of *Eozapus prosimilis* from the early Miocene of Mongolia. The most ancient *Eozapus* (early Miocene), *E. prosimilis*, was found in Mongolia, and *E. similis* was found in Inner Mongolia in late Miocene. *Eozapus similis* was likely the precursor of *E. setchuanus* in China, whereas *Asiazapus* of China was likely the precursor of *Zapus* and then *Napaeozapus* in the Miocene of North America. The dipodoid line leading to *Napaeozapus* suggests the emergence of a *Napaeozapus* ancestor in late Eocene and the attainment of the primitive level of *Plesiosminthus* by upper Eocene. *Zapus* appeared in upper Miocene and *Napaeozapus* in mid-Pleistocene. The relationships of the five living species of zapodids were studied using DNA sequence data, and results indicated that the three genera and five species are valid.

If zapodids evolved in Asia, how did they get into North America? North American groups can be called sister groups to the Asian genera *Asiazapus* and *Eozapus*; they also are sister species to many of the Asian trees such as *Magnolia* and *Liriodendron*, both Magnoliaceae; *Sassafras* (Lauraceae); and *Liquidamber* (Altingiaceae). During the early Tertiary geological period, about 60–70 million years ago, Asia and North America were connected by a wide land bridge across the Bering Strait. This was a low moist area and was much warmer than is currently the case in Eurasia and northern North America. Over the next few million years, continental drifting occurred, and this led to mountain building, including the North American Rockies, European Alps, Pyrenees, and Asian Himalayas (the latter may have been present but either arose or rose in height). As land masses elevated, the Northern Hemisphere cooled considerably ending in the onset of the Ice Ages of the late Pliocene and Pleistocene. As the climate continued to cool during the Pleistocene, the temperate forests migrated southward over several thousand years. Formation of the mountains changed wind flow and precipitation, causing development of huge rain shelters on the lee side of the mountains, leading to development and expansion of extensive grasslands and deserts. With continued cooling and drought patterns, the once extensive circumpolar temperate hardwood forests fragmented, and fragments migrated southward, eastward, and westward to environments suitable to temperate hardwood species of eastern North America, Western Europe, and South-east Asia where these habitats exist today. The north/south Appalachian Mountain chain with refuges in the coves provided a route to the southern Appalachians, and it is here where many of the temperate hardwood tree species still reside. It is no co-

The Woodland Jumping Mouse is brightly colored compared with other zapodids. Its fur is light brown, with a distinctive yellow or reddish tint. A dark brown dorsal band runs from the forehead to the rump. Its underparts are white. When startled, it is capable of jumping at least 2 m at heights of nearly 1 m. Woodland Jumping Mice occur in cool moist environments, almost entirely in forests, and where they are found together, Zapus species tend to be absent from woodlands. Although Zapus and Napaeozapus show a close evolutionary relationship, molecular studies indicate that they are valid genera.

Napaeozapus insignis
McDonough State Forest, Chenango
County, New York, USA.
Photo: Robert Miesner

Jumping mice can remain in hibernation for half a year or more, depending on species, latitude and elevation. In preparation, the Woodland Jumping Mouse will accumulate a third of its body weight in fat. An individual takes about two weeks to reach hibernation weight, although the process takes a total of around six weeks for a population, with older individuals entering hibernation first. Late-born young may not be able to put on sufficient fat to survive hibernation. During hibernation, the jumping mouse rolls into a ball with its nose in its abdomen, and its tail curled around its body. Its respiration rate falls from 200 breaths/minute during normal sleep, to 12 breaths/minute. Males are the first to emerge from hibernation in spring, and are in breeding condition when the females emerge.

Napaeozapus insignis
Dingmans Ferry, Pennsylvania, USA.
Photo: Photo Researchers/FLPA

Mongolia gave rise to *Asiazapus ingens* from the Akshar formation of Kazakhstan. *Eozapus* may have been related to *Zapus* and *Napaeozapus* only through a common *Plesiosminthus* stock. *Zapus* and *Napaeozapus* are more similar to each other than either is to *Eozapus*. The earliest known zapodids were from the middle Miocene. *Asiazapus* apparently gave rise to *Zapus*, and *Napaeozapus* and the discovery of *Asiazapus* in Asia in early Miocene indicates that *Zapus* and *Napaeozapus* evolved from Asian stocks. It could be the precursor of the Chinese Jumping Mouse. *Eozapus*, *Zapus*, and *Napaeozapus* evolved as a progressive series in the late Miocene. *Megasminthus* was found in the middle Pliocene of North America and was structurally transitional between smithids and zapodids. *Megasminthus* appears to be the earliest progenitor genus recognizable as a zapodid. An Asian origin of zapodids was suggested based on a tooth

Jumping mice are primarily seed-eaters, but they also eat a variety of fruits, and invertebrates such as caterpillars and other larvae, beetles, centipedes, and earthworms. Animal food is important in early spring, when little vegetable food is available, but as the year progresses, the mice eat more seeds, fruits, and fungi. The Western Jumping Mouse will bite through a grass stem as high as it can reach, and pull it down until it can get at the seed head. The cut grass stems can be found in little stacks on the ground. Other major foods of this species include salmonberries, blueberries and junebugs. Like other North American zapodids, it eats fungi of the family Endogonaceae, which distribute their spores via the feces of small rodents.

Zapus princeps
Photo: Shattil & Rozinski/
naturepl.com

incidence that Great Smoky Mountains National Park in south-eastern USA has more species of temperate hardwood trees than any place in the world. It is similar to the Arctic Tertiary forest of 60–70 million years ago. It would appear that many other groups, including the zapodids, were affected in the same way.

Most subspecies in Zapodidae are populations or groups of populations that are separated from other such populations, but they are described based on morphology alone and thus not considered true subspecies by all mammalogists and probably should be synonymized.

Morphological Aspects

The tail, hindlegs, and hindfeet of jumping mice are characteristically elongated, and the front legs and feet are normally sized. The fur is reddish or yellowish scattered with long dark guard hairs. The number and distribution of guard hairs cause much of the variation in color of jumping mice. Species of *Zapus* tend to be yellow or orange tinged on the sides, whereas *Napaeozapus* and *Eozapus* tend to be reddish. Nevertheless, all three species of *Zapus* have some populations well within the coloration of *Napaeozapus*. A dark brownish dorsal band that runs from the forehead to the rump is present in all species within this family. The underparts are usually white. Members of the genus *Eozapus* have a distinctive light brown stripe that runs the length of the body on the venter. The tail is bicolored, dark on top and white below, with or without a white tip. Females are slightly larger in overall size than males. The infraorbital foramen is large and oval. The zygomatic plate is nearly horizontal rather than oblique and is narrower than, and completely beneath, the infraorbital foramen. The nasal bones project considerably beyond the incisors. The incisive foramina of the rostrum are short. The incisors are orange or yellow, and the upper incisors contain deep grooves on their anterior surfaces. The genus *Eozapus* has the last premolar (P^4) reduced in size, but it is even smaller in *Zapus* and absent in *Napaeozapus*. There are three upper molars. The molars are rooted and flat-crowned and have a complicated pattern of reentrant folds, islands, and valleys. Dental formula is I 1/1, C 0/0, P 0–1/0, M 3/3 (×2) = 16 or 18.

Habitat

Zapodids occur in a great variety of habitats, but they generally occur in grasslands, brushy fields, and woodlands. They are

usually in areas with good herbaceous ground cover. They also occur in marshy areas, along ponds and streams, and in bogs and swamps. Jumping mice often occur along water, not because of the water but because other requirements are fulfilled, particularly adequate ground cover. The Woodland Jumping Mouse (*Napaeozapus insignis*) occurs in cool moist environments almost entirely in forests. When the grassland species, the Meadow Jumping Mouse (*Zapus hudsonius*), occurs with the Woodland Jumping Mouse, it remains mostly in fields but will inhabit woods with adequate ground cover to some extent. The Woodland Jumping Mouse generally occurs in conifer forests such as spruce-fir (*Picea-Abies*) or hemlock (*Tsuga*), all Pinaceae, and in hardwood forests of north-eastern USA and south-eastern Canada. Spruce-fir associations are common in the north and at higher elevations, and hemlock forests are more common in the south parts of its distribution. The hemlock-northern hardwood forest, besides hemlock, consists mainly of white pine (*Pinus* subgenus *Strobus*, Pinaceae), beech (*Fagus*, Fagaceae), sugar maple (*Acer saccharum*, Sapindaceae), yellow birch (*Betula alleghaniensis*, Betulaceae), basswood (*Tilia*, Malvaceae), and red maple (*A. rubrum*), striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*), all Sapindaceae. Further south, basswood, buckeye (*Aesculus*, Sapindaceae), tulip tree (*Liriodendron*, Magnoliaceae), magnolia (*Magnolia*, Magnoliaceae), and mountain laurel (*Kalmia latifolia*, Ericaceae) are often found. The particular species of tree is not important to jumping mice, but a moist environment is conducive to their presence.

General Habits

Jumping mice are some of the most profound of hibernators, remaining in hibernation for nearly one-half of a year or more, depending on latitude and elevation. Accumulation of adequate fat stores from which energy is derived is necessary for successful hibernation. This process takes place over about six weeks, and individuals enter hibernation gradually as they put on fat. Jumping mice without adequate fat stores generally die during hibernation. Although called jumping mice, these animals typically walk or crawl through the grass. They can swim but seldom climb. When chased, most can hop up to about 1 m, although Woodland Jumping Mice can jump at least 2 m. They then often stop and hide in vegetation. Jumping mice are quite docile, seldom attempt to bite, and do not appear to be antagonistic toward each other. They often wash their faces, feet, and tails. The long tail is passed all the way through the mouth

*As the season progresses and vegetable foods replace invertebrates in its diet, the **Meadow Jumping Mouse** eats a variety of grass, herb and tree seeds. Elm, touch-me-not, chickweed, sheep sorrel, cinquefoil, and wood sorrel may all be important. Like the Western Jumping Mouse, the Meadow Jumping Mouse cuts down grass stems by biting through the stalk repeatedly and pulling the sections down until it can reach the seed heads. This species will also climb the stalk to bite off the seed head and bring it to the ground, and it frequently forages in the canopy of herbaceous vegetation. Late in the season, fungi, mostly subterranean species of the family Endogonaceae, can comprise up to 100% by volume of the diet.*

Zapus hudsonius
Lapeer County, Michigan, USA.
Photo: John Gerlach/DRK

*The many predators of jumping mice include coyotes and foxes, domestic cats and bobcats, skunks, minks and weasels, rattlesnakes and milksnakes, green frogs, hawks and harriers, and, as here, the western scrub-jay (Aphelocoma californica). Owls, however, especially barn owls (Tyto), seem to be the prevalent predators of the **Meadow Jumping Mouse**. Similarly, in western Oregon, the Pacific Jumping Mouse (Zapus trinotatus) makes up 16% of the barn owl's diet. Like other zapodids, the Meadow Jumping Mouse is widely distributed, common, and not in decline throughout most of its extensive distribution, and is classified as Least Concern on the IUCN Red List. However, in some areas, such as South Dakota and New Mexico, it is regarded as threatened because of habitat loss.*

Zapus hudsonius
California, USA.
Photo: Max Allen/Alamy Stock Photo

when washing. Most activity is at night, although there may be some activity during the day. Jumping mice typically live 1–2 years, rarely up to five years.

Communication

Adult jumping mice are usually silent, but they may make squeaking sounds when fighting and a clucking sound when excited. Some, or perhaps all, species of jumping mice also make drumming sounds with their tails against the ground when they are excited. Young jumping mice make high-pitched squeaking sounds. Unfortunately, the functions of most of these calls are not understood. Jumping mice have a keen sense of smell, and they likely use scent as a means of communication.

Food and Feeding

Diets of jumping mice are quite variable. Seeds are primary foods eaten, but a variety of fruits and berries also are consumed. Fungi are very important to most species of jump-ing mice, particularly fungi of the family Endogonaceae, but spores of other fungi are also eaten. Some have questioned if fungi might be taken incidentally along with other foods. This does not seem to be the case because some of the stomachs contain nearly 100% fungi. Spores on the chests of some jumping mice indicate that they probably find the fungi using olfaction and then dig them up. Other important foods are caterpillars, beetles, fly larvae, and other invertebrates such as spiders, centipedes, and earthworms. Seasonal changes in diets of jumping mice vary depending on food availability. In early spring, diets consist of about 50% animal material and 20% seeds; few fungi are consumed. As the year progresses, more fungi and seeds are eaten, and there is a decline in ingestion of animal material.

Breeding

Male jumping mice emerge from hibernation before females, and mating occurs soon after females emerge. Gestation lasts between 17 and 21 days, with the longer periods occurring in lactating females. There are usually 1–2 litters per year and, seldom if at all, three litters. Number of young per litter ranges from two to nine, averaging 4–6 young. Newborn jumping mice are naked and produce a high squeaking noise that can be heard for about 1 m. During their first week of life, young can crawl but not stand. The external auditory meatus opens, and young can react to sound at about day 20. The eyes open about day 25, and young begin to emerge from the nest and eat solid food. Suckling may continue for a time after this, but by the end of week four, young are fully furred and can fend for themselves. Nests are generally underground, often about 15 cm below the surface. Nests have also been found in grassy hummocks in open fields, under planks, in hollow logs, and in other protected areas. One nest was found in the base of a living oak tree (*Quercus*, Fagaceae), and another containing five early stage young was found about 1·4 m above the ground in the crook of a coastal redwood (*Sequoia sempervirens*, Cupressaceae). Another jumping mouse took over a junco nest (*Junco hyemalis*, Passerellidae), ate the four eggs present, lined the nest with the egg shells, and built a dome over the nest with dry grass and hair of Wapiti (*Cervus canadensis*). Many young produced late in the year do not survive winter because they cannot accumulate sufficient fat reserves to survive hibernation.

Movements, Home range and Social organization

Densities of jumping mice can be quite high, up to 37·1 ind/ha. Home ranges vary from about 0·8 ha to 2·4 ha in females and from 0·04 ha to 3·6 ha in males, and they can overlap. There are occasional shifts in home ranges; however, individuals might leave their home ranges during the transition between winter hibernation and the active season, although typically distances moved are not great. Hibernacula are often located in summer home ranges when necessary conditions, such as small banks or piles of dirt, are present.

Relationship with Humans

Jumping mice have no appreciable effects on humans, and most humans do not realize they are around. Jumping mice do not enter buildings or cause noteworthy harm. Nevertheless, farmers working in hayfields often see them. Many Meadow Jumping Mice can be captured by leaping off a tractor and catching them by hand when mowing hayfields.

Status and Conservation

All five species of jumping mice are listed as Least Concern on *The IUCN Red List*. Declines in populations are probably caused by loss of habitat; therefore, setting aside and creating more grassy habitat will benefit jumping mice.

