

Pseudomys higginsii. By Michael M. Driessen and Robert K. Rose

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Pseudomys higginsii (Trouessart, 1897)

Long-tailed Mouse

Mus leucopus Higgins and Petterd, 1883:174. Type locality "from Kentishbury, Tasmania, Australia." Not *Musculus leucopus* Rafinesque, 1818, a *Peromyscus*.

Mus (Epimys) higginsii Trouessart, 1897:473. [*nom. nov.* for *Mus leucopus* Higgins and Petterd, 1883].

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Murinae, genus *Pseudomys*, with 25 Recent species in the genus (Musser and Carleton, 1993). *Mastacomys fuscus* is now placed in the genus *Pseudomys* (Musser and Carleton, 1993; Watts et al., 1992), an assignment not embraced by all investigators in Australia, including Strahan (1995). Almost one-third of the species in the genus *Pseudomys* are listed as threatened in Australia, and one species, *P. gouldii*, is presumed extinct (Lee, 1995). *Pseudomys higginsii* is found only on the island state of Tasmania, Australia. No extant subspecies are recognized, but the extinct form from mainland Australia is considered to be a different subspecies.

DIAGNOSIS. There is no existing key to the genus *Pseudomys*; however, Watts and Aslin (1981) provide a diagnosis for each of the species. *P. higginsii* is among the largest species in the genus, and has proportionately larger feet than most of its congeners. Only two other species of *Pseudomys*, *P. novaehollandiae* and *P. fuscus*, occur in Tasmania. Compared with *P. higginsii*, *P. novaehollandiae*, the New Holland mouse, is much smaller (15–26 g), lighter gray, and restricted to coastal heath communities in the north and east of the state. *P. fuscus*, the broad-toothed mouse, is larger (97–145 g) than *P. higginsii*, brown in color and in Tasmania only occurs in buttongrass moorland. In contrast, *P. higginsii* is rarely found in buttongrass moorland habitat and then only at the ecotone. In Tasmania, specimens of *P. higginsii* are the only long-tailed grayish mice with a mass of 30–70 g.

GENERAL CHARACTERS. *Pseudomys higginsii* is a long-tailed mouse with grayish brown dorsal pelage, a matching bicolored tail, and a white venter (Fig. 1). Slightly built, its rather delicate and long-legged appearance is accentuated by its nervous disposition (Green, 1968). The face is somewhat pointed with the prominent eyes set well forward. The ears are large, prominent and well-rounded, and when pressed forward they cover the eyes. The slender and finely tapered tail is often carried in a posteriorly directed crescent, well clear of the ground. The distinctly bicolored tail is sparsely covered with fine brown bristle-like hairs above and similar white hairs below. A few individuals may have a white 15-mm tail tip. The four nipples are abdominal (Green, 1968), as in all hydromyine rodents (Watts and Aslin, 1981). The overall appearance is grayish brown; darkest on the mid-dorsum and merging to pale gray underneath in both sexes. Young animals are more uniformly gray than adults (Green, 1968). The range of adult body mass is 60–70 g, but some individuals of both sexes can reach 90 g. In a fully mature adult, the length of head and body is about 130 mm and the tail (slightly longer in males) is about 170 mm. The out-sized hind feet of *P. higginsii* were hypothesized to be an adaptation for rock-hopping behavior (Stoddart and Challis, 1993), but a closer examination failed to reveal any evidence to support that claim (Wapstra, 1994).

Average measurements (in mm) of males and females of *P. higginsii* are as follows: total length, 301.1, 302.7, $n = 23, 16$; length of tail, 169.7, 170.8, $n = 23, 16$; length of head and body, 131.1, 131.7, $n = 29, 26$; length of hind foot, 33.7, 33.2, $n = 29, 26$; length of ear, 23.4, 24.2, $n = 29, 26$; greatest length of skull, 33.64, 35.38, $n = 10, 10$; depth of rostrum, 7.58, 7.68, $n = 10, 10$; cranial breadth, 5.2, 5.37, $n = 10, 10$; zygomatic breadth,

16.84, 17.32, $n = 10, 10$; length of maxillary toothrow, 6.3, 6.48, $n = 10, 10$; and length of molariform teeth in mandibular toothrow, 6.45, 6.35, $n = 10, 10$ (Fig. 2). The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16, the typical rodent pattern (Green, 1968).

