
A. calamianensis
A. kuhlii
A. porcinus
Blastocerus [Genus]
B. dichotomus [Species]
Capreolus [Genus]
C. capreolus [Species]
C. pygargus
Cervus [Genus]
C. albirostris [Species]
C. alfredi
C. duvaucelii
C. elaphus
C. eldii
C. mariannus
C. nippon
C. schomburgki
C. timorensis
C. unicolor
Dama [Genus]
D. dama [Species]
D. mesopotamica
Elaphodus [Genus]
E. cephalophus [Species]
Elaphurus [Genus]
E. davidianus [Species]
Hippocamelus [Genus]
H. antisensis [Species]
H. bisulcus
Hydropotes [Genus]
H. inermis [Species]
Mazama [Genus]
M. americana [Species]
M. bricenii
M. chunyi
M. gouazoupira
M. nana
M. rufina
Moschus [Genus]
M. berezovskii [Species]
M. chrysogaster
M. fuscus
M. moschiferus
Muntiacus [Genus]
M. atherodes [Species]
M. crinifrons
M. feae
M. gongshanensis

M. muntjak
M. reevesi
Odocoileus [Genus]
O. hemionus [Species]
O. virginianus
Ozotoceros [Genus]
O. bezoarticus [Species]
Pudu [Genus]
P. mephistophiles [Species]
P. puda
Rangifer [Genus]
R. tarandus [Species]

Giraffidae [Family]
Giraffa [Genus]
G. camelopardalis [Species]
Okapia [Genus]
O. johnstoni [Species]

Antilocapridae [Family]
Antilocapra [Genus]
A. americana [Species]

Bovidae [Family]
Addax [Genus]
A. nasomaculatus [Species]
Aepyceros [Genus]
A. melampus [Species]
Alcelaphus [Genus]
A. buselaphus [Species]
Ammodorcas [Genus]
A. clarkei [Species]
Ammotragus [Genus]
A. lervia [Species]
Antidorcas [Genus]
A. marsupialis [Species]
Antilope [Genus]
A. cervicapra [Species]
Bison [Genus]
B. bison [Species]
B. bonasus
Bos [Genus]
B. frontalis [Species]
B. grunniens
B. javanicus
B. sauveli
B. taurus
Boselaphus [Genus]
B. tragocamelus [Species]
Bubalus [Genus]
B. bubalis [Species]
B. depressicornis
B. mephistopheles
B. mindorensis
B. quarlesi
Budorcas [Genus]
B. taxicolor [Species]
Capra [Genus]
C. caucasica [Species]
C. cylindricornis
C. falconeri
C. hircus
C. ibex
C. nubiana
C. pyrenaica
C. sibirica
C. walie
Cephalophus [Genus]
C. adersi [Species]
C. callipygus
C. dorsalis
C. harveyi
C. jentinki
C. leucogaster
C. maxwellii
C. monticola
C. natalensis
C. niger
C. nigrifrons
C. ogilbyi
C. rubidus
C. rufilatus
C. silvicultor
C. spadix
C. weynsi
C. zebra
Connochaetes [Genus]
C. gnou [Species]
C. taurinus
Damaliscus [Genus]
D. hunteri [Species]
D. lunatus
D. pygargus
Dorcatragus [Genus]
D. megalotis [Species]
Gazella [Genus]
G. arabica [Species]
G. bennettii
G. bilkis
G. cuvieri
G. dama
G. dorcas
G. gazella
G. granti
G. leptoceros
G. rufifrons
G. rufina
G. saudiya
G. soemmerringii
G. spekei
G. subgutturosa
G. thomsonii
Hemitragus [Genus]
H. hylocrius [Species]
H. jayakari
H. jemlahicus
Hippotragus [Genus]
H. equinus [Species]
H. leucophaeus
H. niger
Kobus [Genus]
K. ellipsiprymnus [Species]
K. kob
K. leche
K. megaceros
K. vardonii
Litocranius [Genus]
L. walleri [Species]
Madoqua [Genus]
M. guentheri [Species]
M. kirkii
M. piacentinii
M. saltiana
Naemorhedus [Genus]
N. baileyi [Species]
N. caudatus
N. crispus
N. goral
N. sumatraensis
N. swinhoei
Neotragus [Genus]
N. batesi [Species]
N. moschatus
N. pygmaeus
Oreamnos [Genus]
O. americanus [Species]
Oreotragus [Genus]
O. oreotragus [Species]
Oryx [Genus]
O. dammah [Species]
O. gazella
O. leucoryx
Ourebia [Genus]
O. ourebi [Species]
Ovibos [Genus]
O. moschatus [Species]
Ovis [Genus]
O. ammon [Species]
O. aries
O. canadensis
O. dalli
O. nivicola
O. vignei
Pantholops [Genus]
P. hodgsonii [Species]
Pelea [Genus]
P. capreolus [Species]
Procapra [Genus]
P. gutturosa [Species]
P. picticaudata
P. przewalskii
Pseudois [Genus]
P. nayaur [Species]
P. schaeferi
Raphicerus [Genus]
R. campestris [Species]
R. melanotis
R. sharpei
Redunca [Genus]
R. arundinum [Species]
R. fulvorufula
R. redunca

Rupicapra [Genus]
R. pyrenaica [Species]
R. rupicapra
Saiga [Genus]
S. tatarica [Species]
Sigmoceros [Genus]
S. lichtensteinii [Species]
Sylvicapra [Genus]
S. grimmia [Species]
Syncerus [Genus]
S. caffer [Species]
Taurotragus [Genus]
T. derbianus [Species]
T. oryx
Tetracerus [Genus]
T. quadricornis [Species]
Tragelaphus [Genus]
T. angasii [Species]
T. buxtoni
T. eurycerus
T. imberbis
T. scriptus
T. spekii
T. strepsiceros

Pholidota [Order]

Manidae [Family]
Manis [Genus]
M. crassicaudata [Species]
M. gigantea
M. javanica
M. pentadactyla
M. temminckii
M. tetradactyla
M. tricuspis

Rodentia [Order]

Aplodontidae [Family]
Aplodontia [Genus]
A. rufa [Species]

Sciuridae [Family]
Aeretes [Genus]
A. melanopterus [Species]
Aeromys [Genus]
A. tephromelas [Species]
A. thomasi
Ammospermophilus [Genus]
A. harrisii [Species]
A. insularis
A. interpres
A. leucurus
A. nelsoni
Atlantoxerus [Genus]
A. getulus [Species]
Belomys [Genus]
B. pearsonii [Species]
Biswamoyopterus [Genus]
B. biswasi [Species]
Callosciurus [Genus]
C. adamsi [Species]
C. albescens
C. baluensis
C. caniceps
C. erythraeus
C. finlaysonii
C. inornatus
C. melanogaster
C. nigrovittatus
C. notatus
C. orestes
C. phayrei
C. prevostii
C. pygerythrus
C. quinquestriatus
Cynomys [Genus]
C. gunnisoni [Species]
C. leucurus
C. ludovicianus
C. mexicanus
C. parvidens
Dremomys [Genus]
D. everetti [Species]
D. lokriah
D. pernyi
D. pyrrhomerus
D. rufigenis
Epixerus [Genus]
E. ebii [Species]
E. wilsoni
Eupetaurus [Genus]
E. cinereus [Species]
Exilisciurus [Genus]
E. concinnus [Species]
E. exilis
E. whiteheadi
Funambulus [Genus]
F. layardi [Species]
F. palmarum
F. pennantii
F. sublineatus
F. tristriatus
Funisciurus [Genus]
F. anerythrus [Species]
F. bayonii
F. carruthersi
F. congicus
F. isabella
F. lemniscatus
F. leucogenys
F. pyrropus
F. substriatus
Glaucomys [Genus]
G. sabrinus [Species]
G. volans
Glyphotes [Genus]
G. simus [Species]
Heliosciurus [Genus]
H. gambianus [Species]
H. mutabilis
H. punctatus
H. rufobrachium
H. ruwenzorii
H. undulatus
Hylopetes [Genus]
H. alboniger [Species]
H. baberi
H. bartelsi
H. fimbriatus
H. lepidus
H. nigripes
H. phayrei
H. sipora
H. spadiceus
H. winstoni
Hyosciurus [Genus]
H. heinrichi [Species]
H. ileile
Iomys [Genus]
I. horsfieldi [Species]
I. sipora
Lariscus [Genus]
L. hosei [Species]
L. insignis
L. niobe
L. obscurus
Marmota [Genus]
M. baibacina [Species]
M. bobak
M. broweri
M. caligata
M. camtschatica
M. caudata
M. flaviventris
M. himalayana
M. marmota
M. menzbieri
M. monax
M. olympus
M. sibirica
M. vancouverensis
Menetes [Genus]
M. berdmorei [Species]
Microsciurus [Genus]
M. alfari [Species]
M. flaviventer
M. mimulus
M. santanderensis
Myosciurus [Genus]
M. pumilio [Species]
Nannosciurus [Genus]
N. melanotis [Species]
Paraxerus [Genus]
P. alexandri [Species]
P. boehmi
P. cepapi
P. cooperi
P. flavovittis
P. lucifer