Bibliography
Brown (1967a, 1967b, 1970), Corbet & Hill (1992), Cranford (1977, 1978), Fahlbusch (1992), Fan Zhenxin et al. (2009), Fischer von Waldheim (1917), Gannon (1988, 1999), Gidley & Gazin (1938), Giraudoux et al. (1998), Green (1977), Hafner et al. (1981), Hall (1981), Hamilton (1935), Hart et al. (2004), Jones (1981), Jones et al. (1978), Kardos (1954), Klingener (1964), Korth (1994), Krutzsch (1954), Latham (1950), Lawrence et al. (1965), Lebedev et al. (2013), Lichtenfels & Haley (1968), Lopatin & Zazhigin (2000a), Orrock et al. (2003), Ovaska & Herman (1988), Preble (1899), Quéré et al. (2009), Quimby (1951), Rodrigues et al. (2011), Sheldon (1936, 1938), Shenbrot (1992), Smith & Yan Xie (2008), Stein (1990), Svihla & Svihla (1933), Townsend (1935), Wang Sung & Yan Xie (2009), Whitaker (1963a, 1963b, 1970, 1972), Whitaker & Mumford (1970), Whitaker & Wrigley (1972), Wilson & Reeder (2005), Yan Xie et al. (2009), Zhang Qian et al. (2013).

*Jumping mice will drink free water, but probably obtain much of their water from their food. They are often found near water, in swamps, damp meadows, ponds, and streams. Studies however suggest no significant relationship between occurrence of jumping mice and distance to water, and the mice are likely taking advantage of the denser ground cover in such places. The **Meadow Jumping Mouse** is abundant in stands of touch-me-not (Impatiens), which often grows in wet places, and which is also an important source of seeds eaten by this species.*

Zapus hudsonius
Hamilton County, Ohio, USA.
Photo: Steve & Dave Maslowski/
Maslowski Wildlife Productions

PLATE 4

inches 4
cm 10

Genus *SCARTURUS*
Gloger, 1841

15. Williams's Jerboa   *Scarturus williamsi*
French: Gerboise de Williams / **German:** Türkei-Pferdespringer / **Spanish:** Jerbo de Williams

Taxonomy. *Allactaga williamsi* Thomas, 1897, "Van, alt. 5000 ft. [1524 m]," Turkey. Previously included in the genus *Allactaga* and later *Paralactaga*, which has recently been found to be a junior synonym of *Scarturus*. In the past, *S. williamsi* was synonymized with *S. euphraticus*. Phylogenetically, it is a member of subgenus *Paralactaga*, being the sister species of *S. aulacotis*. Recently found in the Kopet Dagh Mountains of north-eastern Iran, *Scarturus* cf. *williamsi*, named by K. Hamidi and colleagues in 2016, is a separate species that needs to be formally described; it is also possible that it is closely related to *S. euphraticus caprimulga*. Monotypic.

Distribution. Turkey (Anatolia), Armenia, SE Georgia, Azerbaijan, NW & W Iran, and Lebanon; individuals of still unresolved specific status have been recently found in NE Iran (Kopet Dagh Mts).

Descriptive notes. Head–body 102–146 mm, tail 167–255 mm, ear 38–51 mm, hindfoot 61–74 mm; weight 54–143 g. There is no significant secondary sexual dimorphism. Condylo-basal lengths of skulls are 29·5–33·2 mm, zygomatic breadths are 21·4–24·8 mm, and maxillary tooth row lengths are 6·3–7·6 mm. Head and dorsum are brownish ocherous; sides and ventral pelage are pure white; and tail banner is wide and well flattened, with short (20 mm) bright-ocherous basal ring, relatively long (40 mm) black subterminal field, and relatively long (20 mm) white terminal tuft. Toes of hindfeet are covered from below with short soft white (with admixture of black) hairs not forming brushes; conic calluses at bases of toes are large, with wide bases and rounded apexes. Auditory bullae are weakly inflated. Mastoid cavity is medium-sized and not subdivided into sections; tympanic cavity is extremely small. Front surfaces of incisors are white; incisors are weakly deflected forward. P[1] is relatively small and about twice as small as in diameter than M[3]. Molars are low-crowned, with tuberculous masticatory surfaces; crown heights of unworn molars are c.70% of their lengths. Glans penis is egg-shaped, 2·5–3·9 mm long and 1·8–2·4 mm wide, slightly compressed in dorso-ventral direction, subdivided by deep longitudinal dorsal fold into two lateral lobes; surfaces of lobes are covered by single-vertex, backward-directed aciculae increasing in size in backward direction; and aciculae are arranged in 4–5 concentric rows with 12–14 aciculae in each row. Os penis (baculum) is absent. Chromosomal complement has 2n = 48 and FN = 96.

Habitat. Mainly semi-deserts and mountain dry steppes but also subalpine meadows up to elevations of c.2500 m. Williams's Jerboa is a habitat generalist and frequents different habitats including saltwort (Amaranthaceae) vegetation, semi-stabilized sand dunes, and rock outcrops, preferring patches of sparse sagebrush (*Artemisia*, Asteraceae) and herbaceous vegetation.

Food and Feeding. Diet of Williams's Jerboa is mainly composed of seeds and insects and to a lesser extent of green plant material and bulbs. It mainly eats insects and green plant parts in spring, vegetative and generative plant parts in summer, and seeds in autumn.

Breeding. Breeding of Williams's Jerboa was recorded in late March–June and August–October. Litters have 2–8 young (average varies within the same year 3–6·3). Overwintering females can produce two litters per year. Length of gestation was estimated at 25–30 days.

Activity patterns. Williams's Jerboas are nocturnal. Aboveground activity usually starts 1·5–2 hours after sunset and ends before morning dusk. Hibernation occurs in November–February.

Movements, Home range and Social organization. Burrows of Williams's Jerboa are simple and usually have one tunnel with 1–3 turns. Tunnel starts at ground surface, with typically plugged entrance, and ends with nest chamber 12–14 cm in diameter and 20–80 cm deep; lengths of tunnels are 90–200 cm. In some cases, burrows have 1–2 additional tunnels ending with emergency exits. In captivity, initial contacts between individuals of the same or opposite sex are aggressive; after two hours of intense fighting, individuals become peaceful; and in some cases, these interactions can lead to serious wounds or death.

Status and Conservation. Classified as Least Concern on *The IUCN Red List* (as *Allactaga williamsi*).

Bibliography. Arslan & Zima (2010), Atallah & Harrison (1969), Çolak & Yiğit (1998b), Çolak et al. (1994), Dianat et al. (2013), Hamidi et al. (2016), Kryštufek & Vohralík (2005), Kryštufek et al. (2013), Lay (1967), Naderi et al. (2014), Shenbrot et al. (2008), Toyran & Albayrak (2009).

16. Syrian Five-toed Jerboa   *Scarturus aulacotis*
French: Gerboise de Wagner / **German:** Syrien-Pferdespringer / **Spanish:** Jerbo pentadáctilo de Siria

Taxonomy. *Dipus aulacotis* Wagner, 1840, "West coast of Arabia" (probably NE of Aqaba in present-day Jordan).
Previously included in the genus *Allactaga* and later *Paralactaga*, which has recently been found to be a junior synonym of *Scarturus*. In the past, *S. aulacotis* was synonymized with *S. euphraticus*. Phylogenetically, it is in the subgenus *Paralactaga*, being sister species of *S. williamsi*. The name *Dipus aulacotis* was considered a synonym of *Allactaga major* by J. R. Ellerman and T. C. S. Morrison-Scott in 1951 and appeared with a "?" and without any comment in M. E. Holden and G. G. Musser in 2005. Nevertheless, definite indication of the place of origin of the type specimen in the original description and type dimensions typical for *euphraticus* group, allow applying this name to the species in the *euphraticus* group, occurring west of Euphrates River. Monotypic.

Distribution. Extreme SC Turkey (Kilis) and NW Arabian Peninsula W of Euphrates River (W Syria, Jordan, and NW Saudi Arabia); in N Syria, probably, also occurs on the left bank of Euphrates.

Descriptive notes. Head–body 96–128 mm, tail 158–199 mm, ear 30–42 mm, hindfoot 51–61 mm. No specific data are available for body weight. Condylo-basal lengths of skulls are 27·8–31·7 mm, zygomatic breadths are 21–23·2 mm, and maxillary tooth row lengths are 6–6·8 mm. In general appearance and skull and molar morphologies, the Syrian Five-toed Jerboa is similar to the Euphrates Jerboa (*S. euphraticus*). Morphology of glans penis and chromosomal complement have not been described.

Habitat. Arid habitats, preferring foothills especially near "wadi" (ephemeral riverbeds) systems and grassy areas of "hamada" (barren, hard, rocky plateaus) desert; avoids sandy habitats.

Food and Feeding. No information.

Breeding. Breeding of the Syrian Five-toed Jerboa was recorded in April. Litters have 6–9 young.

Activity patterns. The Syrian Five-toed Jerboa is nocturnal.

Movements, Home range and Social organization. No information.

Status and Conservation. Not assessed on *The IUCN Red List*.

Bibliography. Amr et al. (2004), Atallah & Harrison (1969), Ellerman & Morrison-Scott (1951), Holden & Musser (2005), Kryštufek et al. (2013), Qumsiyeh (1996).

17. Euphrates Jerboa   *Scarturus euphraticus*
French: Gerboise de l'Euphrate / **German:** Euphrat-Pferdespringer / **Spanish:** Jerbo del Éufrates
Other common names: Montane Jerboa

Taxonomy. *Allactaga euphratica* Thomas, 1881, "Mesopotamia [= Iraq]."
Previously included in the genus *Allactaga* and later *Paralactaga*, which has recently been found to be a junior synonym of *Scarturus*. Phylogenetically, *S. euphraticus* is in the subgenus *Paralactaga*, being the sister species of the *S. williamsi* + *S. aulacotis* clade. The form *kivanci* named by E. Çolak and N. Yiğit in 1998 is genetically identical to the nominate form; moreover, *kivanci* was described based on comparison of specimens from southern Turkey with *S. aulacotis* from Syria rather than with true *S. euphraticus*. Two subspecies recognized.

Subspecies and Distribution.
S. e. euphraticus Thomas, 1881 – definitely known from SE Turkey, Iraq E of Euphrates River and SW Iran; probably, occurs also in Syria E of Euphrates, C & S Iraq W of Euphrates, Kuwait, and N Saudi Arabia.
S. e. caprimulga Ellerman, 1948 – Afghanistan.

Descriptive notes. Head–body 77–140 mm, tail 144–210 mm, ear 29–52 mm, hindfoot 50–68 mm; weight 48–92 g. There is no significant secondary sexual dimorphism. Condylo-basal lengths of skulls are 25·4–31 mm, zygomatic breadths are 19·4–23·6 mm, and maxillary tooth row lengths are 5·8–7 mm. Head and dorsum are grayish buff; sides and ventral pelage are pure white; and tail banner is wide and well flattened, with short white (often with narrow longitudinal dorsal dark strip) (nominate *euphraticus*) or ocherous (*caprimulga*) basal ring, relatively long black subterminal field, and medium-length white terminal tuft. Toes of hindfeet are covered from below with short soft white hairs, mixed with black, not forming brushes; conic calluses at bases of toes are large, with wide bases and rounded apexes. Auditory bullae are weakly inflated. Mastoid cavity is medium-sized and not subdivided into sections; tympanic cavity is extremely small. Front surfaces of incisors are white; incisors are weakly deflected forward. P[1] is relatively small and 1·6–2 times smaller in diameter than M[3]. Molars are low-crowned, with tuberculous masticatory surfaces; crown heights of unworn molars are c.70% of their lengths. Glans penis is egg-shaped, 5·6–6·6 mm long and 3·3–3·9 mm

On following pages: 18. Hotson's Five-toed Jerboa (*Scarturus hotsoni*); 19. Small Five-toed Jerboa (*Scarturus elater*); 20. Vinogradov's Jerboa (*Scarturus vinogradovi*); 21. Four-toed Jerboa (*Scarturus tetradactylus*); 22. Greater Fat-tailed Jerboa (*Pygeretmus shitkovi*); 23. Lesser Fat-tailed Jerboa (*Pygeretmus platyurus*); 24. Dwarf Fat-tailed Jerboa (*Pygeretmus pumilio*); 25. Comb-toed Jerboa (*Paradipus ctenodactylus*); 26. Northern Three-toed Jerboa (*Dipus sagitta*); 27. Mongolian Three-toed Jerboa (*Stylodipus andrewsi*); 28. Thick-tailed Three-toed Jerboa (*Stylodipus telum*); 29. Dzungarian Three-toed Jerboa (*Stylodipus sungorus*); 30. Lichtenstein's Jerboa (*Eremodipus lichtensteini*); 31. Greater Egyptian Jerboa (*Jaculus orientalis*); 32. Blanford's Jerboa (*Jaculus blanfordi*); 33. Lesser Egyptian Jerboa (*Jaculus jaculus*); 34. African Hammada Jerboa (*Jaculus hirtipes*); 35. Arabian Jerboa (*Jaculus loftusi*).

CLASS MAMMALIA
ORDER RODENTIA
SUBORDER MYOMORPHA
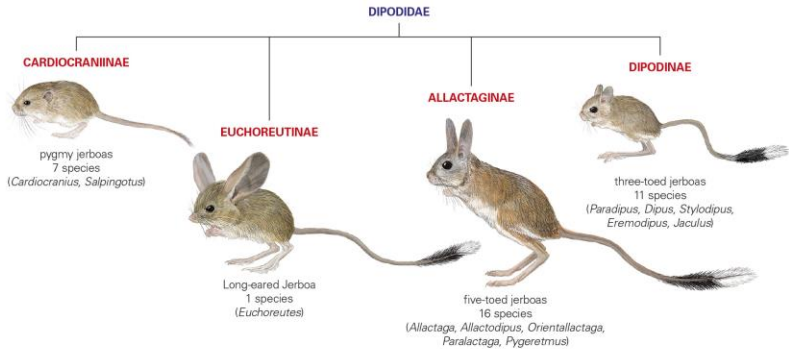SUPERFAMILY DIPODOIDEA

Family DIPODIDAE (JERBOAS)
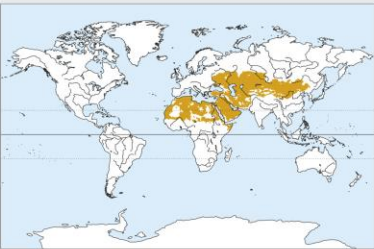
- Small to medium-sized, bipedal and characterized by short forelimbs and long strong hindlimbs and long tails, often ending with black and white brush of long hairs.
- 10–50 cm.

- Palearctic and Afrotropical regions.
- Terrestrial species, desert, semi-desert and steppe habitats.
- 13 genera, 35 species, 91 taxa.
- 1 species Vulnerable; none Extinct since 1600.