There is no consensus on sexual dimorphism in *Pseudomys higginsii*. Mean measurements of females slightly exceed those of males in all dimensions except length of hind foot (Green, 1968). Throughout a 15-month study in wet sclerophyll forest, male *P. higginsii* (66.4 ± 1.2 g) were found to be heavier than females (60.1 ± 1.4 g), but at no time was this difference in body mass significant (Monamy, 1995). However, although similar in length of head and body, males have significantly longer tails and hind feet and greater body mass than females (Stoddart and Challis, 1991). Furthermore, females (but not males) from western Tasmanian forests are significantly heavier than those from eastern (drier) forests (Stoddart and Challis, 1991). Thus, there is detectable geographic variation.

DISTRIBUTION. *Pseudomys higginsii* is endemic to Tasmania, though it is known in the fossil record from locations in eastern New South Wales and in Victoria, Australia (Wakefield, 1972a). *P. higginsii* is believed to have a statewide distribution (Rounsevell et al., 1991), but has been recorded from only one offshore island (Bruny Island; Fig. 3). This mouse ranges from near sea level to 1,200 m and seems suited for life in high rainfall areas such as the wet sclerophyll forests and rainforests found at higher elevations. *P. higginsii* is most common in the western half of the island (Green, 1968), whereas in the drier climatic zones of eastern Tasmania populations mostly are confined to rock screes and some drainage lines within dry forests.

FOSSIL RECORD. *Pseudomys higginsii* is known from Late Pleistocene deposits from the Broom fauna of Wombeyan Caves of eastern New South Wales and from Pyramids Cave in eastern Victoria, Australia, where its disappearance seems to be associated with an early Holocene phase of aridity (Fig. 3; Wakefield, 1972a). Fragmentary skull remains have been found among subfossil deposits in limestone caves at Flowery Gully in southern Tasmania (Green, 1968). Although not presently found on any island in Bass Strait (which separates Tasmania from the Australian mainland), subfossils of *P. higginsii* are known from sand dunes on King Island and 8,000-year-old specimens have been taken from Ranga Cave on Flinders Island, Tasmania (Hope, 1972).

An extinct subspecies, *P. higginsii australiensis*, from Pyramids Cave in eastern Victoria, Australia, is distinguished from the extant Tasmanian form by its greater mean tooth size (Wakefield, 1972b). In comparisons of *P. h. australiensis* and *P. h. higginsii*,



FIG. 1. *Pseudomys higginsii*. Photograph courtesy of Hans Wapstra.