P. ochraceus
P. palliatus
P. poensis
P. vexillarius
P. vincenti
Petaurillus [Genus]
P. emiliae [Species]
P. hosei
P. kinlochii
Petaurista [Genus]
P. alborufus [Species]
P. elegans
P. leucogenys
P. magnificus
P. nobilis
P. petaurista
P. philippensis
P. xanthotis
Petinomys [Genus]
P. crinitus [Species]
P. fuscocapillus
P. genibarbis
P. hageni
P. lugens
P. sagitta
P. setosus
P. vordermanni
Prosciurillus [Genus]
P. abstrusus [Species]
P. leucomus
P. murinus
P. weberi
Protoxerus [Genus]
P. aubinnii [Species]
P. stangeri
Pteromys [Genus]
P. momonga [Species]
P. volans
Pteromyscus [Genus]
P. pulverulentus [Species]
Ratufa [Genus]
R. affinis [Species]
R. bicolor
R. indica
R. macroura
Rheithrosciurus [Genus]
R. macrotis [Species]
Rhinosciurus [Genus]
R. laticaudatus [Species]
Rubrisciurus [Genus]
R. rubriventer [Species]
Sciurillus [Genus]
S. pusillus [Species]
Sciurotamias [Genus]
S. davidianus [Species]
S. forresti
Sciurus [Genus]
S. aberti [Species]
S. aestuans
S. alleni
S. anomalus
S. arizonensis
S. aureogaster
S. carolinensis
S. colliaei
S. deppei
S. flammifer
S. gilvigularis
S. granatensis
S. griseus
S. ignitus
S. igniventris
S. lis
S. nayaritensis
S. niger
S. oculatus
S. pucheranii
S. pyrrhinus
S. richmondi
S. sanborni
S. spadiceus
S. stramineus
S. variegatoides
S. vulgaris
S. yucatanensis
Spermophilopsis [Genus]
S. leptodactylus [Species]
Spermophilus [Genus]
S. adocetus [Species]
S. alashanicus
S. annulatus
S. armatus
S. atricapillus
S. beecheyi
S. beldingi
S. brunneus
S. canus
S. citellus
S. columbianus
S. dauricus
S. elegans
S. erythrogenys
S. franklinii
S. fulvus
S. lateralis
S. madrensis
S. major
S. mexicanus
S. mohavensis
S. mollis
S. musicus
S. parryii
S. perotensis
S. pygmaeus
S. relictus
S. richardsonii
S. saturatus
S. spilosoma
S. suslicus
S. tereticaudus
S. townsendii
S. tridecemlineatus
S. undulatus
S. variegatus
S. washingtoni
S. xanthoprymnus
Sundasciurus [Genus]
S. brookei [Species]
S. davensis
S. fraterculus
S. hippurus
S. hoogstraali
S. jentinki
S. juvencus
S. lowii
S. mindanensis
S. moellendorffi
S. philippinensis
S. rabori
S. samarensis
S. steerii
S. tenuis
Syntheosciurus [Genus]
S. brochus [Species]
Tamias [Genus]
T. alpinus [Species]
T. amoenus
T. bulleri
T. canipes
T. cinereicollis
T. dorsalis
T. durangae
T. merriami
T. minimus
T. obscurus
T. ochrogenys
T. palmeri
T. panamintinus
T. quadrimaculatus
T. quadrivittatus
T. ruficaudus
T. rufus
T. senex
T. sibiricus
T. siskiyou
T. sonomae
T. speciosus
T. striatus
T. townsendii
T. umbrinus
Tamiasciurus [Genus]
T. douglasii [Species]
T. hudsonicus
T. mearnsi
Tamiops [Genus]
T. macclellandi [Species]
T. maritimus
T. rodolphei
T. swinhoei
Trogopterus [Genus]

- *T. xanthipes* [Species]
- *Xerus* [Genus]
  - *X. erythropus* [Species]
  - *X. inauris*
  - *X. princeps*
  - *X. rutilus*

Castoridae [Family]
- *Castor* [Genus]
  - *C. canadensis* [Species]
  - *C. fiber*

Geomyidae [Family]
- *Geomys* [Genus]
  - *G. arenarius* [Species]
  - *G. bursarius*
  - *G. personatus*
  - *G. pinetis*
  - *G. tropicalis*
- *Orthogeomys* [Genus]
  - *O. cavator* [Species]
  - *O. cherriei*
  - *O. cuniculus*
  - *O. dariensis*
  - *O. grandis*
  - *O. heterodus*
  - *O. hispidus*
  - *O. lanius*
  - *O. matagalpae*
  - *O. thaeleri*
  - *O. underwoodi*
- *Pappogeomys* [Genus]
  - *P. alcorni* [Species]
  - *P. bulleri*
  - *P. castanops*
  - *P. fumosus*
  - *P. gymnurus*
  - *P. merriami*
  - *P. neglectus*
  - *P. tylorhinus*
  - *P. zinseri*
- *Thomomys* [Genus]
  - *T. bottae* [Species]
  - *T. bulbivorus*
  - *T. clusius*
  - *T. idahoensis*
  - *T. mazama*
  - *T. monticola*
  - *T. talpoides*
  - *T. townsendii*
  - *T. umbrinus*
- *Zygogeomys* [Genus]
  - *Z. trichopus* [Species]

Heteromyidae [Family]
- *Chaetodipus* [Genus]
  - *C. arenarius* [Species]
  - *C. artus*
  - *C. baileyi*
  - *C. californicus*
  - *C. fallax*
  - *C. formosus*
  - *C. goldmani*
  - *C. hispidus*
  - *C. intermedius*
  - *C. lineatus*
  - *C. nelsoni*
  - *C. penicillatus*
  - *C. pernix*
  - *C. spinatus*
- *Dipodomys* [Genus]
  - *D. agilis* [Species]
  - *D. californicus*
  - *D. compactus*
  - *D. deserti*
  - *D. elator*
  - *D. elephantinus*
  - *D. gravipes*
  - *D. heermanni*
  - *D. ingens*
  - *D. insularis*
  - *D. margaritae*
  - *D. merriami*
  - *D. microps*
  - *D. nelsoni*
  - *D. nitratoides*
  - *D. ordii*
  - *D. panamintinus*
  - *D. phillipsii*
  - *D. spectabilis*
  - *D. stephensi*
  - *D. venustus*
- *Microdipodops* [Genus]
  - *M. megacephalus* [Species]
  - *M. pallidus*
- *Heteromys* [Genus]
  - *H. anomalus* [Species]
  - *H. australis*
  - *H. desmarestianus*
  - *H. gaumeri*
  - *H. goldmani*
  - *H. nelsoni*
  - *H. oresterus*
- *Liomys* [Genus]
  - *L. adspersus* [Species]
  - *L. irroratus*
  - *L. pictus*
  - *L. salvini*
  - *L. spectabilis*
- *Perognathus* [Genus]
  - *P. alticola* [Species]
  - *P. amplus*
  - *P. fasciatus*
  - *P. flavescens*
  - *P. flavus*
  - *P. inornatus*
  - *P. longimembris*
  - *P. merriami*
  - *P. parvus*
  - *P. xanthanotus*