Systematics

The superfamily Dipodoidea (Rodentia, Myomorpha) is the sister group of Muroidea. As noted by J. Michaux and colleagues in 2001, this close relationship, based on morphological and molecular data, confirmed the suprafamilial Myodonta concept, associating both superfamilies. As summarized by V. S. Lebedev and colleagues in 2013 and M. E. Holden and G. G. Musser in 2005, birch mice, jumping mice, and jerboas have been traditionally recognized in a single family Dipodidae or placed in up to six families within superfamily Dipodoidea. Four of them included morphologically specialized bipedal, arid-dwelling jerboas (Cardiocraniinae, pygmy jerboas; Euchoreutinae, Long-eared Jerboa; Dipodinae, three-toed jerboas; and Allactaginae, five-toed jerboas), and the other two were represented by more generalized quadrupedal taxa (Zapodinae, jumping mice, and Sminthinae, birch mice). Despite important effort from morphologists, the taxonomy and phylogeny of Dipodoidea remains controversial. More particularly, the family-level classification has long been a matter of debate, with the number of recognized families ranging from one to six. This lack of consensus on dipodoid taxonomy is linked by the fact that, until recently, phylogenetic relationships among the main lineages were not unambiguously established.

Traditional classifications based mainly on morphological similarities included two related families: Dipodidae, including all jerboas, and Zapodidae, including jumping mice and birch mice. This morphology-based system reflected the evolution of locomotory adaptations, with subfamilies (or families) corresponding to grades of evolutionary development from primitive quadrupedal to specialized bipedal locomotion. Other studies noted that a simple dichotomy between bipedal and non-bipedal taxa was inadequate to explain significant morphological variation within the superfamily. The use of traits that are not directly associated with locomotion appeared to be more reasonable to develop phylogenetic studies less subject to homoplasy. This approach was performed in 1992 by G. I. Shenbrot in a cladistic analysis based on characteristics of dentition, male reproductive systems, and auditory bullae. This study did not reveal any synapomorphies to support the monophyly of the bipedal taxa and proposed to divide Dipodoidea into four families: Allactagidae, Dipodidae (including *Paradipus* and Cardiocraniinae), Sminthidae (with Euchoreutinae), and Zapodidae. Following the same strategy, recent paleontological studies proposed another classification with three main families: Zapodidae (containing Sminthinae/ Sicistinae and Zapodinae), Allactagidae (containing Allactaginae and Euchoreutinae), and Dipodidae (including Cardiocraniinae, Dipodinae, and the extinct Lophocricetinae, even

though this last subfamily was included within Cardiocraniinae by some authors). These last two classifications suggested that the evolution of Dipodoidea was a complex process involving independent and parallel locomotory, trophic, and substrate adaptations.

Recent genetic studies based on several nuclear and mitochondrial markers resulted a new taxonomic revision and supported the recognition of only three families: Sminthidae (synonym of Sicistinae, 14 species), Zapodidae (five species), and Dipodidae, which included Cardiocraniinae (seven species), Euchoreutinae (one species), Dipodinae (eleven species), and Allactaginae (16 species) as subfamilies. This arrangement was chosen to emphasize the monophyly of all bipedal taxa within Dipodoidea, which appears extremely clear with molecular markers. It is also interesting that the number of species of Dipodidae is still highly debated and that several cryptic species probably still need to be identified. This is particularly the case for the subfamily Allactaginae. The use of new molecular and morphological markers and better sampling will help to decipher the correct number of species existing for this still poorly known rodent group.

Concerning their phylogeny, these recent genetic studies also highlighted the basal position of Sminthidae, followed by Zapodidae. This last family appears therefore as the sister group of the monophyletic jerboas. This result was already proposed in earlier morphological studies that generally considered Sminthidae as representing the most primitive dipodids morphologically. In contrast, this pattern contradicts the view that the non-bipedal birch mice (Sminthinae) and jumping mice (Zapodinae) constitute a monophyletic group, as proposed by several other morphologists and paleontologists. Indeed, two Oligocene lineages, *Heosminthus-Plesiosminthus* and *Sinosminthus-Parasminthus*, were generally considered to be the ancestral groups of Zapodinae-Sminthinae and Allactaginae-Dipodinae, respectively. Nevertheless, analyses performed by Lebedev and colleagues in 2013 clearly rejected the monophyly of the former association, thus suggesting that fossil data should be revised to determine which of the Paleogene taxa represent stem-groups of the three, but not two, main dipodoid clades.

Another important result based on recent morphological and molecular analyses concerns the monophyly of bipedal

*The jerboa family Dipodidae is part of the superfamily Dipodoidea, along with the birch mice (Sminthidae) and jumping mice (Zapodidae). There are four jerboa subfamilies. Cardiocraniinae includes seven species of primitively bipedal pygmy jerboas. The genus Cardiocranius consists of a single species, the **Five-toed Pygmy Jerboa**, a very small jerboa (9–19 g) with short, tubiform ears, and a short, fat tail without a brush at its tip. Its hindfeet have five toes, which have conical calluses at the bases, and are covered from below with brushes of short soft hairs. Pygmy jerboas move in a series of jumps using both hindfeet simultaneously, but lack the speed, long-jumping capacity and endurance of the larger and more specialized jerboas.*

Cardiocranius paradoxus
N Gobi Desert, Mongolia.
Photo: Konstantin Mikhailov

Subdivision of the Dipodidae

[Figure Toni Llobet]

DIPODIDAE

CARDIOCRANIINAE

pygmy jerboas
7 species
(*Cardiocranius, Salpingotus*)

EUCHOREUTINAE

Long-eared Jerboa
1 species
(*Euchoreutes*)

ALLACTAGINAE

five-toed jerboas
16 species
(*Allactaga, Allactodipus, Orientallactaga, Paralactaga, Pygeretmus*)

DIPODINAE

three-toed jerboas
11 species
(*Paradipus, Dipus, Stylodipus, Eremodipus, Jaculus*)

FAMILY
SUBFAMILY

*There are six species of pygmy jerboa in the genus Salpingotus. Weighing as little as 6 g, the **Thick-tailed Pygmy Jerboa** is among the smallest species in the genus—the very smallest, the 4-g Balochistan Pygmy Jerboa (S. michaelis), is probably the world's smallest rodent. Its "thick" tail contains deposits of fat and tapers gradually from the base— where the fat stores are greatest—to the tip. The tail is almost twice the head–body length and terminates in a short, gray tuft.*

Salpingotus crassicauda
Zaysan Depression,
E Kazakhstan.
Photo: Oleg Belyalov

At home in the true and extra-arid deserts of northern China and southern Mongolia, the **Long-eared Jerboa** must be ready to eat whatever it finds. This photograph appears to be the first record of an egg in its diet, but this otherwise mainly insectivorous jerboa is reported to catch and eat sleeping variegated toadhead agamas (Phrynocephalus versicolor) a small (total lenght up to 13 cm) species of lizard found in desert areas of Mongolia and China.

Euchoreutes naso
Flaming Mountains, Turpan City, Xinjiang, China.
Photo: Liu Jian/Xinhua/NHPA

Communication

Little is known about communication systems of dipodids. Many species of dipodids use dust baths, and even if they do not have well-developed skin glands for scent marking, dust bathing is often considered a kind of chemical communication. Other specific marking behavior, such as touching substrate with the anogenital area, has been observed in the Long-eared Jerboa. Good hearing of dipodids suggests they may use sounds and vibrations to communicate with one another, even if they are generally silent. Tactile communication probably exists between mates and between mothers and their young.

Food and Feeding

Most dipodids are omnivorous, with diets of vegetation, fruits, fungi, insects, and relatively soft seeds. Some species are mostly insectivorous, particularly eating beetles or moths. Dipodids do not store food. Some species of jerboas, such as the Great Jerboa, Severtzov's Jerboa, and the Siberian Jerboa (*Orientallactaga sibirica*), are omnivorous, feeding on what they find in arid habitats of Central Asia. They mostly eat seeds, fruits, fungi, and insects, but they also eat plant parts such as green stems and leaves, roots, and bulbs. The Northern Three-toed Jerboa has a relatively generalized diet composed of seeds and flowers (36–73%, average 51%), green plant material (16–54%, aver-

Jerboas breed 1–3 times per year, depending on the species. The **Arabian Jerboa**, which does not appear to hibernate, has been recorded breeding between February and November. There are 2–7 young in a litter, born after a gestation estimated at 25 days. Jerboas generally breed after their first winter, from the age of 10–11 months, but in a few species, some individuals born in spring may breed in the autumn of the same year. In species and populations that hibernate, mating usually occurs shortly after emergence.

Jaculus loftusi
Sharjah Breeding Centre, United Arab Emirates.
Photo: Björn Jordan

age 35%), roots and bulbs (0–40%, average 10%), and insects (1–11%, average 4%). Composition of plant species in diets of Northern Three-toed Jerboas varies geographically and seasonally. Locally, Northern Three-toed Jerboas include 15–40 species of shrubs, grasses, and forbs in their diets.

Diets of other species of jerboas range from near-pure insectivory where plant material is less than 5% of the diet (e.g. Long-eared Jerboa) to granivory–insectivory where seeds and insects are eaten in roughly equal amounts (e.g. Thick-tailed Pygmy Jerboa and Kozlov's Pygmy Jerboa, *Salpingotus kozlovi*), near-pure granivory where mainly seeds of *Stipa* sp. (Poaceae) are eaten (e.g. Five-toed Pygmy Jerboa), granivory–folivory (e.g. Thick-tailed Three-toed Jerboa, Small Five-toed Jerboa, and Lichtenstein's Jerboa), and folivory (e.g. Bobrinski's Jerboa, *Pygeretmus* sp., and Comb-toed Jerboa).

Hunting strategies of insectivorous jerboas are sometimes impressive. Long-eared Jerboas and Siberian Jerboas can precisely locate flying insects such as moths, using their long and flexible auricles, and then catch them after fast vertical jumps. Kozlov's Pygmy Jerboa uses its large auricles to detect the presence of insect larvae in sand dunes, and it uses its nose and long vibrissae to dig in the sand until it catches its prey. The Comb-toed Jerboa forages by climbing in *Haloxylon* (Amaranthaceae) shrubs, using its forelimbs and incisors to cut green stems at heights up to 1.5 m.

Breeding

Dipodids generally give birth to litters of 2–9 young after gestations of 19–42 days. They breed 1–3 times/year, depending on the species. Jerboas are polygamous, and their breeding biology can be divided into three groups. Species in the first group breed only one time in spring or summer (warm season). This group includes Lichtenstein's Jerboa, Kozlov's Pygmy Jerboa, the Lesser Fat-tailed Jerboa, the Thick-tailed Three-toed Jerboa, and the Mongolian Three-toed Jerboa. Species in the second group have one and, less regularly, two litters during the warm period and include the Great Jerboa, the Balikun Jerboa (*Orientallactaga balikunica*), the Gobi Jerboa (*Orientallactaga bullata*), the Siberian Jerboa, the Thick-tailed Pygmy Jerboa, Heptner's Pygmy Jerboa (*Salpingotus heptneri*), the Pallid Pygmy Jerboa, the Long-eared Jerboa, and the Lesser Fat-tailed Jerboa. Five-toed Pygmy Jerboas very rarely have two litters during spring or summer. Litters of species in these two groups have 2–9 young, with

an average of five young. Their sexual maturity occurs about a year later after the first hibernation, and mating usually occurs after awakening from hibernation. Species in the third group breed 2–3 times a year. Overwintering individuals in this group can produce two litters in spring and early summer without interruption (only one in the case of the Greater Fat-tailed Jerboa) and one in autumn after an interruption in breeding in late summer. This group includes the Small Five-toed Jerboa, Severtzov's Jerboa, Bobrinski's Jerboa, the Northern Three-toed Jerboa, the Dwarf Fat-tailed Jerboa, and the Greater Fat-tailed Jerboa. Litters in this group have 1–8 young, with an average of four young. Juveniles born in spring can produce one litter in the following autumn.

Breeding of the **Greater Egyptian Jerboa** has been recorded from the end of March to August. During a study of the courtship and copulation of another Jaculus species, the African Hammada Jerboa (J. hirtipes), the male began by standing in front of the female, bobbing up and down with his tail horizontal or erect. He sniffed her genital region, then moved to face her with his nostrils close to hers, before moving behind her, and hopping forward with his hindlegs either side of her tail. Copulation was very brief. Afterwards he moved forward over the female so his genitals and belly rubbed her back. [Happold 1970]

Jaculus orientalis
(captive) Plzeň Zoo, Czech Republic.
Photo: Klaus Rudloff

Jerboas develop very slowly compared to other rodents of similar size. Despite their unusually long gestation, they are born naked, blind, and helpless. Details of the development of young **Arabian Jerboas** are not available, but the young shown here are around two weeks old and soft black hair has begun to appear on their dorsal region, starting on the lower part of the back. Their eyes are swollen and eye slits are just visible. In a study of captive African Hammada Jerboa (Jaculus hirtipes), hair did not begin to appear until 22 days after birth and eyes began to open at 38 days. Age at weaning of jerboas ranges from 30–45 days, according to species. The young of Jaculus species are nursed for 42–45 days.

Jaculus loftusi
Sharjah Breeding Centre, United Arab Emirates.
Photo: Björn Jordan

PLATE 5

inches 2
cm 5

Genus PLATACANTHOMYS

Blyth, 1859

1. Malabar Spiny Tree Mouse   *Platacanthomys lasiurus*

French: Loir-épineux de Malabar / German: Südindien-Stachelbilch / Spanish: Ratón arborícola de Malabar
Other common names: Malabar Spiny Dormouse, Malabar Spiny Mouse

Taxonomy. *Platacanthomys lasiurus* Blyth, 1859, Alipi (= Allepey), Malabar (= Kerala State), India.
This species is monotypic.
Distribution. Endemic to the Western Ghats of S India, from 14° to 8° N latitude in Karnataka, Kerala, and Tamil Nadu.
Descriptive notes. Head–body 118–140 mm, tail 76–106 mm. No specific data are available for body weight. The Malabar Spiny Tree Mouse is the largest platacanthomyid, but a small rodent with large, mostly naked ears and distinctive, white-tipped, flattened spines interspersed throughout dorsal pelage. Dorsum is light brown, with lighter venter; whiskers are long; long tail is lightly furred near base but densely furred at tip (resembling a bottle brush); and hair at tip of tail is white in some individuals (including juveniles).
Habitat. Tropical evergreen forests and deciduous riparian forests at elevations of 600–900 m in the Western Ghats.
Food and Feeding. The Malabar Spiny Tree Mouse is granivorous and frugivorous. It is known to feed on fruits and seeds from more than 25 different plant species, including crops like black pepper and cacao.
Breeding. Poorly known. The Malabar Spiny Tree Mouse might have two distinct breeding seasons.
Activity patterns. Malabar Spiny Tree Mice are nocturnal and nest in leaf-lined tree cavities and rock crevices during the day, emerging to forage in the canopy after dusk.
Movements, Home range and Social organization. Home ranges of Malabar Spiny Tree Mice are c.5 ha and sometimes overlap. Mating system is possibly polygynous. Multiple adult females and their offspring will live with a single adult male in a nest, and males sometimes live alone. Individuals sometimes forage in mixed groups.
Status and Conservation. Classified as Vulnerable on *The IUCN Red List* in 2008. The Malabar Spiny Tree Mouse is considered a pest by some farmers and is sometimes killed. It will occasionally forage in cropland, but it tends to avoid secondary forest. Less than 2000 km² of suitable evergreen forest remains in the Western Ghats. If habitat destruction continues and protected areas are threatened, conservation status of this endemic Indian species will likely be downgraded. It has never been included in a molecular genetic analysis, so any genetically distinct populations (or potential undescribed, morphologically similar species) are unknown.
Bibliography. Carleton & Musser (1984), Chetana & Ganesh (2013), Corbet & Hill (1992), Ganesh & Devy (2006), Gopakumar & Motwani (2013), Jayahari & Jayson (2007), Jayson (2006), Jayson & Jayahari (2009), Molur & Nameer (2008), Molur & Singh (2009), Molur et al. (2005), Mudappa et al. (2010), Musser & Carleton (2005).

