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Pentalagus furnessi.

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Pentalagus Lyon, 1904

Caprolagus: Stone, 1900:460. Part, not *Caprolagus* Blyth, 1845: 247.

Pentalagus Lyon, 1904:428. Type species *Caprolagus furnessi* Stone, 1900, by original designation.

CONTEXT AND CONTENT. Order Lagomorpha, family Leporidae, subfamily Leporinae, genus *Pentalagus*. *Pentalagus* is monotypic (Corbet 1983; Hoffmann 1993; Lyon 1904).

Pentalagus furnessi (Stone, 1900)

Amami Rabbit

Caprolagus furnessi Stone, 1900:460. Type locality "Liu Kiu Islands," restricted to "Amami-Ohshima Island, Kagoshima, Japan" (Uchida 1920:61).

Pentalagus furnessi: Lyon, 1904:428. First use of current name combination.

CONTEXT AND CONTENT. Content as for genus. *P. furnessi* is monotypic (Corbet 1983; Hoffmann 1993).

DIAGNOSIS. Relative to other leporids, rostrum of *Pentalagus furnessi* (Fig. 1) is shorter and heavier and posterior projection of superorbital process is well developed, heavier, and more blunt (Fig. 2; Lyon 1904). Incisive foramina are narrow, their sides approximately parallel, resembling in shape those in *Pronolagus*, but very much smaller. Audital bullae are very small, more reduced in size than in *Pronolagus*. P2 of *Pentalagus* has 3 grooves compared with 2 grooves in *Brachylagus idahoensis*, *Nesolagus netscheri*, and *Romerolagus diazi*. Unlike *Romerolagus diazi*, the anterior reentrant angle is present in *P. furnessi*. The anterointernal reentrant angle is present in *P. furnessi* but absent in *Lepus*, *Oryctolagus*, and *Sylvilagus*. Only *Pentalagus* has all 5 reentrant angles and the most complicated enamel crenulation in the Leporidae (Dawson 1958; Hibbard 1963; Tomida and Jin 2002).

GENERAL CHARACTERS. *Pentalagus furnessi* (Fig. 1) is a medium-sized rabbit. Pelage is thick and wooly, dark brown above, becoming more reddish-brown on sides. Underparts are light reddish-brown. Soft underfur is plumbeous. Long hair is coarse and hispid, brownish black, much with buff annulations or tips, becoming mahogany on the rump and brighter yellowish brown on the feet, except at base of claws and tail (Stone 1900). Hind feet, tail, and ears are short; eyes are small. Heavy, curved claws are very large and strong (10–20 mm in length), nearly straight on the forefeet, but curved on the hind feet (Stone 1900). Mean external measurements (mm) for 4 male adults and 3 female adults, respectively, from Kawauchi, Sumiyo, Amami-Ohshima Island are (range in parentheses): total length, 451 (430–470), 452 (397–530); length of tail, 27 (20–35), 30 (25–33); length of ear, 44 (40–50), 45 (42–49); length of hind foot, 86 (80–92), 89 (83–92); body mass (in g), 2,226 (2,030–2,675), 2,477 (2,000–2,880); measurements of 1 male adult from Mt. Amagi, Amagi, Tokuno-Shima Island, are: total length, 470; length of tail, 25; length of ear, 44; length of hind foot, 85; body mass (in g), 2240 (F. Yamada, in litt.).

Skull is low, flat, and broad between the orbits. Nasals are very short and broad, as wide in front as behind. Sutures of interparietal are obliterated. Bony plate is long. Zygoma is moderately heavy, its posterior free extremity moderately long, antero-inferior angle is slightly enlarged but flared outward. Anterior projection of superorbital process is absent. Mandible has a very large, rounded angular process, which is separated from the condyle by a small, shallow notch (Lyon 1904). M3 is sometimes absent (Abe 1931; Corbet 1983; Hayashida et al. 1967; Lyon 1904). Type specimen (Lyon 1904) is on deposit at the Philadelphia Academy of Natural Science as ANSP#20645.

Mean cranial and mandible measurements (mm) of 9 adults (sex known only for 2 males and 1 female) from the Collection of the National Science Museum, Tokyo (Endo et al. 2001) and the Amami Laboratory of Injurious Animals of the Institute of Medical Science at the University of Tokyo are (range in parentheses): greatest length, 82.0 (76.1–85.4); zygomatic breadth, 40.4 (38.0–42.2); postorbital constriction, 17.5 (16.4–19.1); length of nasals, 26.1 (23.8–28.3); width of nasals, 13.9 (13.0–15.4); length of maxillary tooth row, 17.5 (16.0–18.5); breadth of braincase, 29.5 (28.4–30.5); length of palatal bridge, 12.4 (10.7–16.2); palatal height, 18.4 (16.4–20.3); length of tympanic bulla, 7.7 (7.3–8.1); length of mandible, 60.7 (53.0–65.7); and height of mandible, 40.7 (36.1–44.4—F. Yamada, pers. comm.).

Radius and ulna are short, heavy bones and radius is distinctly shorter than humerus; hind foot is short and stout; tarsal bones are relatively wide; and metatarsals are especially short and heavy with a basal width that is the broadest in Leporidae (Lyon 1904). Transverse processes of lumbar vertebrae are broad (Corbet 1983).