Dipodidae [Family]
- *Allactaga* [Genus]
  - *A. balikunica* [Species]
  - *A. bullata*
  - *A. elater*
  - *A. euphratica*
  - *A. firouzi*
  - *A. hotsoni*
  - *A. major*
  - *A. severtzovi*
  - *A. sibirica*
  - *A. tetradactyla*
  - *A. vinogradovi*
- *Allactodipus* [Genus]
  - *A. bobrinskii* [Species]
- *Cardiocranius* [Genus]
  - *C. paradoxus* [Species]
- *Dipus* [Genus]
  - *D. sagitta* [Species]
- *Eozapus* [Genus]
  - *E. setchuanus* [Species]
- *Eremodipus* [Genus]
  - *E. lichtensteini* [Species]
- *Euchoreutes* [Genus]
  - *E. naso* [Species]
- *Jaculus* [Genus]
  - *J. blanfordi* [Species]
  - *J. jaculus*
  - *J. orientalis*
  - *J. turcmenicus*
- *Napaeozapus* [Genus]
  - *N. insignis* [Species]
- *Paradipus* [Genus]
  - *P. ctenodactylus* [Species]
- *Pygeretmus* [Genus]
  - *P. platyurus* [Species]
  - *P. pumilio*
  - *P. shitkovi*
- *Salpingotus* [Genus]
  - *S. crassicauda* [Species]
  - *S. heptneri*
  - *S. kozlovi*
  - *S. michaelis*
  - *S. pallidus*
  - *S. thomasi*
- *Sicista* [Genus]
  - *S. armenica* [Species]
  - *S. betulina*
  - *S. caucasica*
  - *S. caudata*
  - *S. concolor*
  - *S. kazbegica*
  - *S. kluchorica*
  - *S. napaea*
  - *S. pseudonapaea*
  - *S. severtzovi*
  - *S. strandi*
  - *S. subtilis*
  - *S. tianshanica*
- *Stylodipus* [Genus]

S. andrewsi [Species]
S. sungorus
S. telum
Zapus [Genus]
Z. hudsonius [Species]
Z. princeps
Z. trinotatus

Muridae [Family]
Abditomys [Genus]
A. latidens [Species]
Abrawayaomys [Genus]
A. ruschii [Species]
Acomys [Genus]
A. cahirinus [Species]
A. cilicicus
A. cinerasceus
A. ignitus
A. kempi
A. louisae
A. minous
A. mullah
A. nesiotes
A. percivali
A. russatus
A. spinosissimus
A. subspinosus
A. wilsoni
Aepeomys [Genus]
A. fuscatus [Species]
A. lugens
Aethomys [Genus]
A. bocagei [Species]
A. chrysophilus
A. granti
A. hindei
A. kaiseri
A. namaquensis
A. nyikae
A. silindensis
A. stannarius
A. thomasi
Akodon [Genus]
A. aerosus [Species]
A. affinis
A. albiventer
A. azarae
A. bogotensis
A. boliviensis
A. budini
A. cursor
A. dayi
A. dolores
A. fumeus
A. hershkovitzi
A. illuteus
A. iniscatus
A. juninensis
A. kempi
A. kofordi
A. lanosus
A. latebricola
A. lindberghi
A. longipilis
A. mansoensis
A. markhami
A. mimus
A. molinae
A. mollis
A. neocenus
A. nigrita
A. olivaceus
A. orophilus
A. puer
A. sanborni
A. sanctipaulensis
A. serrensis
A. siberiae
A. simulator
A. spegazzinii
A. subfuscus
A. surdus
A. sylvanus
A. toba
A. torques
A. urichi
A. varius
A. xanthorhinus
Allocricetulus [Genus]
A. curtatus [Species]
A. eversmanni
Alticola [Genus]
A. albicauda [Species]
A. argentatus
A. barakshin
A. lemminus
A. macrotis
A. montosa
A. roylei
A. semicanus
A. stoliczkanus
A. stracheyi
A. strelzowi
A. tuvinicus
Ammodillus [Genus]
A. imbellis [Species]
Andalgalomys [Genus]
A. olrogi [Species]
A. pearsoni
Andinomys [Genus]
A. edax [Species]
Anisomys [Genus]
A. imitator [Species]
Anonymomys [Genus]
A. mindorensis [Species]
Anotomys [Genus]
A. leander [Species]
Apodemus [Genus]
A. agrarius [Species]
A. alpicola
A. argenteus
A. arianus
A. chevrieri
A. draco
A. flavicollis
A. fulvipectus
A. gurkha
A. hermonensis
A. hyrcanicus
A. latronum
A. mystacinus
A. peninsulae
A. ponticus
A. rusiges
A. semotus
A. speciosus
A. sylvaticus
A. uralensis
A. wardi
Apomys [Genus]
A. abrae [Species]
A. datae
A. hylocoetes
A. insignis
A. littoralis
A. microdon
A. musculus
A. sacobianus
Arborimus [Genus]
A. albipes [Species]
A. longicaudus
A. pomo
Archboldomys [Genus]
A. luzonensis [Species]
Arvicanthis [Genus]
A. abyssinicus [Species]
A. blicki
A. nairobae
A. niloticus
A. somalicus
Arvicola [Genus]
A. sapidus [Species]
A. terrestris
Auliscomys [Genus]
A. boliviensis [Species]
A. micropus
A. pictus
A. sublimis
Baiomys [Genus]
B. musculus [Species]
B. taylori
Bandicota [Genus]
B. bengalensis [Species]
B. indica
B. savilei
Batomys [Genus]
B. dentatus [Species]
B. granti
B. salomonseni
Beamys [Genus]
B. hindei [Species]

B. major
Berylmys [Genus]
B. berdmorei [Species]
B. bowersi
B. mackenziei
B. manipulus
Bibimys [Genus]
B. chacoensis [Species]
B. labiosus
B. torresi
Blanfordimys [Genus]
B. afghanus [Species]
B. bucharicus
Blarinomys [Genus]
B. breviceps [Species]
Bolomys [Genus]
B. amoenus [Species]
B. lactens
B. lasiurus
B. obscurus
B. punctulatus
B. temchuki
Brachiones [Genus]
B. przewalskii [Species]
Brachytarsomys [Genus]
B. albicauda [Species]
Brachyuromys [Genus]
B. betsileoensis [Species]
B. ramirohitra
Bullimus [Genus]
B. bagobus [Species]
B. luzonicus
Bunomys [Genus]
B. andrewsi [Species]
B. chrysocomus
B. coelestis
B. fratrorum
B. heinrichi
B. penitus
B. prolatus
Calomys [Genus]
C. boliviae [Species]
C. callidus
C. callosus
C. hummelincki
C. laucha
C. lepidus
C. musculinus
C. sorellus
C. tener
Calomyscus [Genus]
C. bailwardi [Species]
C. baluchi
C. hotsoni
C. mystax
C. tsolovi
C. urartensis
Canariomys [Genus]
C. tamarani [Species]
Cannomys [Genus]
C. badius [Species]
Cansumys [Genus]
C. canus [Species]
Carpomys [Genus]
C. melanurus [Species]
C. phaeurus
Celaenomys [Genus]
C. silaceus [Species]
Chelemys [Genus]
C. macronyx [Species]
C. megalonyx
Chibchanomys [Genus]
C. trichotis [Species]
Chilomys [Genus]
C. instans [Species]
Chiromyscus [Genus]
C. chiropus [Species]
Chinchillula [Genus]
C. sahamae [Species]
Chionomys [Genus]
C. gud [Species]
C. nivalis
C. roberti
Chiropodomys [Genus]
C. calamianensis [Species]
C. gliroides
C. karlkoopmani
C. major
C. muroides
C. pusillus
Chiruromys [Genus]
C. forbesi [Species]
C. lamia
C. vates
Chroeomys [Genus]
C. andinus [Species]
C. jelskii
Chrotomys [Genus]
C. gonzalesi [Species]
C. mindorensis
C. whiteheadi
Clethrionomys [Genus]
C. californicus [Species]
C. centralis
C. gapperi
C. glareolus
C. rufocanus
C. rutilus
C. sikotanensis
Coccymys [Genus]
C. albidens [Species]
C. ruemmleri
Colomys [Genus]
C. goslingi [Species]
Conilurus [Genus]
C. albipes [Species]
C. penicillatus
Coryphomys [Genus]
C. buhleri [Species]
Crateromys [Genus]
C. australis [Species]
C. paulus
C. schadenbergi
Cremnomys [Genus]
C. blanfordi [Species]
C. cutchicus
C. elvira
Cricetomys [Genus]
C. emini [Species]
C. gambianus
Cricetulus [Genus]
C. alticola [Species]
C. barabensis
C. kamensis
C. longicaudatus
C. migratorius
C. sokolovi
Cricetus [Genus]
C. cricetus [Species]
Crossomys [Genus]
C. moncktoni [Species]
Crunomys [Genus]
C. celebensis [Species]
C. fallax
C. melanius
C. rabori
Dacnomys [Genus]
D. millardi [Species]
Dasymys [Genus]
D. foxi [Species]
D. incomtus
D. montanus
D. nudipes
D. rufulus
Delanymys [Genus]
D. brooksi [Species]
Delomys [Genus]
D. dorsalis [Species]
D. sublineatus
Dendromus [Genus]
D. insignis [Species]
D. kahuziensis
D. kivu
D. lovati
D. melanotis
D. mesomelas
D. messorius
D. mystacalis
D. nyikae
D. oreas
D. vernayi
Dendroprionomys [Genus]
D. rousseloti [Species]
Deomys [Genus]
D. ferrugineus [Species]
Dephomys [Genus]
D. defua [Species]
D. eburnea
Desmodilliscus [Genus]
D. braueri [Species]