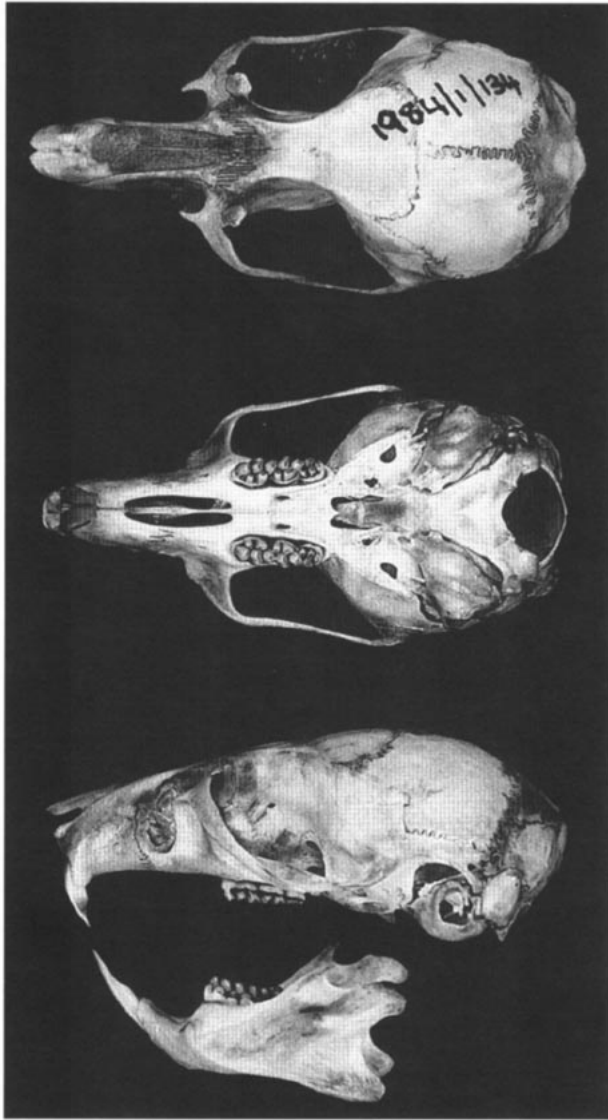


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Pseudomys higginsi*. Condylobasal length is 33.6 mm.

the upper molar row at alveolar level in the former subspecies is 8% longer, the lower molar row at alveolar level is 12% longer, and the maximum crown width of m1 is 8% greater. Furthermore, the height of the zygomatic plate from the anterior-most point of alveolus of M1 to its junction with the length of the zygomatic plate is 5% less in *P. h. australiensis* than in *P. h. higginsi*, whereas the length of the zygomatic plate is 12% longer. Thus, the ratio of height to length of the zygomatic arch is much greater in *P. h. australiensis* than in *P. h. higginsi* (Wakefield, 1972b).

FORM AND FUNCTION. The cheek teeth are rooted and animals can be aged by degree of tooth wear. The exceptionally long and tufted tail is 1.3 times longer than the combined head and body length. This long tail is probably important for balance when leaping in habitat such as boulder scree (Wapstra, 1994).

The iris is dark brown, the pink nostrils are naked, and the short hairs on the extreme tip of the nose are white. The incisors are slender, the upper pair being orange on the anterior face and rising to 4 mm above the gums, whereas the lower pair is pale yellow and protrudes 6 mm (Green, 1968). The hind feet are well covered with short pale hairs; undersurfaces of toes are white, but with a pale grayish tone towards the heel. The pads do not differ greatly in size. The manus is always white, with rounded, smooth and prominent pads (Green, 1968).

ONTOGENY AND REPRODUCTION. Breeding is sea-

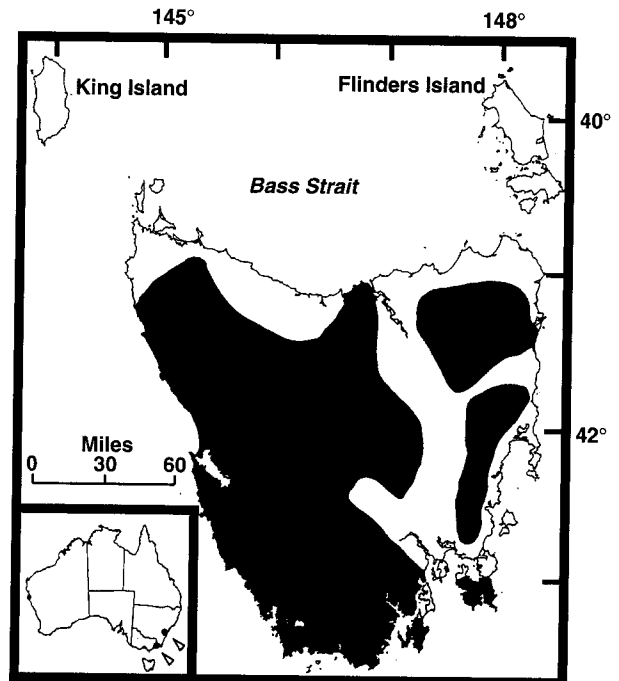


FIG. 3. Distribution of *Pseudomys higginsi*, which is endemic to Tasmania. Areas not occupied by the species are mostly agricultural lands or coastal heathlands. Fossil sites in New South Wales and Victoria are indicated by arrowheads on inset of Australia.