Genus TYPHLOMYS

Milne-Edwards, 1877

2. Chapa Tree Mouse   *Typhlomys chapensis*

French: Loir-pygmée de Chapa / German: Vietnam-Zwergbilch / Spanish: Ratón arborícola de Chapa
Other common names: Chapa Pygmy Dormouse, Vietnamese Pygmy Dormouse

Taxonomy. *Typhlomys cinereus chapensis* Osgood, 1932, "Chapa [= Sa Pa], Tonkin," Lào Cai Province, Vietnam.
Typhlomys chapensis currently comprises two former subspecies of *T. cinereus* (chapensis and jingdongensis). Monotypic.
Distribution. SW China (W of the Red River in SW Yunnan) and NW Vietnam (Lào Cai Province).

Descriptive notes. Head–body 61–115 mm, tail 80–126 mm, weight 7·7–22·6 g. Braincase is dome-shaped. The Chapa Tree Mouse is larger than the Soft-furred Tree Mouse (*T. cinereus*) and the Dwarf Tree Mouse (*T. nanus*); dorsal pelage is dark gray to black; venter is yellowish-white; ears are large and naked; eyes are very small; whiskers are long; long tail is lightly furred near base but densely furred at tip (resembling a bottle brush); and hair at tip of tail is white in some individuals.
Habitat. Tropical montane forests above 200 m in elevation.
Food and Feeding. Poorly known. The Chapa Tree Mouse is likely granivorous and frugivorous.
Breeding. No information.
Activity patterns. Poorly known. Like other small forest-dwelling rodents, the Chapa Tree Mouse is likely nocturnal.
Movements, Home range and Social organization. Poorly studied in most respects. Recent behavioral studies of wild-caught animals in laboratory enclosures suggest that this species uses ultrasonic echolocation to navigate among tree branches. Little is known about its behavior in the wild. Like the Soft-furred Tree Mouse, it has been trapped on low branches in trees and on the ground.
Status and Conservation. Not yet assessed on *The IUCN Red List*. Because distribution appears to be small and it occupies threatened tropical forests, it will likely be classified as more threatened than the Soft-furred Tree Mouse after it is assessed by conservationists.
Bibliography. Abramov et al. (2014), Carleton & Musser (1984), Cheng Feng et al. (2017), Musser & Carleton (2005), Osgood (1932), Panyutina et al. (2017), Smith & Yan Xie (2008), Wu Deling & Wang Guanghuan (1984).

3. Soft-furred Tree Mouse   *Typhlomys cinereus*

French: Loir-pygmée de Chine / German: China-Zwergbilch / Spanish: Ratón arborícola de pelaje suave
Other common names: Chinese Pigmy Dormouse, Pygmy Dormouse, Soft-furred Pygmy-dormouse

Taxonomy. *Typhlomys cinereus* Milne-Edwards, 1877, W. Fujian, China.
Typhlomys cinereus was formerly considered conspecific with *T. chapensis* and *T. daloushanensis*. Two subspecies recognized.
Subspecies and Distribution.
T. c. cinereus Milne-Edwards, 1877 – SE China (Anhui, Zhejiang, Jiangxi, and Fujian).
T. c. guangxiensis Wang Yingxiang & Chen Zhiping, 1996 – S China (Guangxi).
Descriptive notes. Head–body 71–76 mm, tail 96–102 mm; weight 15–32 g. Braincase is flattened. The Soft-furred Tree Mouse is the second smallest platacanthomyid; dorsal pelage is medium gray; venter is grayish white; ears are large and naked; eyes are small; whiskers are long; long tail is lightly furred near base but densely furred at tip (resembling a bottle brush); and hair at tip of tail is white in some individuals.
Habitat. Tropical and subtropical montane forests above 200 m in elevation, including bamboo stands and mixed-bamboo forests.
Food and Feeding. Poorly known. The Soft-furred Tree Mouse is likely granivorous and frugivorous, but some reports also mention that it eats leaves and stems.
Breeding. Poorly known. Litter sizes appear to be small, with 1–4 young/litter.
Activity patterns. Poorly known. The Soft-furred Tree Mouse is probably nocturnal. Some reports suggest that it might dig burrows, but this could be speculation based on its reduced eye size.
Movements, Home range and Social organization. Other than reports of its presence in certain habitats, the Soft-furred Tree Mouse has never been the focus of ecological research. Like the Chapa Tree Mouse (*T. chapensis*), it has been trapped both on low branches in trees and on the ground, suggesting that it is less arboreal than the Malabar Spiny Tree Mouse (*Platacanthomys lasiurus*). Given its close evolutionary relationship with the Chapa Tree Mouse and its similar morphology (including exceptionally small eyes), it is possible that this species also uses ultrasonic echolocation for navigation.
Status and Conservation. Classified as Least Concern on *The IUCN Red List*. The Soft-furred Tree Mouse has a wide distribution in China, where it has been regionally listed as least concern. Morphologically distinct and geographically isolated subspecies could be raised to full species status with additional genetic data.

Bibliography. Abramov et al. (2014), Carleton & Musser (1984), Cheng Feng et al. (2017), Cong Haiyan et al. (2013), Corbet & Hill (1992), Lunde & Smith (2008), Musser & Carleton (2005), Osgood (1932), Smith & Yan Xie (2008), Wang Yingxiang et al. (1996).

4. Dalou Mountains Tree Mouse   *Typhlomys daloushanensis*

French: Loir-pygmée du Dalou Shan / German: Dalou Shan-Zwergbilch / Spanish: Ratón arborícola de Dalou

Taxonomy. *Typhlomys cinereus daloushanensis* Wang Yingxiang & Li Chongyun, 1996, "Mt. Jingfu (107° 10' E, 29° 02' N), Nanchuan co., soutern [sic] Sichuan, alt. 2 000 m," China.
This species is monotypic.
Distribution. C China (SE Gansu, S Shaanxi, E Sichuan, Chongqing, W Hubei, and N Guizhou).
Descriptive notes. Head–body 72–105 mm, tail 105–129 mm; weight 15·4–31 g. The Dalou Mountains Tree Mouse is the largest species of *Typhlomys*. Dorsum is charcoal gray; venter is slate gray, with white hairs interspersed throughout; ears are large and naked; eyes are small; whiskers are long; long tail is lightly furred near base but densely furred at tip (resembling a bottle brush); and hair at tip of tail is white in some individuals. Braincase is flattened.
Habitat. Tropical montane forests at elevations above 200 m.
Food and Feeding. Poorly known, but the Dalou Mountains Tree Mouse is probably granivorous and frugivorous.
Breeding. No information.
Activity patterns. Poorly known, but the Dalou Mountains Tree Mouse is probably nocturnal as are other forest-dwelling rodents.
Movements, Home range and Social organization. Poorly known, but given its close evolutionary relationship with the Chapa Tree Mouse (*T. chapensis*) and similar morphologies (including exceptionally small eyes), it is possible that the Dalou Mountains Tree Mouse also uses ultrasonic echolocation for navigation.
Status and Conservation. Not yet assessed on *The IUCN Red List*.
Bibliography. Carleton & Musser (1984), Cheng Feng et al. (2017), Musser & Carleton (2005), Smith & Yan Xie (2008), Wang Yingxiang et al. (1996).

5. Dwarf Tree Mouse   *Typhlomys nanus*

French: Loir-pygmée du Jiaozi / German: Zwergbilch / Spanish: Ratón arborícola enano

Taxonomy. *Typhlomys nanus* Cheng Feng et al., 2017, "Mt. Jiaozi (26° 08' N, 102° 85' E), Wumeng township, Luquan County, Kunming, Yunnan, China; elevation approximately 3,252 m asl."
This species is monotypic.
Distribution. Known only from Mt Jiaozi and Mt Dawei in Yunnan (SW China).
Descriptive notes. Head–body 65–74 mm, tail 97–106 mm; weight 8·8–13·2 g. The Dwarf Tree Mouse is the smallest species of *Typhlomys*. Pelage is distinctly bicolored, with ash-gray dorsum and creamy white venter and cheeks; ears are large and naked; eyes are small; whiskers are long; long tail is lightly furred near base but densely furred at tip (resembling a bottle brush); and hair at tip of tail is white in some individuals. Braincase is dome-shaped.
Habitat. Only known from secondary forests on two mountains at elevations of 2000–3000 m. Forests had acidic, red soil and were composed mostly of George's fir (*Abies forrestii* var. *georgei*, Pinaceae) with undergrowth of bamboo and rhododendron (*Rhododendron*, Ericaceae).
Food and Feeding. Poorly known, but the Dwarf Tree Mouse is probably granivorous and frugivorous.
Breeding. No information.
Activity patterns. Poorly known, but the Dwarf Tree Mouse is probably nocturnal as are other forest-dwelling rodents.
Movements, Home range and Social organization. Poorly known, but given its close evolutionary relationship with the Chapa Tree Mouse (*T. chapensis*) and similar morphologies (including exceptionally small eyes), it is possible that the Dwarf Tree Mouse also uses ultrasonic echolocation for navigation.
Status and Conservation. Not assessed on *The IUCN Red List*.
Bibliography. Cheng Feng et al. (2017).

CLASS MAMMALIA

ORDER RODENTIA

SUBORDER MYOMORPHA

SUPERFAMILY MUROIDEA

Family PLATACANTHOMYIDAE (TREE MICE)

- Small rodents with dormouse-like body forms, large ears, and long tails that resemble a bottle-brush.
- 15–25 cm.

- Palearctic and Indo-Malayan Regions.
- Tropical and subtropical montane forests.
- 2 genera, 5 species, 7 taxa.
- 1 species Vulnerable; none Extinct since 1600.

Systematics

Comprising only two genera and five extant species, the family Platacanthomyidae is among the most poorly studied of all mammalian families. This may soon change, given the recent remarkable discovery that at least one platacanthomyid species may be capable of ultrasonic echolocation. That species, the Chapa Tree Mouse (*Typhlomys chapensis*), is restricted to northern Vietnam and southern China. Its closest relatives are the Soft-furred Tree Mouse (*Typhlomys cinereus*), the Dwarf Tree Mouse (*Typhlomys nanus*), and the Dalou Mountains Tree Mouse (*Typhlomys daloushanensis*), all restricted to China. The Malabar Spiny Tree Mouse (*Platacanthomys lasiurus*), found in the montane forests of south-western India, is the only member of its genus. Although the two genera occur thousands of kilometers apart and differ markedly in external appearance, many skeletal characteristics support the hypothesis that *Platacanthomys* and *Typhlomys* are more closely related to each other than to any other living rodent lineage.

Platacanthomys and *Typhlomys* have long been the subject of taxonomic debate due to their unusual combination of anatomical traits. Conspicuous ears, long-haired tails, and superficial characteristics of the molars led some taxonomists to group these genera with the dormice (Gliridae). Different interpretations of the morphological evidence led others to posit that *Platacanthomys* and *Typhlomys* were allied with muroid rodents, with disagreement about the position of these genera relative to other lineages within the superfamily and debate regarding whether or not the taxon should be designated a tribe, subfamily, or family. Recent morphological assessments that include extinct taxa follow the latter scheme, with Platacanthomyidae nested within Muroidea at the family rank. DNA sequence data from the Soft-furred Tree Mouse confirms this arrangement, clearly demonstrating that Platacanthomyidae is part of Muroidea. Intriguingly, these molecular phylogenies show that Platacanthomyidae is on an isolated long branch and is sister to a clade that comprises all other extant muroid rodent families, which underpins historical biogeographical reconstructions suggesting that the hugely diverse Muroidea had its origin in Eurasia.

A time-calibrated molecular phylogeny of Myomorpha dates the divergence between Platacanthomyidae and the clade comprising the remaining muroid families to 40–45 million years ago in the middle Eocene, although no fossils attributable to Platacanthomyidae have been described from the Eocene or Oligocene. The oldest known platacanthomyid fossils are from the extinct genus *Neocometes* from early Miocene deposits (17–18 million years ago). *Neocometes* had a much wider distribution than either extant platacanthomyid genus. Fossils attributable to *Neocometes* are rare, but they have been recovered across a broad geographical area spanning Eurasia, from modern-day Spain to South Korea. Paleontologists have hypothesized that *Neocometes* is more closely related to *Typhlomys* than *Platacanthomys* based on molar morphology. The oldest fossils belonging to the extant genera *Platacanthomys* and *Typhlomys* are from late Miocene deposits in southern China.

Platacanthomys has been considered monotypic since it was first described in the 19th century. *Typhlomys*, with its much broader distribution, has been recognized as containing anywhere from two to five taxa. New material and data from China and Vietnam have reshaped our understanding of the diversity of *Typhlomys*, including the recent re-elevation of the Chapa Tree Mouse (formerly *T. cinereus chapensis*) and the Dalou Mountains Tree Mouse (formerly *T. cinereus daloushanensis*) to species status, and the discovery of the Dwarf Tree Mouse, a new species. Evidence from DNA sequences and morphology convincingly demonstrate that all four *Typhlomys* species are readily diagnosable, with some species having been separated from one another for millions of years. *Platacanthomys* might also contain more species than are currently recognized, but a taxonomic revision that includes molecular and morphological data has never been published. If platacanthomyids are like other poorly studied small mammal taxa that inhabit tropical and subtropical montane forests, revisionary work that includes molecular data will almost certainly lead to an increase in the family's recognized species-level diversity.