Desmodillus [Genus]
D. auricularis [Species]
Dicrostonyx [Genus]
D. exsul [Species]
D. groenlandicus
D. hudsonius
D. kilangmiutak
D. nelsoni
D. nunatakensis
D. richardsoni
D. rubricatus
D. torquatus
D. unalascensis
D. vinogradovi
Desmomys [Genus]
D. harringtoni [Species]
Dinaromys [Genus]
D. bogdanovi [Species]
Diomys [Genus]
D. crumpi [Species]
Diplothrix [Genus]
D. legatus [Species]
Echiothrix [Genus]
E. leucura [Species]
Eropeplus [Genus]
E. canus [Species]
Eligmodontia [Genus]
E. moreni [Species]
E. morgani
E. puerulus
E. typus
Eliurus [Genus]
E. majori [Species]
E. minor
E. myoxinus
E. penicillatus
E. tanala
E. webbi
Ellobius [Genus]
E. alaicus [Species]
E. fuscocapillus
E. lutescens
E. talpinus
E. tancrei
Eolagurus [Genus]
E. luteus [Species]
E. przewalskii
Eothenomys [Genus]
E. chinensis [Species]
E. custos
E. eva
E. inez
E. melanogaster
E. olitor
E. proditor
E. regulus
E. shanseius
Euneomys [Genus]
E. chinchilloides [Species]
E. fossor
E. mordax
E. petersoni
Galenomys [Genus]
G. garleppi [Species]
Geoxus [Genus]
G. valdivianus [Species]
Gerbillurus [Genus]
G. paeba [Species]
G. setzeri
G. tytonis
G. vallinus
Gerbillus [Genus]
G. acticola [Species]
G. allenbyi
G. andersoni
G. bilensis
G. bottai
G. burtoni
G. cheesmani
G. dalloni
G. diminutus
G. dunni
G. floweri
G. gerbillus
G. grobbeni
G. henleyi
G. hoogstraali
G. juliani
G. lowei
G. maghrebi
G. mesopotamiae
G. nancillus
G. nigeriae
G. percivali
G. poecilops
G. pulvinatus
G. pyramidum
G. riggenbachi
G. ruberrimus
G. somalicus
G. syrticus
G. vivax
Golunda [Genus]
G. ellioti [Species]
Grammomys [Genus]
G. aridulus [Species]
G. caniceps
G. dolichurus
G. gigas
G. macmillani
G. rutilans
Graomys [Genus]
G. domorum [Species]
G. griseoflavus
Gymnuromys [Genus]
G. roberti [Species]
Habromys [Genus]
H. chinanteco [Species]
H. lepturus
H. lophurus
H. simulatus
Hadromys [Genus]
H. humei [Species]
Haeromys [Genus]
H. margarettae [Species]
H. minahassae
H. pusillus
Hapalomys [Genus]
H. delacouri [Species]
H. longicaudatus
Heimyscus [Genus]
H. fumosus [Species]
Hodomys [Genus]
H. alleni [Species]
Holochilus [Genus]
H. brasiliensis [Species]
H. chacarius
H. magnus
H. sciureus
Hybomys [Genus]
H. basilii [Species]
H. eisentrauti
H. lunaris
H. planifrons
H. trivirgatus
H. univittatus
Hydromys [Genus]
H. chrysogaster [Species]
H. habbema
H. hussoni
H. neobrittanicus
H. shawmayeri
Hylomyscus [Genus]
H. aeta [Species]
H. alleni
H. baeri
H. carillus
H. denniae
H. parvus
H. stella
Hyomys [Genus]
H. dammermani [Species]
H. goliath
Hyperacrius [Genus]
H. fertilis [Species]
H. wynnei
Hypogeomys [Genus]
H. antimena [Species]
Ichthyomys [Genus]
I. hydrobates [Species]
I. pittieri
I. stolzmanni
I. tweedii
Irenomys [Genus]
I. tarsalis [Species]
Isthmomys [Genus]
I. flavidus [Species]
I. pirrensis
Juscelinomys [Genus]
J. candango [Species]

J. vulpinus
Kadarsanomys [Genus]
K. sodyi [Species]
Komodomys [Genus]
K. rintjanus [Species]
Kunsia [Genus]
K. fronto [Species]
K. tomentosus
Lagurus [Genus]
L. lagurus [Species]
Lamottemys [Genus]
L. okuensis [Species]
Lasiopodomys [Genus]
L. brandtii [Species]
L. fuscus
L. mandarinus
Leggadina [Genus]
L. forresti [Species]
L. lakedownensis
Leimacomys [Genus]
L. buettneri [Species]
Lemmiscus [Genus]
L. curtatus [Species]
Lemmus [Genus]
L. amurensis [Species]
L. lemmus
L. sibiricus
Lemniscomys [Genus]
L. barbarus [Species]
L. bellieri
L. griselda
L. hoogstraali
L. linulus
L. macculus
L. mittendorfi
L. rosalia
L. roseveari
L. striatus
Lenomys [Genus]
L. meyeri [Species]
Lenothrix [Genus]
L. canus [Species]
Lenoxus [Genus]
L. apicalis [Species]
Leopoldamys [Genus]
L. edwardsi [Species]
L. neilli
L. sabanus
L. siporanus
Leporillus [Genus]
L. apicalis [Species]
L. conditor
Leptomys [Genus]
L. elegans [Species]
L. ernstmayri
L. signatus
Limnomys [Genus]
L. sibuanus [Species]
Lophiomys [Genus]
L. imhausi [Species]
Lophuromys [Genus]
L. cinereus [Species]
L. flavopunctatus
L. luteogaster
L. medicaudatus
L. melanonyx
L. nudicaudus
L. rahmi
L. sikapusi
L. woosnami
Lorentzimys [Genus]
L. nouhuysi [Species]
Macrotarsomys [Genus]
M. bastardi [Species]
M. ingens
Macruromys [Genus]
M. elegans [Species]
M. major
Malacomys [Genus]
M. cansdalei [Species]
M. edwardsi
M. longipes
M. lukolelae
M. verschureni
Malacothrix [Genus]
M. typica [Species]
Mallomys [Genus]
M. aroaensis [Species]
M. gunung
M. istapantap
M. rothschildi
Malpaisomys [Genus]
M. insularis [Species]
Margaretamys [Genus]
M. beccarii [Species]
M. elegans
M. parvus
Mastomys [Genus]
M. angolensis [Species]
M. coucha
M. erythroleucus
M. hildebrandtii
M. natalensis
M. pernanus
M. shortridgei
M. verheyeni
Maxomys [Genus]
M. alticola [Species]
M. baeodon
M. bartelsii
M. dollmani
M. hellwaldii
M. hylomyoides
M. inas
M. inflatus
M. moi
M. musschenbroekii
M. ochraceiventer
M. pagensis
M. panglima
M. rajah
M. surifer
M. wattsi
M. whiteheadi
Mayermys [Genus]
M. ellermani [Species]
Megadendromus [Genus]
M. nikolausi [Species]
Megadontomys [Genus]
M. cryophilus [Species]
M. nelsoni
M. thomasi
Megalomys [Genus]
M. desmarestii [Species]
M. luciae
Melanomys [Genus]
M. caliginosus [Species]
M. robustulus
M. zunigae
Melasmothrix [Genus]
M. naso [Species]
Melomys [Genus]
M. aerosus [Species]
M. bougainville
M. burtoni
M. capensis
M. cervinipes
M. fellowsi
M. fraterculus
M. gracilis
M. lanosus
M. leucogaster
M. levipes
M. lorentzii
M. mollis
M. moncktoni
M. obiensis
M. platyops
M. rattoides
M. rubex
M. rubicola
M. rufescens
M. specht
Meriones [Genus]
M. arimalius [Species]
M. chengi
M. crassus
M. dahli
M. hurrianae
M. libycus
M. meridianus
M. persicus
M. rex
M. sacramenti
M. shawi
M. tamariscinus
M. tristrami
M. unguiculatus
M. vinogradovi
M. zarudnyi