sonal in *Pseudomys higginsi*, extending from September to June (Stoddart and Challis, 1991). The nonbreeding season includes the winter months of July and August, when neither sex shows any evidence of current or impending reproduction: females have non-perforate vaginae, males have abdominal testes, and the distance from the anus to the penis is reduced from that seen in breeding males.

Ovulation is spontaneous, with a mean ($\pm SE$) estrous cycle of 10.7 ± 3.0 days in adults. The vagina normally is closed in the nonbreeding season, but as the breeding season approaches, a lip appears in the proto-vaginal area. As it deepens and finally opens, the external vagina is formed (Stoddart and Challis, 1991).

Spermatazoa of *P. higginsi* are 98–115 μm long and structurally resemble those of some other *Pseudomys* species and other genera of hydromyine rodents. The sperm head has a broad base which tapers to three hooks, behind which is a prominent midpiece (Breed and Sarafis, 1978). Scrotal development is not obvious outside the breeding season, when the testes are carried inguinally. Testes of subadult males are usually 5 by 3 mm during the winter months and those of adults are ca. 12 by 5 mm. With the approach of summer and the onset of breeding, testes descend into the scrotum and increase in size to as much as 20 by 11 mm (Green, 1968). Recrudescence of testes precedes the appearance of perforate vaginae (an indication of the estrous cycle) by 1–2 months, a common feature in rodent breeding cycles. However, it is unusual for the testes to regress 1–2 months before breeding ends, while a small fraction (10–20%) of females is still perforate and therefore cycling. Thus, in April perhaps 2–3 times more females than males are deemed to be fertile (Stoddart and Challis, 1991).

Before December, the first month when the majority of both sexes are in breeding condition, males have had scrotal testes for three months but few if any females are perforate. This early development of males compared to females may allow dominance relationships or territories to be formed before females are ready for mating. At the end of the breeding season, males lose their breeding condition first (usually starting in April), followed by the females 1–2 months later (Stoddart and Challis, 1991).

Gestation of two females in captivity was ca. 33 days, but a gestation period of 31–32 days has been reported (Green, 1968). The median number of embryos from wild-caught animals is three, and most captive-bred litters have three and sometimes four young

(Green, 1968; Stoddart and Challis, 1991). Birth have been recorded as early as mid-November (Stoddart and Challis, 1991) and pregnancies are common in December. Pregnant females have been found as late as April, when the first weanlings enter the population (Monamy, 1995). Nipples are difficult to discern in subadults, but they become progressively more obvious with lactation, when suckling causes loss of up to 5 mm of fur around each (Green, 1968). Some females can raise two litters in a season. The sex ratios for a cohort did not differ significantly from unity (Monamy, 1995).

In the laboratory, at birth incisors but not molar teeth are visible in both jaws. The upper incisors are 0.4-mm wide, pale yellow on the anterior face, and extend about 0.5 mm above the gums. Each is slightly bicuspid and directed prominently towards the throat. The chisel-pointed lower incisors are white and slightly longer and narrower than the upper incisors; like the upper incisors they are set in a pronounced inward direction. Soon after birth, the young fasten themselves to the nipples. When the young are so attached, the mother may suddenly "explode" from the nest if alarmed and take evasive action in the face of danger, while at the same time transporting the young with her by dragging them along between her hind legs (Green, 1968).