Morphological Aspects

The two genera of Platacanthomyidae do not share many external morphological traits. *Platacanthomys* and *Typhlomys* do, however, possess pale ventral fur, large ears, and long, brush-like tails, tipped with bushy (sometimes white) hairs. They are small rodents and somewhat resemble dormice, with head and body lengths of 70–140 mm and tail lengths of 76–135 mm. The Malabar Spiny Tree Mouse has a longer body and is heavier than the four *Typhlomys* species, but its tail is shorter. Perhaps the most striking difference between the two genera is in the dorsal pelage. In *Platacanthomys*, this region is light brown and interspersed with white-tipped, flattened spines, whereas all species of *Typhlomys* have soft, dark gray dorsal pelage and no spines. *Typhlomys* species also have very small eyes (approximately 1 mm in diameter in the Chapa Tree Mouse)—much smaller than the Malabar Spiny Tree Mouse, other arboreal rodents, and even most bats—a feature that has led some researchers to refer to them as the "blind" tree mice. Histological examinations of the eyes of Chapa Tree Mice show degraded retinas and vision-associated neurons, supporting the hypothesis that *Typhlomys* species have limited vision.

Despite their divergence in external appearance, distinctive skulls and molars of *Platacanthomys* and *Typhlomys* strongly support the hypothesis that these genera belong to the same evolutionary lineage. Their three molars possess flattened arrays of parallel, oblique ridges somewhat similar to those of the dormice (Gliridae) or the Sleek-furred Ground Rat (*Gymnuromys roberti*, Nesomyidae). Morphological assessments that include extinct and extant species have shown that these similarities evolved convergently. In platacanthomyids, the third molars are noticeably smaller than the first two. Platacanthomyids follow the typical muroid dental formula: I 1/1, C 0/0, P 0/0, M 3/3 (×2) = 16. A relatively large braincase and short rostrum contribute to their dormouse-like appearance. The auditory bullae of platacanthomyids lack septa and are much smaller than those of true dormice.

The Malabar Spiny Tree Mouse lacks a cecum—another intriguing anatomical parallel to the dormice. The Soft-furred Tree Mouse has a cecum, although it is small (c.25 mm). The digestive tract of other *Typhlomys* species has yet to be examined. The Malabar Spiny Tree Mouse has two pairs of mammae, but the Soft-furred Tree Mouse has four pairs. Platacanthomyids have relatively long tails and digits suggestive of an arboreal lifestyle. The front feet have four clawed digits and a thumb with a nail. Both genera have five digits on their hindfeet, claws on all except for the hallux of the Malabar Spiny Tree Mouse (which could be semi-opposable). The Malabar Spiny Tree Mouse has been observed moving nimbly high in the forest canopy and often builds its nests in tree holes. It is occasionally observed and trapped on the ground. Little is known about the locomotion of the four *Typhlomys* species, but individuals are often caught on the ground and at least one species (the Chapa Tree Mouse) moves adeptly among branches while echolocating, suggesting a partially arboreal lifestyle.

Habitat

Platacanthomyids occur in evergreen forests and deciduous riparian corridors in only two parts of the world: the Western Ghats of southern India (*Platacanthomys*) and highlands of central China through northern Vietnam (*Typhlomys*). Both genera occur in mountainous regions at elevations of 300–3000 m above sea level. Malabar Spiny Tree Mice prefer habitats with closed canopies and high densities of lianas. Rocky hillsides interspersed among forested habitats are also used. Large tracts of primary forest are preferred over small, fragmented patches, but Malabar Spiny Tree Mice have been observed foraging in neighboring cropland. Chapa Tree Mice, Dalou Mountains Tree Mice, and Soft-furred Tree Mice have been captured in bamboo stands and
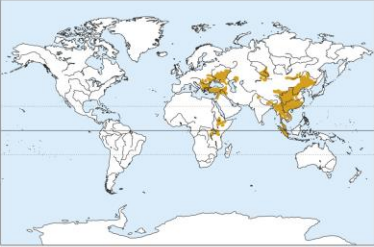

The **Malabar Spiny Tree Mouse**, found only in the montane forests of south-western India, is named from the flattened, white-tipped spines that are interspersed with the light brown hairs of its dorsal pelage. Its tail, lightly furred toward the base but with a dense brush at the tip, contributes to the dormouse-like appearance. The Malabar Spiny Tree Mouse has a longer body and proportionally shorter tail than the other members of the family, one of a number of marked external differences between Platacanthomys and Typhlomys.

Platacanthomys lasiurus
Indira Gandhi Wildlife Sanctuary and National Park, Tamil Nadu, India.
Photo: Kalyan Varma

The **Soft-furred Tree Mouse** is the smallest platacanthomyid. The two Typhlomys species have tails that are much longer than their bodies, but like the Malabar Spiny Tree Mouse (Platacanthomys lasiurus), their tails are lightly furred toward the base and brush-like at the tip. They are found in northern Vietnam and in central and southern China, thousands of kilometers away from the Malabar Spiny Tree Mouse, other arboreal rodents. Fossil evidence indicates that the family once had a far wider distribution, from Spain to South Korea, and that the platacanthomyids diverged from the clade comprising all other extant muroid (mouse-like) rodent families 40–45 million years ago.

Typhlomys cinereus
(captive) Moscow Zoo, Russia.
Photo: Klaus Rudloff

CLASS MAMMALIA
ORDER RODENTIA
SUBORDER MYOMORPHA
SUPERFAMILY MUROIDEA

Family SPALACIDAE (MUROID MOLE-RATS)

- Small to medium-sized rodents with adaptations for subterranean lifestyle such as cylindrical bodies, enlarged incisors and reduced tails, eyes, and ear pinnae.
- 13–70 cm.

- Palearctic, Afrotropical, and Indo-Malayan Regions.
- Steppe, grassland, meadows, forests, bamboo thickets, and farmland from sea level to elevations of 4500 m.
- 7 genera, 28 species, 45 taxa.
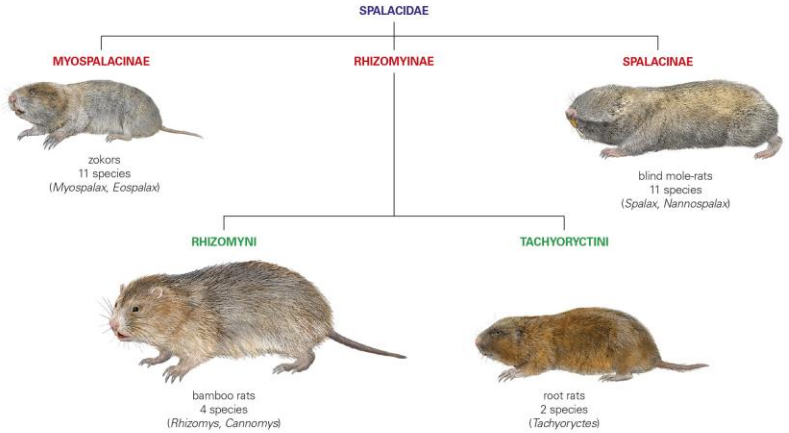- 2 species Endangered, 1 species Vulnerable; none Extinct since 1600.

Systematics

The family Spalacidae unites several distinct groups of Old World subterranean and fossorial muroid rodents. All members of the family exhibit multiple specialized characteristics for life underground such as cylindrical bodies, small or subcutaneous eyes, small or absent ear pinnae, short or absent tails, and enlarged incisors. No popular common name exists for the group, but all members have been referred to as mole-rats at some point or another, and the family is collectively referred to here as the "muroid mole-rats." The muroid mole-rats should not be mistaken for other groups of unrelated burrowing rodents that have also been called mole-rats such as the Naked Mole-rat (*Heterocephalus glaber*, Heterocephalidae), the African mole-rats (Bathyergidae), or various fossorial murines.

Muroid mole-rats are divided into three subfamilies: Myospalacinae that contains the zokors of Asia, Rhizomyinae that contains the bamboo rats of Asia and the root rats of East Africa, and Spalacinae that contains the blind mole-rats of East-ern Europe, Western Asia, and the Middle East. Despite their shared subterranean lifestyle, the three subfamilies of muroid mole-rats had traditionally been considered as separate evolutionary radiations until molecular studies, beginning in 2004, demonstrated that they form a monophyletic group.

Although all living muroid mole-rats exhibit a subterranean or fossorial lifestyle, L. J. Flynn in 2009 outlined paleontological evidence that indicated that members of the family evolved this way of life on multiple occasions convergently. Thus, many characteristics of the family listed by R. W. Norris and colleagues in 2004, such as reduction of eyes and ear pinnae, triangular braincase, and extensive neck musculature, were probably independently derived adaptations to life underground. Muroid mole-rats do appear to share a certain degree of modification in their myomorphy. They lack a narrow ventral slit in the infraorbital foramen, potentially due to their divergence along the muroid line prior to the evolution of the complete myomorphy seen in the Eumuroida—a clade defined by S. J. Steppan and colleagues in 2004 to unite the families Calomyscidae, Nesomyidae, Cricetidae, and Muridae.

SPALACIDAE

MYOSPALACINAE — **RHIZOMYINAE** — **SPALACINAE**

zokors
11 species
(*Myospalax, Eospalax*)

blind mole-rats
11 species
(*Spalax, Nannospalax*)

RHIZOMYNI — **TACHYORYCTINI**

bamboo rats
4 species
(*Rhizomys, Cannomys*)

root rats
2 species
(*Tachyoryctes*)

Subdivision of the Spalacidae

[Figure Toni Llobet]

FAMILY
SUBFAMILY
TRIBE

*The muroid mole-rats are divided into three subfamilies representing three highly distinct lineages. These were traditionally considered as separate evolutionary radiations, until molecular studies demonstrated that they share a common ancestor distinct from all other muroids. The subfamily Myospalacinae includes eleven species of zokors from central and eastern Asia, separated into two genera by the shape of the back of the skull. The "flat occiput" zokors of the genus Myospalax, including the **Altai Zokor**, are distributed in Kazakhstan, Russia, Mongolia, and China. Zokors have small eyes and ear pinnae, which are often hidden in their fur. They have large curved claws on their enlarged forelimbs, which they use for digging, and which fold under their feet when they are walking.*

Myospalax myospalax
Photo: Alexander Zhigalin

Although it was not widely adopted until the application of genetic techniques, the idea of a group that unites Myospalacinae, Rhizomyinae, and Spalacinae can be traced to T. Tullberg's seminal work in 1899. The taxonomic history of muroid mole-rats is complex, and G. G. Musser and M. D. Carleton in 2005 provided a particularly thorough overview. Many taxonomic arrangements have been proposed for these subfamilies. For example, numerous authors have historically adopted approaches combining two of the three subfamilies to the exclusion of the third. E. R. Alston in 1876 and O. Thomas in 1897 united Rhizomyinae and Spalacinae into the family Spalacidae to the exclusion of Myospalacinae. G. S. Miller and J. W. Gidley in 1918 and G. M. Allen in 1940 united Myospalacinae and Spalacinae in the family Spalacidae to the exclusion of Rhizomyinae. Likewise, individual subfamilies have been placed in various locations across the muroid tree. Myospalacinae was treated as a family by I. Ya. Pavlinov and O. L. Rossolimo in 1987, or as allied to cricetines by I. M. Gromov and I. Ya. Polyakov in 1977, or arvicolines by Miller in 1896, M. Kretzoi in 1955, and others. Rhizomyinae in particular is often treated as a separate family, especially in paleontological literature. Root rats in the genus *Tachyoryctes* were separated from Rhizomyinae by R. Lavocat in 1978, who proposed that they were more closely related to Nesomyidae. Spalacinae has also been treated as a separate family by numerous authorities or as allied to cricetids. Monophyly of the subfamilies of muroid mole-rats has rarely been challenged, with the exception of Rhizomyinae, where the grouping of its African (*Tachyoryctes*) and Asian (*Rhizomys* and *Cannomys*) taxa has been disputed as noted above.

The phylogenetic position of muroid mole-rats began to clarify with the introduction of molecular data. DNA-DNA hybridization studies first suggested that muroid mole-rats might be rather distantly related to core muroids such as *Mus* in the late 1980s. As early as 1997, M. F. Robinson and colleagues indicated a sister relationship between an early diverging clade of fossorial muroids (including Spalacinae and Rhizomyinae) and most of the remaining muroid rodents, but with only moderate support. These results were soon confirmed with more

There are currently six recognized species of "convex occiput" zokors in the genus Eospalax. They are found only in China. Five of the six species are found in Sichuan. The individual shown here is one of three possible, very similar species that were recently separated—either the Qinling Zokor (E. rufescens), the Gansu Zokor (E. cansus), or the Plateau Zokor (E. baileyi). All these forms have at various times been considered subspecies or synonyms of one another or of Fontanier's Zokor (E. fontanierii). Studies of mtDNA, cranial morphology, molar shape, and hair morphology support treating them as distinct species. Further species may well be found, particularly among geographically separated populations of E. cansus and E. baileyi.

Eospalax sp.
Sichuan, China.
Photo: Zhang Ming

*The **Lesser Bamboo Rat** is nocturnal and leaves its burrow to feed. Unlike some of the Rhizomys bamboo rats, it builds extensive burrows, reaching lengths of 58 m and depths of 60 cm. The burrow is plugged during the day. Densities of Lesser Bamboo Rat can reach 600 ind/ha. A study of the density and biomass of large herbivores and other mammals in a dry tropical forest in Western Thailand found that the Lesser Bamboo Rat comprised about 15% of total mammal biomass. As well as providing a major prey source for small carnivores, the researchers suggested that the Lesser Bamboo Rat probably influences the dynamics of the overlying plant community because of the scale of its burrowing.*

Cannomys badius
(captive) Berlin Zoo, Germany.
Photo: Klaus Rudloff

*Muroid mole-rat burrows vary in size and complexity. They usually include a nest chamber lined with dry vegetation, one or more toilet chambers, several food storage chambers, and feeding tunnels. The **Chinese Bamboo Rat** digs a central den chamber of 20–25 cm diameter, lined with bamboo leaves. The burrows are up to 45 m long and extend up to 20–30 cm below the surface. There are 4–7 external entrances, indicated by spoil mounds 50–80 cm in diameter and 20–40 cm high. After about a year, when the food resources in the surrounded area have been used up, the solitary occupant abandons the burrow. Bamboo rats spend more time aboveground than other spalacids and some individuals maintain more than one burrow.*

Rhizomys sinensis
(captive) Wolong National Nature
Reserve, Sichuan, China.
Photo: Keith & Liz Laidler/ardea.com

ing. Incisors are ungrooved and not used for excavation to the same degree as other spalacids. Diploid number is 2n = 44–64.

Bamboo rats range in size from the Lesser Bamboo Rat (head and body length c.200 mm, weight c.500 g) to the Indomalayan Bamboo Rat (head and body length c.370 mm, weight c.3 kg). Tails are short and sparsely haired in *Cannomys* or naked in *Rhizomys*. Although still fossorial, they may not qualify as subterranean. Bamboo rats probably spend more time aboveground than other spalacids, and this is reflected in their morphology. Eyes and ears are small but visible. Pelage is gray, brownish, or reddish. Southern forms have sparser and coarser hair than is present in other spalacids. Claws are large

but do not reach the extremes seen in zokors. Incisors are orange, and the mouth closes behind them to allow for digging without soil getting in the mouth. Incisors are oriented nearly vertically in *Rhizomys*, but they protrude forward in *Cannomys*. Diploid number is usually 2n = 50.