Mesembriomys [Genus]
M. gouldii [Species]
M. macrurus
Mesocricetus [Genus]
M. auratus [Species]
M. brandti
M. newtoni
M. raddei
Microdillus [Genus]
M. peeli [Species]
Microhydromys [Genus]
M. musseri [Species]
M. richardsoni
Micromys [Genus]
M. minutus [Species]
Microryzomys [Genus]
M. altissimus [Species]
M. minutus
Microtus [Genus]
M. abbreviatus [Species]
M. agrestis
M. arvalis
M. bavaricus
M. breweri
M. cabrerae
M. californicus
M. canicaudus
M. chrotorrhinus
M. daghestanicus
M. duodecimcostatus
M. evoronensis
M. felteni
M. fortis
M. gerbei
M. gregalis
M. guatemalensis
M. guentheri
M. hyperboreus
M. irani
M. irene
M. juldaschi
M. kermanensis
M. kirgisorum
M. leucurus
M. limnophilus
M. longicaudus
M. lusitanicus
M. majori
M. maximowiczii
M. mexicanus
M. middendorffi
M. miurus
M. mongolicus
M. montanus
M. montebelli
M. mujanensis
M. multiplex
M. nasarovi
M. oaxacensis
M. obscurus
M. ochrogaster
M. oeconomus
M. oregoni
M. pennsylvanicus
M. pinetorum
M. quasiater
M. richardsoni
M. rossiaemeridionalis
M. sachalinensis
M. savii
M. schelkovnikovi
M. sikimensis
M. socialis
M. subterraneus
M. tatricus
M. thomasi
M. townsendii
M. transcaspicus
M. umbrosus
M. xanthognathus
Millardia [Genus]
M. gleadowi [Species]
M. kathleenae
M. kondana
M. meltada
Muriculus [Genus]
M. imberbis [Species]
Mus [Genus]
M. baoulei [Species]
M. booduga
M. bufo
M. callewaerti
M. caroli
M. cervicolor
M. cookii
M. crociduroides
M. famulus
M. fernandoni
M. goundae
M. haussa
M. indutus
M. kasaicus
M. macedonicus
M. mahomet
M. mattheyi
M. mayori
M. minutoides
M. musculoides
M. musculus
M. neavei
M. orangiae
M. oubanguii
M. pahari
M. phillipsi
M. platythrix
M. saxicola
M. setulosus
M. setzeri
M. shortridgei
M. sorella
M. spicilegus
M. spretus
M. tenellus
M. terricolor
M. triton
M. vulcani
Mylomys [Genus]
M. dybowskii [Species]
Myomys [Genus]
M. albipes [Species]
M. daltoni
M. derooi
M. fumatus
M. ruppi
M. verreauxii
M. yemeni
Myopus [Genus]
M. schisticolor [Species]
Myospalax [Genus]
M. aspalax [Species]
M. epsilanus
M. fontanierii
M. myospalax
M. psilurus
M. rothschildi
M. smithii
Mystromys [Genus]
M. albicaudatus [Species]
Nannospalax [Genus]
N. ehrenbergi [Species]
N. leucodon
N. nehringi
Neacomys [Genus]
N. guianae [Species]
N. pictus
N. spinosus
N. tenuipes
Nectomys [Genus]
N. palmipes [Species]
N. parvipes
N. squamipes
Nelsonia [Genus]
N. goldmani [Species]
N. neotomodon
Neofiber [Genus]
N. alleni [Species]
Neohydromys [Genus]
N. fuscus [Species]
Neotoma [Genus]
N. albigula [Species]
N. angustapalata
N. anthonyi
N. bryanti
N. bunkeri
N. chrysomelas
N. cinerea
N. devia
N. floridana
N. fuscipes
N. goldmani

N. lepida
N. martinensis
N. mexicana
N. micropus
N. nelsoni
N. palatina
N. phenax
N. stephensi
N. varia
Neotomodon [Genus]
N. alstoni [Species]
Neotomys [Genus]
N. ebriosus [Species]
Nesomys [Genus]
N. rufus [Species]
Nesokia [Genus]
N. bunnii [Species]
N. indica
Nesoryzomys [Genus]
N. darwini [Species]
N. fernandinae
N. indefessus
N. swarthi
Neusticomys [Genus]
N. monticolus [Species]
N. mussoi
N. oyapocki
N. peruviensis
N. venezuelae
Niviventer [Genus]
N. andersoni [Species]
N. brahma
N. confucianus
N. coxingi
N. cremoriventer
N. culturatus
N. eha
N. excelsior
N. fulvescens
N. hinpoon
N. langbianis
N. lepturus
N. niviventer
N. rapit
N. tenaster
Notiomys [Genus]
N. edwardsii [Species]
Notomys [Genus]
N. alexis [Species]
N. amplus
N. aquilo
N. cervinus
N. fuscus
N. longicaudatus
N. macrotis
N. mitchellii
N. mordax
Nyctomys [Genus]
N. sumichrasti [Species]
Ochrotomys [Genus]
O. nuttalli [Species]
Oecomys [Genus]
O. bicolor [Species]
O. cleberi
O. concolor
O. flavicans
O. mamorae
O. paricola
O. phaeotis
O. rex
O. roberti
O. rutilus
O. speciosus
O. superans
O. trinitatis
Oenomys [Genus]
O. hypoxanthus [Species]
O. ornatus
Oligoryzomys [Genus]
O. andinus [Species]
O. arenalis
O. chacoensis
O. delticola
O. destructor
O. eliurus
O. flavescens
O. fulvescens
O. griseolus
O. longicaudatus
O. magellanicus
O. microtis
O. nigripes
O. vegetus
O. victus
Ondatra [Genus]
O. zibethicus [Species]
Onychomys [Genus]
O. arenicola [Species]
O. leucogaster
O. torridus
Oryzomys [Genus]
O. albigularis [Species]
O. alfaroi
O. auriventer
O. balneator
O. bolivaris
O. buccinatus
O. capito
O. chapmani
O. couesi
O. devius
O. dimidiatus
O. galapagoensis
O. gorgasi
O. hammondi
O. intectus
O. intermedius
O. keaysi
O. kelloggi
O. lamia
O. legatus
O. levipes
O. macconnelli
O. melanotis
O. nelsoni
O. nitidus
O. oniscus
O. palustris
O. polius
O. ratticeps
O. rhabdops
O. rostratus
O. saturatior
O. subflavus
O. talamancae
O. xantheolus
O. yunganus
Osgoodomys [Genus]
O. banderanus [Species]
Otomys [Genus]
O. anchietae [Species]
O. angoniensis
O. denti
O. irroratus
O. laminatus
O. maximus
O. occidentalis
O. saundersiae
O. sloggetti
O. tropicalis
O. typus
O. unisulcatus
Otonyctomys [Genus]
O. hatti [Species]
Ototylomys [Genus]
O. phyllotis [Species]
Oxymycterus [Genus]
O. akodontius [Species]
O. angularis
O. delator
O. hiska
O. hispidus
O. hucucha
O. iheringi
O. inca
O. nasutus
O. paramensis
O. roberti
O. rufus
Pachyuromys [Genus]
P. duprasi [Species]
Palawanomys [Genus]
P. furvus [Species]
Papagomys [Genus]
P. armandvillei [Species]
P. theodorverhoeveni
Parahydromys [Genus]
P. asper [Species]
Paraleptomys [Genus]
P. rufilatus [Species]