Relatively short at birth, the tail grows rapidly to equal head and body length at about 18 days and thereafter exceeds it. The hind feet also develop rapidly and almost triple in length in the first 5 weeks to reach about 30 mm, or nearly adult size. There is no significant difference in growth between the sexes (Green, 1968).

At 8 days, young *P. higginsii* are active and can crawl readily, despite their closed eyes. By 10 days, young can take active evasive action, although still blind. The eyes open at 15 days, and by 18 days the ears have unfolded. At 33 days, by which time they are weaned, the young are independent. Near-adult size is achieved by 40 days, except for the tail, which grows until about 75 days in both sexes (Stoddart and Challis, 1991). The first molt begins at 50 days, development of the scrotal region is apparent by 74 days, and adult molt is completed by 100 days (Green, 1968). Molar wear already is detectable in 50-g subadults (Green, 1968). Beyond 75 days, asymptotic growth is achieved for all parameters except length of head and body and length of hindfoot, which grow slowly to 90 days (Stoddart and Challis, 1991). Body mass varies too much from day to day to be a useful ageing parameter. Thus, individuals can be reliably classified as juveniles or adults only during the November-to-April period. At other times, adults cannot be distinguished from young by use of any mensurate feature (Stoddart and Challis, 1991).

ECOLOGY. *Pseudomys higginsii* is primarily nocturnal but can be active during the day. When housed in captivity with *R. lutreolus*, a frequent syntopic species, *P. higginsii* always avoids the larger swamp rat and is sometimes killed by it (Green, 1968).

Pseudomys higginsii occupies rainforest, wet scrub, eucalypt scrub, sedgeland, and low alpine vegetation (Taylor et al., 1985) but is rare or absent in dry forests and probably absent from grasslands. Although probably most common in alpine scree slopes and boulder fields (Stoddart and Challis, 1991, 1993), densities in rainforest are up to three times greater than in other communities; few are found in alpine vegetation and sedgeland. Although sometimes recorded from the sedgelands of western Tasmania (Hocking and Guiler, 1983; Taylor et al., 1985), the long-tailed mouse usually is restricted to ecotonal areas. In western Tasmania, *P. higginsii* has been recorded in habitats where the vegetation ranges from very open to very dense (Taylor et al., 1985). On Mt. Wellington, south-eastern Tasmania, in subalpine habitats and lowland wet forests, no relationship was found between success in trapping *P. higginsii* and vegetational structure or floristics (Driessen, 1987). However, in a broader habitat survey in southwestern Tasmania, the species was recorded only where the undergrowth was devoid of cover within 0.5 m of the ground (Hocking and Guiler, 1983). Although terrestrial in habit, *P. higginsii* has been trapped above ground in *Banksia marginata* (banksia), a generally small and bushy tree (Taylor et al., 1985). Its natural retreats or nesting places are in holes in rotting stumps, logs, and litter on the forest floor (Green, 1968).

Specific areas of macrohabitat are used differentially by low-density populations in wet sclerophyll forest (Monamy, 1995). Trapping data indicate that within a wet sclerophyll mosaic *P. higginsii* is significantly more likely to be found in areas of boulder scree than in areas of dense fern cover. Thus, in wet forests at least, *P.*

higginsii may avoid areas where densities of *R. lutreolus* are high (Monamy, 1995).

In the long-tailed mouse, both sexes showed a pattern of seasonal abundance, with numbers increasing in spring and December and decreasing in summer (January and February). Densities in optimal habitat range from 2.6 to 7.8 individuals per ha (Stoddart and Challis, 1991). Differing results have been reported for sex ratios for *P. higginsii*. A sex ratio in favor of males was reported for most of a 20-month trapping study across a variety of habitats (Stoddart and Challis, 1991). Males usually outnumbered females by a factor of four, but the authors were unsure whether this was a true reflection of sex ratio or a result of differential trappability between sexes. The sex ratios reported were not tested statistically. In a 14-month trapping study conducted in the same area as the wet-sclerophyll-forest study (Stoddart and Challis, 1991), no significant difference in sex ratios was reported (Monamy, 1995).