Root rats have approximate head and body lengths of 160–310 mm and approximate weights of 140–930 g. The Giant Root Rat is roughly three times the size of the African Root Rat. Root rats have short well-haired tails that are 20–30% of head and body lengths. They vary widely in color, with individuals being black, gray, brown, and reddish. Albinos are not uncommon. Females tend to be darker than males. Eyes and ear pin-

nae are small but visible. Eyes are positioned distinctively high on the head in the Giant Root Rat. Like bamboo rats, root rats are chisel-diggers and have orange incisors that protrude from the mouth when it is closed. Diploid number is 2n = 48 or 50.

Blind mole-rats have approximate head and body lengths of 130–350 mm and approximate weights of 50–1000 g. They range from the small Middle East Blind Mole-rat to the large Giant Blind Mole-rat. No external tail, pinnae, or eyes are present. They have soft, nearly reversible, pelage that is gray to brown and can be reddish or yellowish. The anterior part of the head is often lighter in color, and a line of tactile bristles extends laterally along the side of the snout forming a keel,

which can provide a mustached appearance. Blind mole-rats are chisel-diggers. Incisors are large and powerful, and lips close behind them. Lower incisors are very long and shovel-like. The wide, flat head serves as a bulldozer to move earth away, an action aided by powerful musculature. The cecum is large, and a spiral valve is present that increases the surface area for absorption. Chromosomes are widely variable; diploid number is 2n = 36–62. Diploid number is virtually unchanged across the genus *Spalax*, whereas extreme variability is present in each *Nannospalax* superspecies.

Blind mole-rats are the only rodents that completely lack an external eye and probably have the most rudimentary eyes

*A single **Lesser Blind Mole-rat** digs around 1·7 m of tunnel daily, throwing out 10 kg of excavated dirt, or more than 20 times its own weight. Its burrows have a main tunnel with secondary tunnels branching off, reaching a total length of 65–195 m, spread over 200–1000 m². An oval shaped, grass-lined nest chamber is located centrally, at a depth of 25–50 cm. Like other spalacids, Lesser Blind Mole Rats are solitary and aggressive toward others of their kind. Blind Mole-rats are polyphasic, with two or three peaks of activity during the day and night. Although their eyes cannot perceive images, the brief exposure to daylight when pushing soil to the surface seems to be sufficient to maintain a circadian rhythm.*

Nannospalax leucodon
Republic of Macedonia.
Photo: Rollin Verlinde

*Root rats use their chisel-like teeth to excavate their burrows. They push the soil behind them with their feet, and when the heap reaches a certain size, they turn round and shove it away with their heads and one forelimb. Temperatures high in Ethiopia's Bale Mountains can fall well below freezing during the night, but rise rapidly when the sun is up. In the dry season, daily temperatures may fluctuate by 30°C or more. At 50 cm below the surface, the **Giant Root Rat**'s preferred burrow depth, these fluctuations are minimized. In January, the temperature at this depth was a constant 9°C throughout the day.*

Tachyoryctes macrocephalus
Bale Mountains National Park,
Ethiopia.
Photo: Neil Bowman/
FLPA/age fotostock

PLATE 7

inches 2
cm 5

1 2 3 4 5 6 7 8

Genus *CALOMYSCUS*
Thomas, 1905

1. Zagros Mountains Brush-tailed Mouse
Calomyscus bailwardi

French: Calomysque de Bailward / **German:** Zagros-Maushamster / **Spanish:** Ratón de cola de cepillo de Zagros

Other common names: Zagros Mountains Calomyscus, Zagros Mountains Mouse-like Hamster

Taxonomy. *Calomyscus bailwardi* Thomas, 1905, "Mala-i-Mir, 70 mi. N.E. of Ahwaz, 4300' [= 1311 m]," SW Persia. Modified by G. G. Musser and M. D. Carleton in 2005 to "Mala-i-Mir (= Izeh), 120 km SE Ahwaz (= Ahaz), Zagros Mtns., Eastern Khuzistan Province, WC Iran."
All currently recognized species of brush-tailed mice, except for *C. urartensis*, have previously been recognized as subspecies of *C. bailwardi*, demonstrating minor differences observed in morphology and color among these taxa. Elevation of these forms to distinct species was originally based on karyotypic differentiation but has been further supported by morphometric and molecular analyses. Six distinct karyotypes, five of which were sampled from a different province, have been reported for *C. bailwardi*. Specimens collected from near the type locality in the Khuzistan Province have a karyotype with a diploid number of 2n = 46 and an autosomal fundamental number of FNa = 44, whereas a karyotype with a 2n = 37 and FNa = 40 has been found in the northwestern Zagros Mountains, Bahtaran (= Kermanshah) Province. In the southern part of this mountain range, karyotypes with a 2n = 52 and FNa = 56 and 2n = 50 and FNa = 48 or 50 have been found in Kerman and Fars provinces respectively. Specimens of *C. bailwardi* from southern and central parts of its distribution (Fars, Kerman, southern Yazd, and central Hormozgan provinces) form a monophyletic clade with material from near the type locality (Khuzestan Province) in phylogenetic analyses of mitochondrial sequences. The level of genetic divergence between the subclade from near the type locality and the clade containing samples southeast of the type locality suggests the presence of more than a single species. In these newer analyses, this clade falls within a "southern clade" that also includes *C. baluchi* and *C. hotsoni*; however, sequences from specimens from more northern areas of the Zagros Mountains are not contained in this southern clade. Material from Kurdistan forms a monophyletic clade that is sister to *C. urartensis*, and material from Kermanshah forms a monophyletic clade that is sister to *C. grandis* within a larger northern clade. Although no subspecies are currently recognized, there is strong evidence that some northern and southern population currently recognized as *C. bailwardi* likely represents undescribed phylogenetic species. B. Kryštufek and V. Vohralík in 2009 reviewed the reports of *Calomyscus* from Turkey (Gaziantep and Hakkâri provinces) and discussed the possibility that *C. bailwardi* occurs in south-eastern and southern Turkey. However, the populations of *Calomyscus* in north-western Iran (West Azerbaizan and Kurdistan provinces) in the closest proximity to the localities reported from Turkey are *C. urartensis* and not *C. bailwardi*. No specimens are available from Turkey to either verify the occurrence or identify the taxon that may be present. Monotypic.
Distribution. Limits of distribution unresolved but currently known from W & S Iran (Zagros Mts as far E as the Kerman Province and the N Genu Mts of Hormozgan Province); it may occur in S & SE Turkey (Gaziantep and Hakkâri provinces).
Descriptive notes. Head–body 80–92 mm, tail 81–92 mm, ear 18–20 mm, hindfoot 19–22 mm; weight 17–22 g. Ears and hindfeet of the Zagros Mountains Brush-tailed Mouse are similar in length, and tail is only slightly longer than head–body length. It is pinkish buff but darker on back due to presence of black-tipped hairs. Head is buffy and slightly paler than back. Belly is pure white, with sharp demarcation with buffy pelage along flanks. White pelage extends to cheeks and nearly to eyes. Dorsal surface of feet is white, and tail is bicolored with grayish buff above and white below. Ears are naked, pale grayish brown, with small white patches at bases. Skull is small and narrow, with condylobasal lengths of 22·4–23·7 mm and zygomatic breadths of 12·2–13·2 mm. M_1 is wider than in most other species of brush-tailed mice.

Habitat. Dry rocky hills, ridge lines, and mountain sides, often with large boulders and scant vegetation. Vegetation is typically xerophylic and includes bunches of grass, thistles, and knapweed (*Centaurea* spp., Asteraceae). The Zagros Mountains Brush-tailed Mouse is also commonly found in rock walls surrounding grain fields.
Food and Feeding. Poorly known. The Zagros Mountains Brush-tailed Mouse likely feeds on grass seeds, including *Bromus* spp. (Poaceae), and thistle buds that have been found in little piles under overhanging rocks in the habitat where these mice are abundant.
Breeding. Juvenile Zagros Mountains Brush-tailed Mice with body weights of 7–16 g have been collected from the southern Zagros Mountains in late April and early May. Lactating females, each with four placental scars, were found in December along with an additional female with two uterine swellings. These data suggest the litter sizes are 2–4 young.
Activity patterns. No information.
Movements, Home range and Social organization. Poorly known. The Zagros Mountains Brush-tailed Mouse is reported to occur in very high density in the lacustrine habitat in the valley above Lake Parishan (= Famur) in Fars Province.
Status and Conservation. Classified as Least Concern on *The IUCN Red List*.
Bibliography. Akbarirad *et al.* (2016c), Ashrafzadeh (2010), Corbet (1978), Graphodatsky *et al.* (2000), Hashemi *et al.* (2006), Karami *et al.* (2008), Kryštufek & Vohralík (2009), Lay (1967), Malikov *et al.* (1999), Musser & Carleton (2005), Morshed & Patton (2002), Norris *et al.* (2003), Shahabi, Ali. (2011), Vorontsov *et al.* (1979), Zarei *et al.* (2013).

2. Hotson's Brush-tailed Mouse   *Calomyscus hotsoni*
French: Calomysque de Hotson / **German:** Hotson-Maushamster / **Spanish:** Ratón de cola de cepillo de Hotson

Other common names: Hotson's Calomyscus, Hotson's Mouse-like Hamster, Hotson's Mouse-tailed Hamster

Taxonomy. *Calomyscus hotsoni* Thomas, 1920, "Gwambuk Kaul, about 30 miles [= 48 Km] S. W. of Panjgur, 2,700' [= 823 m]," Makran District, W Balochistan, SW Pakistan.
Calomyscus hotsoni was originally recognized as a distinct species based primarily on its smaller size. It has been treated as a subspecies of *C. bailwardi* in several revisions in part based on undocumented report of intergradation with *C. baluchi* in southern Pakistan, a species that is morphologically very similar to *C. bailwardi*. Comprehensive revision of the genus in 1979 supported morphological distinctiveness of *C. hotsoni*, and it was returned to specific status. R. W. Norris and colleagues in 2008 demonstrated that *C. hotsoni* was morphologically and molecularly distinct from *C. baluchi*. Morphometric analyses with wider taxon sampling all support morphological distinctiveness of *C. hotsoni*. Phylogenetic analyses recover *C. hotsoni* as either the sister taxon of *C. baluchi* or *C. bailwardi* and consistently place these three taxa in a southern clade. Phylogeographic analyses recover clinal variation in size and molecular sequences among populations in south-eastern Iran. Three karyotypes have been reported from specimens in south-eastern Iran including a 2n = 48 and FNa = 46 from the Bagheran Mountains of South Khorasan Province, a 2n = 48 and FNa = 48 from the Birk and Malek Siah Kuh Mountains, and a 2n = 50 and FNa = 48 from the Birk Mountains of Sistan and Baluchestan Province. This demonstrates geographical variation among populations inhabiting these mountain ranges and polymorphism within the population in the Birk Mountains. While some of the specimens from the Bashagard Mountains (Hormozgan Province), the highlands in northern Fanuj (Sistan and Baluchestan Province), and Anbar Abad (Kerman Province) of south-eastern Iran reported as *C. hotsoni* by A. Khajeh and colleagues in 2015 likely represent this species, two of these localities are closer to known populations of *C. bailwardi* and so they may be representatives of that species. Monotypic.
Distribution. E & SE Iran, from Bagheran Mts of S Khorasan Province and desert mountain ranges (Abkhan, Malek Siah Kuh, and Birk) of Sistan and Baluchestan Province, E to dry coastal hills, the Central Makran Range and intermountain desert ranges of Balochistan in SW Pakistan, and Southern Kirthar Mts in Sindh Province of S Pakistan; it may occur in the Bashagard Mts, highlands in N Fanuj, and Anbar Abad of SE Iran.
Descriptive notes. Head–body 67–85 mm, tail 73–90 mm, ear 12–20 mm, hindfoot 16–20 mm; weight 14–25 g. Hotson's Brush-tailed Mouse is one of the smaller species of brush-tailed mice, and ears are generally being shorter than hindfoot. Skull has narrow interorbital region, palatal foramina of medium length, and rather small auditory bulla. Greatest length of skull ranges from 22·7 mm to 25·7 mm, with zygomatic breadths of 10·7–12·2 mm. M_1 has long entoconid cusp. Dorsal pelage is darker than in most other species of brush-tailed mice due to blackish tipped hairs.
Habitat. Rocky associated with dwarf palms (*Nannorrhops ritchieana*, Arecaceae) and dry, rocky mountaintops with shrubby vegetation at elevations of 67–1890 m in southern Pakistan and rocky hillsides and along rocky outcrops in association with vegetation including common fig (*Ficus carica*, Moraceae), pistachio (*Pistacia atlantica*, Anacardiaceae), ephedra (*Ephedra* sp., Ephedraceae), and oats (*Avena sativa*, Poaceae) in south-eastern Iran. Hotson's Brush-tailed Mouse appears to be restricted to the Saharo-Sindian phylogeographic region, an area characterized by hot, dry summers and mild winters.

Food and Feeding. In south-eastern Iran, Hotson's Brush-tailed Mice appear to feed on seeds of common fig and pistachio because large amounts of seeds from these plants have been recovered from their burrows.
Breeding. Poorly known. A lactating female Hotson's Brush-tailed Mouse was captured in June, and juveniles have been collected in May.
Activity patterns. No information.
Movements, Home range and Social organization. Based on trap success, Hotson's Brush-tailed Mouse has considerable variation in densities, with 0·6% trap success at dry sparsely vegetated areas and 4–8% trap success at more mesic sites with more vegetation. It has a more calm behavior when handled than some other species of brush-tailed mice. In captivity, it is highly social and does not show any aggressive behavior toward conspecific or congeneric cage mates. It occurs sympatrically with Persian Jird (*Meriones persicus*) and has been found inhabiting the same burrows in south-eastern Iran. Use of burrows of Persian Jirds may allow Hotson's Brush-tailed Mouse to inhabit areas without sufficient rock crevices and voids for their nest sites.
Status and Conservation. Currently classified as Least Concern on *The IUCN Red List*. In 1996, it was classified as Endangered. Downlisting resulted from the known distribution of Hotson's Brush-tailed Mouse being expanded from only its type locality in Balochistan to multiple areas in south-eastern Iran and south-western Pakistan. Prior to downlisting, recommendations had been made to establish a captive breeding population. Populations are known to occur in Kirthar and Hingol national parks in southern Pakistan. Recent surveys in south-eastern Iran have provided a better understanding of the habitat requirements of Hotson's Brush-tailed Mouse.
Bibliography. Akbarirad *et al.* (2016b, 2016c), Corbet (1978), Ellerman (1941), Ellerman & Morrison-Scott (1951), Hamidi *et al.* (2017), Khajeh *et al.* (2015), Mohammadi *et al.* (2013), Molur *et al.* (2005), Norris, Morshed *et al.* (2003), Norris, Woods & Kilpatrick (2008), de Roguin (1988), Shahabi, Aliabadian *et al.* (2013), Shahabi, Zarei & Sahebjam (2010), Vorontsov *et al.* (1979), Zarei *et al.* (2013).