P. wilhelmina
Parotomys [Genus]
P. brantsii [Species]
P. littledalei
Paruromys [Genus]
P. dominator [Species]
P. ursinus
Paulamys [Genus]
P. naso [Species]
Pelomys [Genus]
P. campanae [Species]
P. fallax
P. hopkinsi
P. isseli
P. minor
Peromyscus [Genus]
P. attwateri [Species]
P. aztecus
P. boylii
P. bullatus
P. californicus
P. caniceps
P. crinitus
P. dickeyi
P. difficilis
P. eremicus
P. eva
P. furvus
P. gossypinus
P. grandis
P. gratus
P. guardia
P. guatemalensis
P. gymnotis
P. hooperi
P. interparietalis
P. leucopus
P. levipes
P. madrensis
P. maniculatus
P. mayensis
P. megalops
P. mekisturus
P. melanocarpus
P. melanophrys
P. melanotis
P. melanurus
P. merriami
P. mexicanus
P. nasutus
P. ochraventer
P. oreas
P. pectoralis
P. pembertoni
P. perfulvus
P. polionotus
P. polius
P. pseudocrinitus
P. sejugis
P. simulus
P. sitkensis
P. slevini
P. spicilegus
P. stephani
P. stirtoni
P. truei
P. winkelmanni
P. yucatanicus
P. zarhynchus
Petromyscus [Genus]
P. barbouri [Species]
P. collinus
P. monticularis
P. shortridgei
Phaenomys [Genus]
P. ferrugineus [Species]
Phaulomys [Genus]
P. andersoni [Species]
P. smithii
Phenacomys [Genus]
P. intermedius [Species]
P. ungava
Phloeomys [Genus]
P. cumingi [Species]
P. pallidus
Phyllotis [Genus]
P. amicus [Species]
P. andium
P. bonaeriensis
P. caprinus
P. darwini
P. definitus
P. gerbillus
P. haggardi
P. magister
P. osgoodi
P. osilae
P. wolffsohni
P. xanthopygus
Pithecheir [Genus]
P. melanurus [Species]
P. parvus
Phodopus [Genus]
P. campbelli [Species]
P. roborovskii
P. sungorus
Platacanthomys [Genus]
P. lasiurus [Species]
Podomys [Genus]
P. floridanus [Species]
Podoxymys [Genus]
P. roraimae [Species]
Pogonomelomys [Genus]
P. bruijni [Species]
P. mayeri
P. sevia
Pogonomys [Genus]
P. championi [Species]
P. loriae
P. macrourus
P. sylvestris
Praomys [Genus]
P. delectorum [Species]
P. hartwigi
P. jacksoni
P. minor
P. misonnei
P. morio
P. mutoni
P. rostratus
P. tullbergi
Prionomys [Genus]
P. batesi [Species]
Proedromys [Genus]
P. bedfordi [Species]
Prometheomys [Genus]
P. schaposchnikowi [Species]
Psammomys [Genus]
P. obesus [Species]
P. vexillaris
Pseudohydromys [Genus]
P. murinus [Species]
P. occidentalis
Pseudomys [Genus]
P. albocinereus [Species]
P. apodemoides
P. australis
P. bolami
P. chapmani
P. delicatulus
P. desertor
P. fieldi
P. fumeus
P. fuscus
P. glaucus
P. gouldii
P. gracilicaudatus
P. hermannsburgensis
P. higginsi
P. johnsoni
P. laborifex
P. nanus
P. novaehollandiae
P. occidentalis
P. oralis
P. patrius
P. pilligaensis
P. praeconis
P. shortridgei
Pseudoryzomys [Genus]
P. simplex [Species]
Punomys [Genus]
P. lemminus [Species]
Rattus [Genus]
R. adustus [Species]
R. annandalei
R. argentiventer
R. baluensis
R. bontanus
R. burrus

R. colletti
R. elaphinus
R. enganus
R. everetti
R. exulans
R. feliceus
R. foramineus
R. fuscipes
R. giluwensis
R. hainaldi
R. hoffmanni
R. hoogerwerfi
R. jobiensis
R. koopmani
R. korinchi
R. leucopus
R. losea
R. lugens
R. lutreolus
R. macleari
R. marmosurus
R. mindorensis
R. mollicomulus
R. montanus
R. mordax
R. morotaiensis
R. nativitatis
R. nitidus
R. norvegicus
R. novaeguineae
R. osgoodi
R. palmarum
R. pelurus
R. praetor
R. ranjiniae
R. rattus
R. sanila
R. sikkimensis
R. simalurensis
R. sordidus
R. steini
R. stoicus
R. tanezumi
R. tawitawiensis
R. timorensis
R. tiomanicus
R. tunneyi
R. turkestanicus
R. villosissimus
R. xanthurus
Reithrodon [Genus]
R. auritus [Species]
Reithrodontomys [Genus]
R. brevirostris [Species]
R. burti
R. chrysopsis
R. creper
R. darienensis
R. fulvescens
R. gracilis
R. hirsutus
R. humulis
R. megalotis
R. mexicanus
R. microdon
R. montanus
R. paradoxus
R. raviventris
R. rodriguezi
R. spectabilis
R. sumichrasti
R. tenuirostris
R. zacatecae
Rhabdomys [Genus]
R. pumilio [Species]
Rhagomys [Genus]
R. rufescens [Species]
Rheomys [Genus]
R. mexicanus [Species]
R. raptor
R. thomasi
R. underwoodi
Rhipidomys [Genus]
R. austrinus [Species]
R. caucensis
R. couesi
R. fulviventer
R. latimanus
R. leucodactylus
R. macconnelli
R. mastacalis
R. nitela
R. ochrogaster
R. scandens
R. venezuelae
R. venustus
R. wetzeli
Rhizomys [Genus]
R. pruinosus [Species]
R. sinensis
R. sumatrensis
Rhombomys [Genus]
R. opimus [Species]
Rhynchomys [Genus]
R. isarogensis [Species]
R. soricoides
Saccostomus [Genus]
S. campestris [Species]
S. mearnsi
Scapteromys [Genus]
S. tumidus [Species]
Scolomys [Genus]
S. melanops [Species]
S. ucayalensis
Scotinomys [Genus]
S. teguina [Species]
S. xerampelinus
Sekeetamys [Genus]
S. calurus [Species]
Sigmodon [Genus]
S. alleni [Species]
S. alstoni
S. arizonae
S. fulviventer
S. hispidus
S. inopinatus
S. leucotis
S. mascotensis
S. ochrognathus
Sigmodontomys [Genus]
S. alfari [Species]
S. aphrastus
Solomys [Genus]
S. ponceleti [Species]
S. salamonis
S. salebrosus
S. sapientis
S. spriggsarum
Spalax [Genus]
S. arenarius [Species]
S. giganteus
S. graecus
S. microphthalmus
S. zemni
Spelaeomys [Genus]
S. florensis [Species]
Srilankamys [Genus]
S. ohiensis [Species]
Stenocephalemys [Genus]
S. albocaudata [Species]
S. griseicauda
Steatomys [Genus]
S. caurinus [Species]
S. cuppedius
S. jacksoni
S. krebsii
S. parvus
S. pratensis
Stenomys [Genus]
S. ceramicus [Species]
S. niobe
S. richardsoni
S. vandeuseni
S. verecundus
Stochomys [Genus]
S. longicaudatus [Species]
Sundamys [Genus]
S. infraluteus [Species]
S. maxi
S. muelleri
Synaptomys [Genus]
S. borealis [Species]
S. cooperi
Tachyoryctes [Genus]
T. ankoliae [Species]
T. annectens
T. audax
T. daemon
T. macrocephalus
T. naivashae