The diet of *Pseudomys higginsii*, a generalist omnivore, has been assessed by use of fecal analyses of animals from subalpine woodlands and scree slopes (Driessen, 1999) and from wet sclerophyll forests (Driessen, 1999; Murray, 1980; Stoddart and Challis, 1991). *P. higginsii* is an opportunistic feeder, consuming whatever is locally and seasonally available. Monocotyledons (*Poa*, *Holcus lanatus*, *Gahnia grandis*), subterranean fungi (*Chamonixia*, *Hysterangium*, *Octavianina*, *Gyospora*, *Richoniella*, *Hymenogaster zeylanicus*), fruits of shrubs (*Cyathodes glauca*, *C. parvifolia*, *Coprosma nitida*, *Gaultheria hispida*), and invertebrates (lepidopteran larvae, adult coleopterans, adult dipterans, arachnids, oligochaetes) are the main dietary components of *P. higginsii* throughout the year as measured in fecal analyses. Mosses (*Polytrichum juniperinum*, *Rhacomitrium crispulum*) and a fern (*Blechnum penna-marina*) are most common in the diet during spring (Driessen, 1999; Stoddart and Challis, 1991) whereas monocotyledons (stems and leaves of grasses, and basal stems of *Gahnia grandis*) and some dicotyledons were more common during summer (Driessen, 1999).

By far the most conspicuous ectoparasite of *P. higginsii* is the mite *Laelaps calabyi*. Other ectoparasites of *P. higginsii* include a tick—*Ixodes tasmani*; fleas—*Pygiopsylla hoplia*, *Acanthopsylla rothschildi*, and *Stephanocircus pectinipes*; and a louse—*Hoplopleura calabyi* (Green, 1968).

Possible predators of the long-tailed mouse include the masked owl, *Tyto castanops*, and the eastern quoll, *Dasyurus viverrinus*. The remains of *P. higginsii* have been found in pellets of the masked owl from cave and recent deposits (Mooney, 1993). Before human settlement in Tasmania *P. higginsii* constituted 44% of the diet of masked owls although it is only 1% of its diet today, suggesting greater relative abundance of *P. higginsii* in the past.

BEHAVIOR. *Pseudomys higginsii* is very active and inquisitive. When necessary, it can move swiftly and if suddenly alarmed will often initiate its escape by an explosive leap of at least 30 cm in any direction. When relaxed, *P. higginsii* will sit in a semi-upright position with the forefeet held in a kangaroo-like manner. A faint high-pitched whisper-whistle, almost inaudible to the human ear, often is uttered by caged animals (Green, 1968).

Pseudomys higginsii is easily kept in captivity (Green, 1968). Caged individuals provided with sufficient dry grass or straw readily build domed nests in one corner of a cage or within a nest box. The nest is fairly elaborate and is denser and more frequently visited in 5°C than in 20°C environments (Morris, 1969). When raised at 30°C, long-tailed mice discard nesting material and occupy the empty cage (Nicol, 1969). After the young raised in a nest are weaned, the nest is not maintained (Morris, 1969).

Wild-caught animals are prone to nervous defensive squabbling if housed in confined quarters. Hoarding of food by captive *P. higginsii* is rare, although lactating females do so readily (Morris, 1969). In captivity, adults groom themselves (and other adults) in a manner similar to that seen in other rodents. Female *P. higginsii* continue grooming their young even after they have been weaned, when the young also groom themselves (Morris, 1969).

Pseudomys higginsii is readily trapped by use of snap traps and small live traps. Some tail damage can occur with live traps. A trap success of 5% usually can be expected in suitable habitat (Green, 1968), but trapping success of 35% has been recorded in wet sclerophyll forest (Monamy, 1995). Trapping success varies among habitats: 10% in rainforest, 4% in wet scrub, 3% in eucalypt scrub, 2% in sedgeland, and 0.5% in alpine (Taylor et al., 1985).