3. Pakistan Brush-tailed Mouse   *Calomyscus baluchi*
French: Calomysque du Baloutchistan / **German:** Belutschistan-Maushamster / **Spanish:** Ratón de cola de cepillo de Pakistán

Other common names: Baluchi Brush-tailed Mouse, Baluchi Calomyscus, Baluchi Mouse-like Hamster, Pakistan Mouse-tailed Hamster

Taxonomy. *Calomyscus baluchi* Thomas, 1920, "Kelat District, Baluchistan," W Pakistan.
Calomyscus baluchi was originally described as a distinct but closely related species to *C. bailwardi* that could be differentiated by its smaller ears and longer palatine foramina. Latter revisions treated it as a subspecies of *C. bailwardi* until N. N. Vorontsov and colleagues in 1979 conducted a comprehensive revision of the genus that elevated it to a distinct species. They noted, however, that the two species were morphologically very similar but their distributions were separated by presence of a morphologically distinct species, *C. hotsoni*. Results of molecular phylogenetic analyses support the specific status of *C. baluchi* and its close relationship with *C. bailwardi*. No karyotypic data are available. Two subspecies are recognized, but preliminary phylogeographic analysis failed to provide support for their recognition, analyses with greater geographic coverage are needed.
Subspecies and Distribution.
C. b. baluchi Thomas, 1920 – EC Afghanistan (S Koh-i-Baba Mts) and W Pakistan (N Waziristan to Balochistan).
C. b. mustersi Ellerman, 1948 – NE & NC Afghanistan and NW Pakistan (N Federally Administered Tribal Areas and W Khyber Pakhtunkhwa Province).
Descriptive notes. Head–body 73–97 mm, tail 63–102 mm, ear 16–21 mm, hindfoot 18–25 mm; weight 15–30 g. The Pakistan Brush-tailed Mouse is morphologically similar to the Zagros Mountains Brush-tailed Mouse (*C. bailwardi*) but has smaller ears (mean 17·6 mm compared to 19·4 mm) and long palatal foramina. Two subspecies have been described that are morphologically similar but differ in color, with nominate *baluchi* a sandy buff and *mustersi* a rather grizzled drab gray. Skull is similar to the Zagros Mountains Brush-tailed Mouse with condylobasal lengths of 20·2–23·6 mm and zygomatic breadths of 11·2–13·2 mm but averages somewhat narrower in breadth (12·5 mm compared to 12·7 mm).
Habitat. Primarily steppic forest with junipers (*Juniperus macropoda*, Cupressaceae) and pistachios (*Pistacia khinjuk*, Anacardiaceae) in areas with rocky terrain at elevations of 400–3500 m. In the northern parts of its distribution, the Pakistan Brush-tailed Mouse also has been found in areas with evergreen oaks (*Quercus* sp., Fagaceae). While primarily found in dry, rocky hills, rock walls, and stone piles, the Pakistan Brush-tailed Mouse has also been collected from burrows excavated by the Persian Jird (*Meriones persicus*) but is notably absent from valley floors that are devoid of exposed rocks.
Food and Feeding. The Pakistan Brush-tailed Mouse is granivorous, caching seeds in their burrows and concealing them under stones. It feeds on acorns and seeds of vari-

Skulls of brush-tailed mice are very *Peromyscus*-like. The braincase is broad and rather flat, and the zygomatic plate is straight anteriorly. The tympanic bulla is small, and the jugal is long and rather broad. The coronoid process is thin and long, extending well over the mandibular condyle. Dentition of brush-tailed mice consists of one incisor and three molars in each upper and lower jaw; the dental formula is I 1/1, C 0/0, P 0/0, M 3/3 (×2) = 16. Incisors are smooth and dull yellow. Molars are brachyodont, with an asymmetrical bi-serial arrangement of five cusps on the first two molars and only three cusps on the third molar.

Morphological differences among species of brush-tailed mice are rather cryptic relative to color, size, and cranial and dental measurements. Forms in the genus are so similar in morphology that they were considered conspecific prior to investigations of karyotypic differentiation, hybridization, and mitochondrial sequence divergence.

Habitat

Brush-tailed mice primarily inhabit barren rocky and scarcely vegetated dry mountain sides in deserts, semi-deserts, and arid steppes at elevations near sea level (67 m) to 3500 m. They nest primarily in crevices in rocky outcrops and voids in rock piles and stone walls. A single nest has been observed that consisted of a ball of fine grass and sheep wool. At some high elevations, they occur in old relict cedar forest composed of *Cupressus sempervirens* and Greek juniper (*Juniperus excelsa*), both Cupressaceae, where they use hollows in lower parts of trunks and dead roots of old trees as shelter. At mid-elevations, they are found on rather barren rocky mountain sides with vegetation such as Greek juniper, evergreen oaks (*Quercus*, Fagaceae), dog-rose (*Rosa canina*, Rosaceae), barberry (*Berberis integerrima*, Berberidaceae), and pistachio tree (*Pistacia atlantica*, Anacardiaceae). At lower elevations, they inhabit rocky situations with

*Like all other brush-tailed mice, the **Great Balkhan Brush-tailed Mouse** mostly eats the seeds and fruits of grasses, herbs, and shrubs. Much of what is known about the diet of wild brush-tailed mice comes from caches of food found in their burrows or under overhanging rocks. They are not known to hibernate and in the northern parts of their range, they may be dependant on these caches during the winter. In the warm months, brush-tailed mice are strictly nocturnal, but during cold weather, they may be active in the early morning and afternoon.*

Calomyscus mystax
(captive) Germany.
Photo: Jonas Livet

*Little is known about the reproduction of brush-tailed mice in the wild. Juvenile **Zagros Mountains Brush-tailed Mice** with body weights of 7–16 g (compared with adult weights of 17–22 g) have been collected from the southern Zagros Mountains in late April and early May. Lactating females, each with four placental scars, were found in December. Brush-tailed mice are most frequently characterized as being solitary or occurring in small family groups. In the wild, they have been reported to share favorable shelter sites.*

Calomyscus bailwardi
Ferdowsi University of Mashhad,
Mashhad, Razavi Khorasan, Iran.
Photo: Kordiyeh Hamidi

Captive brush-tailed mice breed throughout the year, but peak production of litters occurs in March–April. The number of litters per female is high: one female produced 15 litters, totaling 41 young, during a 28-month period.

*It is common for wild brush-tailed mice to produce a single litter in the spring or summer; a few individuals may produce a second litter in the fall. In the wild, juvenile and subadult **Goodwin's Brush-tailed Mice** have been captured in spring and summer, but more were captured in summer. The earliest pregnancy reported in any brush-tailed mouse involved a Goodwin's Brush-tailed Mouse of not quite four months old. Generally, the first pregnancy occurs at 6–7 months of age, while males begin to reproduce at five months. Gestation in brush-tailed mice is 29–31 days, which is longer than in other muroid rodents of similar size. Newborns are blind, but have ears separated from their heads. They appear hairless but, when closely examined, are covered with a very thin and fine coat of dark colored hair. By ten days after birth, their coats appear complete.*

Calomyscus elburzensis
Ferdowsi University of Mashhad,
Mashhad, Razavi Khorasan, Iran.
Photos: Kordiyeh Hamidi

PLATE 9

inches 4
cm 10

Subfamily CRICETOMYINAE

Genus *BEAMYS*

Thomas, 1909

34. Greater Long-tailed Pouched Rat   *Beamys major*

French: Grand Rat-hamster / **German**: Große Hamsterratte / **Spanish**: Rata de abazones grande

Other common names: Greater Pouched Rat

Taxonomy. *Beamys major* Dollman, 1914, "Mlanje, Nyasaland," Malawi, south-eastern Africa.
Some authorities have considered it conspecific with *B. hindei* but it is morphologically distinct from that species and occupies a different habitat. Monotypic.
Distribution. N & E Zambia, Malawi, and NC Mozambique (Mt Mabu).
Descriptive notes. Head-body 136–173 mm, tail 126–143 mm, ear 19–21 mm, hindfoot 21–25 mm; weight 95–102 g. The Greater Long-tailed Pouched Rat is medium-sized, with well-developed cheek pouches. Fur is soft and gray dorsally, shading to pure white ventrally. Chin, throat, and upper chest are white. Ears are relatively large. Tail is long and prehensile, with conspicuous white markings. Limbs are relatively short and white, with four digits on forefeet and five digits on hindfeet. Males are on average larger than females, with considerable overlap in measurements between sexes.
Habitat. Montane and riparian forests typically at elevations of 500–1000 m.
Food and Feeding. The Greater Long-tailed Pouched Rat mostly eats fruits and seeds that might be cached in burrows. Insects constitute a smaller proportion of the diet.
Breeding. Pregnant Greater Long-tailed Pouched Rats have been recorded during the rainy season in November–May. Average litter size is 4-6 young. Growth is rapid, with young reaching 43 g within the first four weeks. Gestation in captivity in the closely related Hinde's Long-tailed Pouched Rat (*B. hindei*) is 22–23 days, and longevity is 3–4 years.
Activity patterns. The Greater Long-tailed Pouched Rat is nocturnal. It is mostly terrestrial but may also climb, using its prehensile tail to assist with negotiating thin branches.
Movements, Home range and Social organization. Little is known, but the Greater Long-tailed Pouched Rat is apparently solitary.
Status and Conservation. Not assessed on *The IUCN Red List*. Although the Greater Long-tailed Pouched Rat is not currently under threat of extinction, it does occupy a rapidly disappearing habitat. Its future survival depends on continued protection of forests in north-eastern Zambia, Malawi, and central Mozambique.
Bibliography. Ansell (1978), Ansell & Dowsett (1988), Egoscue (1972), Fitzgibbon *et al.* (1995), Hanney & Morris (1962), Happold (2013e), Monadjem *et al.* (2015).

35. Hinde's Long-tailed Pouched Rat   *Beamys hindei*

French: Petit Rat-hamster / **German**: Kleine Hamsterratte / **Spanish**: Rata de abazones de Hinde

Other common names: Hinde's Pouched Rat

Taxonomy. *Beamys hindei* Thomas, 1909, "Taveta, Coast region [= Kenya], British East Africa. Alt. 2000' [= 610 m]."
Some authorities have considered it conspecific with *B. major*, but it is morphologically distinct from that species and occupies a different habitat. Monotypic.
Distribution. Coastal plains and montane areas of E Kenya and Tanzania.
Descriptive notes. Head-body 125–155 mm, tail 114–127 mm, ear 20–23 mm, hindfoot 22–25 mm; weight 49–76 g. Hinde's Long-tailed Pouched Rat is medium-sized, with well-developed cheek pouches. Fur is soft and gray dorsally, shading to pure white ventrally. Chin, throat, and upper chest are white. Ears are relatively large. Tail is long and prehensile, with conspicuous white markings. Limbs are relatively short and white, with four digits on forefeet and five digits on hindfeet. Males are on average larger than females, with considerable overlap in measurements between sexes.
Habitat. Coastal forests and woodlands below elevations of 400 m (but up to 1200 m in the Usambara Mountains), typically on sandy soils. Hinde's Long-tailed Pouched Rat enters fallow fields and cassava plantations. Sandy soils might facilitate burrow excavation, in which it rests during the day and stores cached seeds and fruits. Another important factor appears to be a dense shrub layer, but reasons for that are not known.
Food and Feeding. Hinde's Long-tailed Pouched Rat mostly eats fruits and seeds, which may be cached in burrows. Insects are also eaten but constitute a smaller proportion of the diet.
Breeding. Juveniles and reproductively active males and females appear throughout the year suggesting aseasonal breeding, but the proportion of lactating female Hinde's Long-tailed Pouched Rats appears to increase during seasonal rains. A large proportion of males are scrotal throughout the year, but individuals enter reproductive condition at different times of the year. Gestation in captivity is 22–23 days, with average litter size of 2·8 young (1–5). Neonates have an average weight of 3·2 g and are pink. Lactation lasts for 5–6 weeks. Growth is rapid, with young reaching 43 g at c.4 weeks old. Longevity is 3–4 years. Equivalent parameters for wild populations are not known.
Activity patterns. Hinde's Long-tailed Pouched Rat is nocturnal and relatively slow moving. It is mostly terrestrial but may also climb, using its prehensile tail to assist with negotiating thin branches.
Movements, Home range and Social organization. Home ranges of adult male Hinde's Long-tailed Pouched Rats are larger than those of females. Densities in good-quality habitat are relatively stable at 14–31 ind/ha.
Status and Conservation. Classified as Least Concern on *The IUCN Red List*. Although Hinde's Long-tailed Pouched Rat is not currently under threat of extinction, it occupies a rapidly disappearing habitat. Its future survival depends on continued protection of coastal and montane forests in Kenya and Tanzania.
**Bibliography**. Christensen (1987), Egoscue (1972), Fitzgibbon *et al.* (1995), Happold (2013e), Hubbard (1970), Monadjem *et al.* (2015), Sabuni *et al.* (2015), Stanley & Goodman (2011).