T. rex
T. ruandae
T. ruddi
T. spalacinus
T. splendens
Taeromys [Genus]
T. arcuatus [Species]
T. callitrichus
T. celebensis
T. hamatus
T. punicans
T. taerae
Tarsomys [Genus]
T. apoensis [Species]
T. echinatus
Tateomys [Genus]
T. macrocercus [Species]
T. rhinogradoides
Tatera [Genus]
T. afra [Species]
T. boehmi
T. brantsii
T. guineae
T. inclusa
T. indica
T. kempi
T. leucogaster
T. nigricauda
T. phillipsi
T. robusta
T. valida
Taterillus [Genus]
T. arenarius [Species]
T. congicus
T. emini
T. gracilis
T. harringtoni
T. lacustris
T. petteri
T. pygargus
Tscherskia [Genus]
T. triton [Species]
Thallomys [Genus]
T. loringi [Species]
T. nigricauda
T. paedulcus
T. shortridgei
Thalpomys [Genus]
T. cerradensis [Species]
T. lasiotis
Thamnomys [Genus]
T. kempi [Species]
T. venustus
Thomasomys [Genus]
T. aureus [Species]
T. baeops
T. bombycinus
T. cinereiventer
T. cinereus
T. daphne
T. eleusis
T. gracilis
T. hylophilus
T. incanus
T. ischyurus
T. kalinowskii
T. ladewi
T. laniger
T. monochromos
T. niveipes
T. notatus
T. oreas
T. paramorum
T. pyrrhonotus
T. rhoadsi
T. rosalinda
T. silvestris
T. taczanowskii
T. vestitus
Tokudaia [Genus]
T. muenninki [Species]
T. osimensis
Tryphomys [Genus]
T. adustus [Species]
Tylomys [Genus]
T. bullaris [Species]
T. fulviventer
T. mirae
T. nudicaudus
T. panamensis
T. tumbalensis
T. watsoni
Typhlomys [Genus]
T. chapensis [Species]
T. cinereus
Uranomys [Genus]
U. ruddi [Species]
Uromys [Genus]
U. anak [Species]
U. caudimaculatus
U. hadrourus
U. imperator
U. neobritanicus
U. porculus
U. rex
Vandeleuria [Genus]
V. nolthenii [Species]
V. oleracea
Vernaya [Genus]
V. fulva [Species]
Volemys [Genus]
V. clarkei [Species]
V. kikuchii
V. millicens
V. musseri
Wiedomys [Genus]
W. pyrrhorhinos [Species]
Wilfredomys [Genus]
W. oenax [Species]
W. pictipes
Xenomys [Genus]
X. nelsoni [Species]
Xenuromys [Genus]
X. barbatus [Species]
Xeromys [Genus]
X. myoides [Species]
Zelotomys [Genus]
Z. hildegardeae [Species]
Z. woosnami
Zygodontomys [Genus]
Z. brevicauda [Species]
Z. brunneus
Zyzomys [Genus]
Z. argurus [Species]
Z. maini
Z. palatilis
Z. pedunculatus
Z. woodwardi

Anomaluridae [Family]
Anomalurus [Genus]
A. beecrofti [Species]
A. derbianus
A. pelii
A. pusillus
Idiurus [Genus]
I. macrotis [Species]
I. zenkeri
Zenkerella [Genus]
Z. insignis [Species]

Pedetidae [Family]
Pedetes [Genus]
P. capensis [Species]

Ctenodactylidae [Family]
Ctenodactylus [Genus]
C. gundi [Species]
C. vali
Felovia [Genus]
F. vae [Species]
Massoutiera [Genus]
M. mzabi [Species]
Pectinator [Genus]
P. spekei [Species]

Myoxidae [Family]
Dryomys [Genus]
D. laniger [Species]
D. nitedula
D. sichuanensis
Eliomys [Genus]
E. melanurus [Species]
E. quercinus
Glirulus [Genus]
G. japonicus [Species]
Graphiurus [Genus]
G. christyi [Species]
G. hueti
G. lorraineus
G. monardi
G. ocularis

G. parvus
G. rupicola
Muscardinus [Genus]
M. avellanarius [Species]
Myomimus [Genus]
M. personatus [Species]
M. roachi
M. setzeri
Myoxus [Genus]
M. glis [Species]
Selevinia [Genus]
S. betpakdalaensis [Species]

Petromuridae [Family]
Petromus [Genus]
P. typicus [Species]

Thryonomyidae [Family]
Thryonomys [Genus]
T. gregorianus [Species]
T. swinderianus

Bathyergidae [Family]
Bathyergus [Genus]
B. janetta [Species]
B. suillus
Cryptomys [Genus]
C. bocagei [Species]
C. damarensis
C. foxi
C. hottentotus
C. mechowi
C. ochraceocinereus
C. zechi
Georychus [Genus]
G. capensis [Species]
Heliophobius [Genus]
H. argenteocinereus
Heterocephalus [Genus]
H. glaber [Species]

Hystricidae [Family]
Atherurus [Genus]
A. africanus [Species]
A. macrourus
Hystrix [Genus]
H. africaeaustralis [Species]
H. brachyura
H. crassispinis
H. cristata
H. indica
H. javanica
H. pumila
H. sumatrae
Trichys [Genus]
T. fasciculata [Species]

Erethizontidae [Family]
Coendou [Genus]
C. bicolor [Species]
C. koopmani
C. prehensilis
C. rothschildi
Echinoprocta [Genus]
E. rufescens [Species]
Erethizon [Genus]
E. dorsatum [Species]
Sphiggurus [Genus]
S. insidiosus [Species]
S. mexicanus
S. pallidus
S. spinosus
S. vestitus
S. villosus

Chinchillidae [Family]
Chinchilla [Genus]
C. brevicaudata [Species]
C. lanigera
Lagidium [Genus]
L. peruanum [Species]
L. viscacia
L. wolffsohni
Lagostomus [Genus]
L. maximus [Species]

Dinomyidae [Family]
Dinomys [Genus]
D. branickii [Species]

Caviidae [Family]
Cavia [Genus]
C. aperea [Species]
C. fulgida
C. magna
C. porcellus
C. tschudii
Dolichotis [Genus]
D. patagonum [Species]
D. salinicola
Galea [Genus]
G. flavidens [Species]
G. spixii
Kerodon [Genus]
K. rupestris [Species]
Microcavia [Genus]
M. australis [Species]
M. niata
M. shiptoni

Hydrochaeridae [Family]
Hydrochaeris [Genus]
H. hydrochaeris [Species]

Dasyproctidae [Family]
Dasyprocta [Genus]
D. azarae [Species]
D. coibae
D. cristata
D. fuliginosa
D. guamara
D. kalinowskii
D. leporina
D. mexicana
D. prymnolopha
D. punctata
D. ruatanica
Myoprocta [Genus]
M. acouchy [Species]
M. exilis

Agoutidae [Family]
Agouti [Genus]
A. paca [Species]
A. taczanowskii

Ctenomyidae [Family]
Ctenomys [Genus]
C. argentinus [Species]
C. australis
C. azarae
C. boliviensis
C. bonettoi
C. brasiliensis
C. colburni
C. conoveri
C. dorsalis
C. emilianus
C. frater
C. fulvus
C. haigi
C. knighti
C. latro
C. leucodon
C. lewisi
C. magellanicus
C. maulinus
C. mendocinus
C. minutus
C. nattereri
C. occultus
C. opimus
C. pearsoni
C. perrensis
C. peruanus
C. pontifex
C. porteousi
C. saltarius
C. sericeus
C. sociabilis
C. steinbachi
C. talarum
C. torquatus
C. tuconax
C. tucumanus
C. validus

Octodontidae [Family]
Aconaemys [Genus]
A. fuscus [Species]
A. sagei
Octodon [Genus]
O. bridgesi [Species]
O. degus
O. lunatus

Octodontomys [Genus]
O. gliroides [Species]
Octomys [Genus]
O. mimax [Species]
Spalacopus [Genus]
S. cyanus [Species]
Tympanoctomys [Genus]
T. barrerae [Species]

Abrocomidae [Family]
Abrocoma [Genus]
A. bennetti [Species]
A. boliviensis
A. cinerea