The home range, as estimated from trapping data, is ca. 2,630 m² for males and ca. 2,080 m² for females (Stoddart and Challis, 1991). This indicates either a need for large areas for feeding, nesting, and other resources or the relative intolerance of conspecifics. These relatively large home ranges and the low population densities (3–8/ha) are compatible with a model of population dispersion in which females occupy more-or-less exclusive home ranges, whereas the home range of a male overlaps those of two or more females. There is evidence to suggest that interspecific interaction between *R. lutreolus* and *P. higginsi* in wet sclerophyll forest may be a determining factor in the use of wet sclerophyll habitat by *P. higginsi*. The absence of *P. higginsi* from areas where cover is densest, a habitat characteristic preferred by *R. lutreolus*, may imply an asymmetric competition based on body mass (Monamy, 1995). This implication was subsequently confirmed by use of a standardized regression technique to assess competition between the two species (Luo et al., 1998). In winter (June–October), competition is low, and it reaches a maximum during the breeding season (November–April). Habitat selection by female *R. lutreolus* drives asymmetric competition and coexistence with *P. higginsi* (Monamy and Fox, 1999). During the nonbreeding season, female *R. lutreolus* occupy areas of thickest ground cover. After the onset of breeding, male *R. lutreolus* visit areas occupied by females. *P. higginsi* occurs more frequently in those areas occupied by male *R. lutreolus* during the nonbreeding season. This shift in habitat occupancy by *P. higginsi* is reflected in a dietary shift (Driessen, 1999). Thus, it is likely that *R. lutreolus* restricts the access of *P. higginsi* to better microhabitats and food supply.

Although a relatively long tail and large hind feet suggest that *P. higginsi* is adapted for bipedality, an analysis of locomotion using a treadmill and video photography revealed that it is never bipedal and that its movements, including the carriage of the tail, more closely resemble the quadrupedal condition. These anatomical features are interpreted as a specialization for leaping only, a behavior which may be advantageous in boulder scree, a preferred habitat in parts of Tasmania (Wapstra, 1994).

GENETICS. The diploid number of *P. higginsi* is $2n = 48$ (Dartnell, 1970), including 21 pairs of telocentric autosomes, two pairs of small metacentric autosomes (numbers 22 and 23), and a pair of telocentric sex chromosomes (XX, XY). Autosome pair 1 is distinguishable by its large size, whereas pairs 2 to 21 form a graded series, with one pair (near number 6), being subacrocentric. X-banding is restricted to the centromere of all autosomes and the X chromosome, but characterizes the entire Y chromosome (Baverstock et al., 1977).

Pseudomys higginsi is genetically most similar to a cluster of *Pseudomys* species from mainland Australia, according to an electrophoretic analysis (Baverstock et al., 1981). Despite much recent work (Watts et al., 1992), the genetic relationships within *Pseudomys* are proving difficult to determine, and the sister taxa to *P. higginsi* remain unclear.

REMARKS. *Pseudomys* is the combined form of the Greek *pseudes*, false and the Latin *mys*, the plural form of Latin *mus*, mouse. The specific name *higginsi* is the latinized surname of E. T. Higgins, physician and natural history dealer, resident of Tasmania from 1882–1887, and describer of this species as *Mus leucopus* in 1882 (Strahan, 1981). Other common names include the long-tailed rat, but it was also called the “short-tailed mouse” by an author who must not have seen any specimens with intact tails (Lord, 1919). We thank H. Wapstra for the use of the photograph, J. Leeming of the Queen Victoria Museum, Launceston, Tasmania for skull photographs, J. Rainbird, also of the Queen Victoria Museum, for specimen measurements, C. Reed of Tasmania Parks and Wildlife Service for developing the distribution map, and C. Watts and V. Monamy for thoughtful and useful comments in their reviews. This account was written while the second author, RKR, was on leave at the institution of the first author, MMD.

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