Genus *CRICETOMYS*

Waterhouse, 1840

36. Forest Giant Pouched Rat   *Cricetomys emini*

French: Cricétome d'Emin / **German**: Emin-Riesenhamsterratte / **Spanish**: Rata de abazones gigante de bosque

Other common names: Emin's Giant Pouched Rat
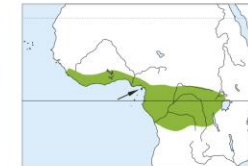
Taxonomy. *Cricetomys gambianus emini* Wroughton, 1910, "Gadda, Monbattu," DR Congo.
Taxonomy of *C. emini* is currently in flux because it represents a species complex. Recent molecular studies have shown presence of at least three, if not four, different species, which are morphologically assignable to *C. emini*. Further studies are required to sort out taxonomic implications. Monotypic.
Distribution. Tropical Africa extending continuously from Sierra Leone E to Uganda, Rwanda, and Burundi, and S to Gabon, Republic of the Congo, DR Congo, and Angola; it also occurs on Bioko.
Descriptive notes. Head-body 300–355 mm, tail 320–429 mm, ear 33–45 mm, hindfoot 64–71 mm; weight 0·5–1·3 kg. The Forest Giant Pouched Rat is a very large muroid rat, with well-developed cheek pouches. Fur is relatively short and soft for a species of *Cricetomys*, bright brown to dark brown dorsally, which is clearly delineated from white or cream venter. Snout is long and pointed. There is no dark ring around eyes, as is typical in other species of *Cricetomys*. Ears are relatively long. Tail is slightly longer than head-body length, with terminal one-half conspicuously white compared with dark proximal one-half. Limbs are relatively short, with four digits on forefeet and five digits on hindfeet.
Habitat. Wide range of forest habitats. The Forest Giant Pouched Rat is often commensal with humans at forest edges, but it is replaced by the Northern Giant Pouched Rat (*C. gambianus*) or the Southern Giant Pouched Rat (*C. ansorgei*) in large forest clearings.
Food and Feeding. The Forest Giant Pouched Rat mostly eats fruits, palm nuts, and seeds, which may be cached in a burrow.
Breeding. Little is known. Litter of Forest Giant Pouched Rats are 2–4 young, and gestation is 42 days. They may survive over four years in captivity.
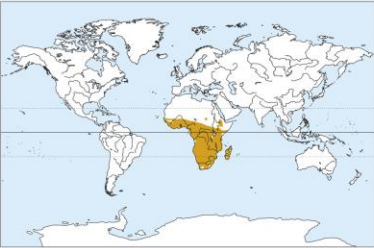**Activity patterns**. The Forest Giant Pouched Rat is nocturnal and terrestrial but may also climb. It excavates a burrow where it rests during the day.
Movements, Home range and Social organization. Forest Giant Pouched Rats are typically solitary, with one individual in each burrow system. Densities are poorly known, and a single study reported densities of 134 ind/km².

On following pages: 37. Northern Giant Pouched Rat (*Cricetomys gambianus*); 38. Kivu Giant Pouched Rat (*Cricetomys kivuensis*); 39. Southern Giant Pouched Rat (*Cricetomys ansorgei*); 40. East African Pouched Mouse (*Saccostomus mearnsi*); 41. Gray-bellied Pouched Mouse (*Saccostomus umbriventer*); 42. Southern African Pouched Mouse (*Saccostomus campestris*); 43. Nikolaus's African Climbing Mouse (*Megadendromus nikolausi*); 44. Lachaise's African Climbing Mouse (*Dendromus lachaisei*); 45. Cameroon African Climbing Mouse (*Dendromus oreas*); 46. Banana African Climbing Mouse (*Dendromus messorius*); 47. Rupp's African Climbing Mouse (*Dendromus ruppi*); 48. Lovat's African Climbing Mouse (*Dendromus lovati*); 49. Mount Kahuzi African Climbing Mouse (*Dendromus kahuziensis*); 50. Montane African Climbing Mouse (*Dendromus insignis*); 51. Vernay's African Climbing Mouse (*Dendromus vernayi*); 52. Monard's African Climbing Mouse (*Dendromus leucostomus*); 53. Kivu African Climbing Mouse (*Dendromus nyasae*); 54. Nyika African Climbing Mouse (*Dendromus nyikae*); 55. Chestnut African Climbing Mouse (*Dendromus mystacalis*); 56. Gray African Climbing Mouse (*Dendromus melanotis*); 57. Brants's African Climbing Mouse (*Dendromus mesomelas*); 58. Velvet African Climbing Mouse (*Dendroprionomys rousseloti*); 59. Bates's African Climbing Mouse (*Prionomys batesi*); 60. North-western Fat Mouse (*Steatomys caurinus*); 61. Dainty Fat Mouse (*Steatomys cuppedius*); 62. Jackson's Fat Mouse (*Steatomys jacksoni*); 63. Pousargues's Fat Mouse (*Steatomys opimus*); 64. Bocage's Fat Mouse (*Steatomys bocagei*); 65. Tiny Fat Mouse (*Steatomys parvus*); 66. Common Fat Mouse (*Steatomys pratensis*); 67. Krebs's Fat Mouse (*Steatomys krebsii*); 68. Long-eared Desert Mouse (*Malacothrix typica*).

CLASS MAMMALIA
ORDER RODENTIA
SUBORDER MYOMORPHA
SUPERFAMILY MUROIDEA

Family NESOMYIDAE (POUCHED RATS, CLIMBING MICE AND FAT MICE)

- Small to medium-sized, with considerable variation in external features such as notably elongated ears and tails to those that are distinctly short; moderate sized eyes; short to relatively drawn out bodies; and short to long legs.
- 10–85 cm.

- Afrotropical Region.
- Large variety of habitats including forests, marshes, savanna, and arid regions from sea level to the alpine zone.
- 21 genera, 68 species, 76 taxa.
- 1 species Critically Endangered, 7 species Endangered, 2 species Vulnerable; none Extinct since 1600.

Systematics

The 68 living species in the family Nesomyidae are restricted to sub-Saharan Africa and Madagascar and have had a varied and complicated taxonomic history. Recent molecular research has brought considerable insight into the evolutionary history of these highly divergent species in that they represent a monophyletic lineage, divided into six different subfamilies, with Nesomyinae endemic to Madagascar and Delanymyinae, Mystromyinae, Petromyscinae, Cricetomyinae, and Dendromurinae, occurring in sub-Saharan Africa and the Tanzanian offshore island of Zanzibar (Unguja). New species are regularly being described, and generic and specific taxonomies and indices of species diversity are at least partially unresolved.

Over the course of the taxonomic history of what is recognized today as an endemic radiation of this family on Madagascar, the Nesomyinae, researchers working on mammalian systematics have placed these rodents in various families, at least in part associated with morphological resemblance to animals found elsewhere in the world. In fact, it was previously mentioned by M. D. Carleton and G. G. Musser in 1984 that the morphological diversity among native Malagasy rodents was exceptional and the only "character" that unified this group was their occurrence on Madagascar. Because dental characteristics have been classically used to define relationships among different groups of rodents and Malagasy taxa show parallels in structure and morphology to numerous extralimital groups, it is not surprising that they were previously considered to be derived from diverse origins. For example, in classification of rodents by J. R. Ellerman in 1941, Malagasy taxa were placed in five different subfamilies of Muridae: Murinae (*Eliurus*), Cricetinae (*Nesomys, Hypogeomys*, and *Macrotarsomys*), Gymnuromyinae (*Gymnuromys*), Tachyoryctinae (*Brachyuromys*), and Microtinae (*Brachytarsomys*). The work of a number of people, in particular R. Lavocat and F. Petter on African fossil rodents, most dating from the Miocene, brought a broader view on the origin, dispersal history, and importance of convergence to discussions on the evolutionary history and different perspectives concerning native rodents on Madagascar. Recent molecular studies indicate the monophyly of the animals considered herein as part of the Nesomyinae and, from a larger perspective, the even more morphologically heterogeneous Nesomyidae. In short, dental morphology shows numerous cases of remarkable levels of convergence and, at least for this family of rodents, is not a viable characteristic to infer phylogenetic relationships.
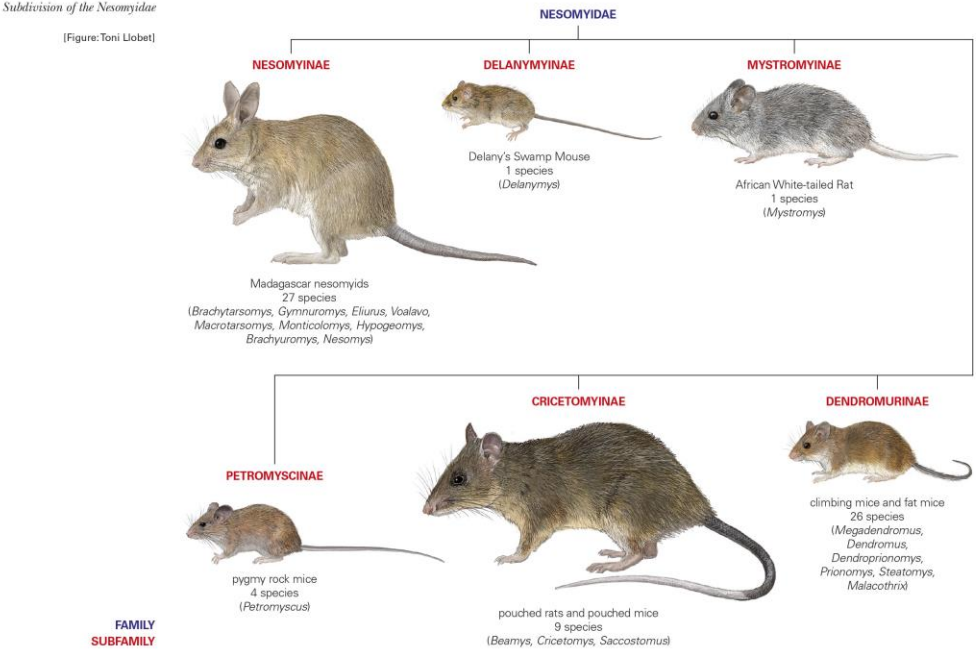
Membership in Nesomyidae has until relatively recently been a matter of contention, and various authors have placed the six subfamilies in different families. The underlying reason for this confusion is the lack of morphological traits unique to the family; hence, recognition of the close relationships of these six subfamilies had to wait until molecular assessment. Furthermore, the generic allocation in subfamilies has also been debated. For example, based on morphological grounds, the subfamily Dendromurinae included the six genera recognized here (*Megadendromus, Dendromus, Dendroprionomys, Prionomys, Steatomys*, and *Malacothrix*) and the two genera (*Deomys* and *Leimacomys*) now included in two separate subfamilies (Deomyinae and Leimacomyinae) in the family Muridae.

Before molecular assessment showed the close relationships between them, the six subfamilies comprising the Nesomyidae were distributed between several rodent families. The subfamily Nesomyinae represents an endemic radiation of this family on Madagascar, resulting in remarkable levels of convergence with rodents elsewhere in the world, including hamsters, voles, squirrels, and kangaroo rats. Their dental characteristics, classically used to define relationships among rodents, also show parallels in structure and morphology to other families. The two extant species of Brachytarsomys, the Hairy-tailed Tree Rat and the White-tailed Tree Rat (B. albicauda), were formerly placed with the voles in Microtinae. Strictly arboreal, they have broad, large-soled hindfeet with elongated fifth digits, sharp claws, and prehensile tails.

Brachytarsomys villosus
Anjanaharibe-Sud Reserve, Madagascar.
Photo: Harald Schütz

Subdivision of the Nesomyidae

[Figure: Toni Llobet]

NESOMYIDAE

NESOMYINAE

Madagascar nesomyids
27 species
(*Brachytarsomys, Gymnuromys, Eliurus, Voalavo, Macrotarsomys, Monticolomys, Hypogeomys, Brachyuromys, Nesomys*)

DELANYMYINAE

Delany's Swamp Mouse
1 species
(*Delanymys*)

MYSTROMYINAE

African White-tailed Rat
1 species
(*Mystromys*)

PETROMYSCINAE

pygmy rock mice
4 species
(*Petromyscus*)

CRICETOMYINAE

pouched rats and pouched mice
9 species
(*Beamys, Cricetomys, Saccostomus*)

DENDROMURINAE

climbing mice and fat mice
26 species
(*Megadendromus, Dendromus, Dendroprionomys, Prionomys, Steatomys, Malacothrix*)

FAMILY
SUBFAMILY

An informative manner to follow changes in the systematics of the Nesomyinae, specifically their higher-level relationships and indices of generic and species richness, is a review of different treatments in the *Mammal Species of the World*. In the first edition, published in 1982, the subfamily Nesomyinae was placed in the broadly distributed Cricetidae and composed of seven genera and ten species. In the second edition, published in 1993, the same subfamily structure was maintained, but it was placed in Muridae and composed of seven genera and 14 species. Field and associated laboratory work over the subsequent decade brought new perspectives to higher relationships of native Malagasy rodents, and certain aspects mentioned in earlier literature were revisited. In the third edition, published in 2005, Nesomyinae was still used for extant species strictly endemic to Madagascar, was placed within the family Nesomyidae, and included nine genera and 23 species. Today, nine genera and 27 species are included, although several undescribed species are known. It is estimated that recognized species richness in this subfamily will reach at least 30 species by 2020.

Taxonomy of the mainland African species of Nesomyidae has remained relatively unchanged over the past decade, mostly because of the lack of critical systematic studies. In the 2005 edition of *Mammal Species of the World*, 38 species were listed from sub-Saharan Africa compared to 40 species documented ten years later in *Rodents of Sub-Saharan Africa*. The difference was due to descriptions of two new species: Rupp's African Climbing Mouse (*Dendromus ruppi*) in 2009 and Lachaise's African Climbing Mouse (*Dendromus lachaisei*) in 2012. Nevertheless, numerous other undescribed species are known within the African members of this family. For example, a recent review of giant rats (*Cricetomys*) in 2012 showed the existence of at least three undescribed species in the tropical forests of Central and West Africa. Another example concerns the Southern African Pouched Mouse (*Saccostomus campestris*) that shows extreme chromosomal variability and associated genetic differences among geographical populations, suggesting the presence of undescribed species. In fact, a new species of *Saccostomus*, the

Gray-bellied Pouched Mouse (*Saccostomus umbriventer*), was elevated to species in 2016. For the most part, species of Nesomyidae remain poorly documented relative to their natural history and distribution.

Molecular genetic work, using nuclear DNA, by S. A. Jansa and M. Weksler in 2004 clarified higher-level systematics of Nesomyidae. Their study was based on an extensive dataset incorporating five of the six subfamilies, with only the subfamily Delanymyinae missing from the analysis, and conclusively demonstrated monophyly of Nesomyidae. The subfamily Nesomyinae is clearly monophyletic, but its relationship with the rest of the family is not clearly resolved. The subfamilies Petromyscinae and Mystromyinae form a well-supported clade that conforms with morphological evidence. Monophyly of subfamilies Dendromurinae and Cricetomyinae has not been conclusively demonstrated, although the most recent studies support this view. A molecular study in 2001, based on mitochondrial DNA, grouped the genera *Cricetomys* and *Saccostomus* in Cricetomyinae and *Dendromus* and *Steatomys* in Dendromurinae. Later, Jansa's study, which included all three putative genera (*Beamys, Cricetomys*, and *Saccostomus*) belonging to Cricetomyinae, failed to support monophyly of this subfamily. Instead, *Saccostomus* grouped with *Dendromus* and *Steatomys* in Dendromurinae, although this was only weakly supported. A 2016 study that included seven genera provided support for inclusion of *Saccostomus* in Cricetomyinae. More molecular work is required to elucidate relationships within Nesomyidae.

In the case of the forms of Nesomyidae on Madagascar, a critical paper by Jansa and colleagues in 1999 used cytochrome-b sequence data from all described genera and a high percentage of named species at that time and concluded that they were all derived from a single colonization event of the island, they were Asiatic in origin, and Africa was secondarily colonized by ancestors of this radiation. While new results have changed some conclusions of this paper, this was the first explicit phylogeny and biogeographic scenario of the native rodents of Madagascar that underlined that they were derived from a single col-