Echimyidae [Family]
Boromys [Genus]
B. offella [Species]
B. torrei
Brotomys [Genus]
B. contractus [Species]
B. voratus
Carterodon [Genus]
C. sulcidens [Species]
Clyomys [Genus]
C. bishopi [Species]
C. laticeps
Chaetomys [Genus]
C. subspinosus [Species]
Dactylomys [Genus]
D. boliviensis [Species]
D. dactylinus
D. peruanus
Diplomys [Genus]
D. caniceps [Species]
D. labilis
D. rufodorsalis
Echimys [Genus]
E. blainvillei [Species]
E. braziliensis
E. chrysurus
E. dasythrix
E. grandis
E. lamarum
E. macrurus
E. nigrispinus
E. pictus
E. rhipidurus
E. saturnus
E. semivillosus
E. thomasi
E. unicolor
Euryzygomatomys [Genus]
E. spinosus [Species]
Heteropsomys [Genus]
H. antillensis [Species]
H. insulans
Hoplomys [Genus]
H. gymnurus [Species]
Isothrix [Genus]
I. bistriata [Species]
I. pagurus
Kannabateomys [Genus]
K. amblyonyx [Species]
Lonchothrix [Genus]
L. emiliae [Species]
Makalata [Genus]
M. armata [Species]
Mesomys [Genus]
M. didelphoides [Species]
M. hispidus
M. leniceps
M. obscurus
M. stimulax
Olallamys [Genus]
O. albicauda [Species]
O. edax
Proechimys [Genus]
P. albispinus [Species]
P. amphichoricus
P. bolivianus
P. brevicauda
P. canicollis
P. cayennensis
P. chrysaeolus
P. cuvieri
P. decumanus
P. dimidiatus
P. goeldii
P. gorgonae
P. guairae
P. gularis
P. hendeei
P. hoplomyoides
P. iheringi
P. longicaudatus
P. magdalenae
P. mincae
P. myosuros
P. oconnelli
P. oris
P. poliopus
P. quadruplicatus
P. semispinosus
P. setosus
P. simonsi
P. steerei
P. trinitatis
P. urichi
P. warreni
Puertoricomys [Genus]
P. corozalus [Species]
Thrichomys [Genus]
T. apereoides [Species]

Capromyidae [Family]
Capromys [Genus]
C. pilorides [Species]
Geocapromys [Genus]
G. brownii [Species]
G. thoracatus
Hexolobodon [Genus]
H. phenax [Species]
Isolobodon [Genus]
I. montanus [Species]
I. portoricensis
Mesocapromys [Genus]
M. angelcabrerai [Species]
M. auritus
M. nanus
M. sanfelipensis
Mysateles [Genus]
M. garridoi [Species]
M. gundlachi
M. melanurus
M. meridionalis
M. prehensilis
Plagiodontia [Genus]
P. aedium [Species]
P. araeum
P. ipnaeum
Rhizoplagiodontia [Genus]
R. lemkei [Species]

Heptaxodontidae [Family]
Amblyrhiza [Genus]
A. inundata [Species]
Clidomys [Genus]
C. osborni [Species]
C. parvus
Elasmodontomys [Genus]
E. obliquus [Species]
Quemisia [Genus]
Quemisia gravis [Species]

Myocastoridae [Family]
Myocastor [Genus]
M. coypus [Species]

Lagomorpha [Order]

Ochotonidae [Family]
Ochotona [Genus]
O. alpina [Species]
O. cansus
O. collaris
O. curzoniae
O. dauurica
O. erythrotis
O. forresti
O. gaoligongensis
O. gloveri
O. himalayana
O. hyperborea
O. iliensis
O. koslowi
O. ladacensis
O. macrotis
O. muliensis
O. nubrica
O. pallasi
O. princeps
O. pusilla
O. roylei

O. rufescens
O. rutila
O. thibetana
O. thomasi
Prolagus [Genus]
P. sardus [Species]

Leporidae [Family]
Brachylagus [Genus]
B. idahoensis [Species]
Bunolagus [Genus]
B. monticularis [Species]
Caprolagus [Genus]
C. hispidus [Species]
Lepus [Genus]
L. alleni [Species]
L. americanus
L. arcticus
L. brachyurus
L. californicus
L. callotis
L. capensis
L. castroviejoi
L. comus
L. coreanus
L. corsicanus
L. europaeus
L. fagani
L. flavigularis
L. granatensis
L. hainanus
L. insularis
L. mandshuricus
L. nigricollis
L. oiostolus
L. othus
L. pequensis
L. saxatilis
L. sinensis
L. starcki
L. timidus
L. tolai
L. townsendii
L. victoriae
L. yarkandensis
Nesolagus [Genus]
N. netscheri [Species]
Oryctolagus [Genus]
O. cuniculus [Species]
Pentalagus [Genus]
P. furnessi [Species]
Poelagus [Genus]
P. marjorita [Species]
Pronolagus [Genus]
P. crassicaudatus [Species]
P. randensis
P. rupestris
Romerolagus [Genus]
R. diazi [Species]
Sylvilagus [Genus]
S. aquaticus [Species]
S. audubonii
S. bachmani
S. brasiliensis
S. cunicularius
S. dicei
S. floridanus
S. graysoni
S. insonus
S. mansuetus
S. nuttallii
S. palustris
S. transitionalis

Macroscelidea [Order]

Macroscelididae [Family]
Elephantulus [Genus]
E. brachyrhynchus [Species]
E. edwardii
E. fuscipes
E. fuscus
E. intufi
E. myurus
E. revoili
E. rozeti
E. rufescens
E. rupestris
Macroscelides [Genus]
M. proboscideus [Species]
Petrodromus [Genus]
P. tetradactylus [Species]
Rhynchocyon [Genus]
R. chrysopygus [Species]
R. cirnei
R. petersi

A brief geologic history of animal life

A note about geologic time scales: A cursory look will reveal that the timing of various geological periods differs among textbooks. Is one right and the others wrong? Not necessarily. Scientists use different methods to estimate geological time—methods with a precision sometimes measured in tens of millions of years. There is, however, a general agreement on the magnitude and relative timing associated with modern time scales. The closer in geological time one comes to the present, the more accurate science can be—and sometimes the more disagreement there seems to be. The following account was compiled using the more widely accepted boundaries from a diverse selection of reputable scientific resources.

Geologic time scale

Era	Period	Epoch	Dates	Life forms
Proterozoic			2,500-544 mya*	First single-celled organisms, simple plants, and invertebrates (such as algae, amoebas, and jellyfish)
Paleozoic	Cambrian		544-490 mya	First crustaceans, mollusks, sponges, nautiloids, and annelids (worms)
	Ordovician		490-438 mya	Trilobites dominant. Also first fungi, jawless vertebrates, starfishes, sea scorpions, and urchins
	Silurian		438-408 mya	First terrestrial plants, sharks, and bony fishes
	Devonian		408-360 mya	First insects, arachnids (scorpions), and tetrapods
	Carboniferous	Mississippian	360-325 mya	Amphibians abundant. Also first spiders, land snails
		Pennsylvanian	325-286 mya	First reptiles and synapsids
	Permian		286-248 mya	Reptiles abundant. Extinction of trilobytes. Most modern insect orders
Mesozoic	Triassic		248-205 mya	Diversification of reptiles: turtles, crocodiles, therapsids (mammal-like reptiles), first dinosaurs, first flies
	Jurassic		205-145 mya	Insects abundant, dinosaurs dominant in later stage. First mammals, lizards, frogs, and birds
	Cretaceous		145-65 mya	First snakes and modern fish. Extinction of dinosaurs and ammonites, rise and fall of toothed birds
Cenozoic	Tertiary	Paleocene	65-55.5 mya	Diversification of mammals
		Eocene	55.5-33.7 mya	First horses, whales, monkeys, and leafminer insects
		Oligocene	33.7-23.8 mya	Diversification of birds. First anthropoids (higher primates)
		Miocene	23.8-5.6 mya	First hominids
		Pliocene	5.6-1.8 mya	First australopithecines
	Quaternary	Pleistocene	1.8 mya-8,000 ya	Mammoths, mastodons, and Neanderthals
		Holocene	8,000 ya-present	First modern humans

*Millions of years ago (mya)