DISTRIBUTION. *Pentalagus furnessi* is endemic to Amami-Ohshima Island (712 km^2) and Tokuno-Shima Island (248 km^2) in the Nansei Archipelago, in southern Japan (Fig. 3). Its vertical range is from sea level to 694 m on Amami-Ohshima Island and to 645 m on Tokuno-Shima Island.

FORM. Dental formula is i 2/1, c 0/0, p 3/2, m 2–3/3, total 26–28. Vertebral formula is 7 C, 12 T, 7 L, 4 S, and 10–11 Ca, total 40–41 (Otsuka et al. 1980).

Body mass of 10 captive rabbits (5 males and 5 females) captured at Amami-Ohshima Island in April and June, 1984, was measured over 2.5 years (Matsuzaki et al. 1989). Body mass decreased after introduction to the cages, but recovered after ca. 1 month. Average maximum body mass was 2,710 g for males and 2,730 g for females after 14–16 months. Body mass of both sexes fluctuated monthly by ca. 100–200 g, and the maximum body mass was reached during August–September seasonally.

FOSSIL RECORD. Two late Pleistocene teeth (right M1 and left P3) of the Amami rabbit are from Tokuno-Shima Island (Tomida and Otsuka 1993). *Pliopentalagus*, ancestral to the extant Amami rabbit (Dawson 1958; Hibbard 1963; Tomida 1997), occurs in

FIG. 1. Photograph of an adult (sex unknown) *Pentalagus furnessi* at Sumiyo, Amami-Ohshima Island. Used with permission of the photographer H. Katsu.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult (sex unknown) *Pentalagus furnesii* (National Science Museum, Tokyo. Collection No. 31591) from Amami-Ohshima Island, Kagoshima, Japan, December 21, 1988. Greatest length of skull is 83.7 mm.

Huainan, Anhui Province, China (Tomida and Jin 2002) and in Moldavia and Slovakia in Europe (Daxner and Fejfar 1967; Gureev 1964). The Chinese materials are from the latest Miocene (ca. 6 million years ago) to late Pliocene (ca. 3 million years ago—Tomida and Jin 2002).

ONTOGENY AND REPRODUCTION. From autumn of 1984 to March of 1989, 1 captive adult pair produced 11 neonates (mean litter size of ca. 1) at the Kagoshima Hirakawa Zoo (Sako et al. 1991). Parturition occurred late March–May (4 juveniles) and September–December (7 juveniles). Females dig burrows for parturition and nursing ca. 1 week before parturition. The entrance is 15 cm in diameter and 150 cm deep, with a chamber (30 cm in diameter) full of leaves. The juvenile stays in the chamber in daytime. Females cover the entrance of the burrow by soil after nursing

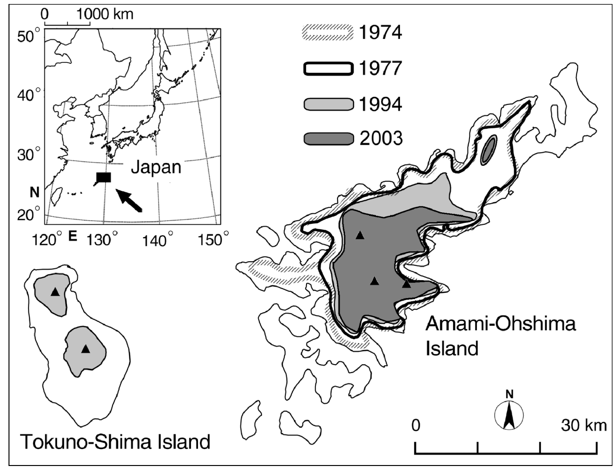

FIG. 3. Geographic distribution of *Pentalagus furnessi* in 1994 and 2003 compared with previous distributions (after Sugimura et al. 2000; Sugimura and Yamada 2004). Triangles show the peaks of main mountains.

28 and 48 days after parturition. Females visit nursing burrows after 2000–2100 h and remove the soil on the entrance. After suckling, the entrance is covered by soil and camouflaged with twigs and leaves, the process taking 30 s. At 3–4 months old, juveniles, 25–35 cm in total length, are driven away by the mother from both the nursing burrow and mother's burrow (Sako et al. 1991).

A captive, neonatal Amami rabbit, 2 days after birth, weighed 100 g, and had short brown hair on the body, closed eyes and ears, erupted incisors, grown nails, of which the white tips rolled filamentously into the limbs, and 3 pairs of nipples (Matsuzaki et al. 1989). External measurements (mm) of a 4-day neonate were body length (from tip of nose to base of tail), 150; length of head, 40; length of ear, 15; length of tail, 5; length of forelimb, 15; length of hind limb, 30 (Matsuzaki et al. 1989).

Scrota of males under anesthesia average 26.5 mm in length (21.8–29.5) and 12.8 mm in width (9.4–14.8; $n = 6$—F. Yamada, in litt.). These males were caught at Kawauchi, Sumiyo, Amami-Ohshima Island, and Mt. Amagi, Amagi, Tokuno-Shima Island, in February, March, July, November, and December. Females have 3 pairs of mammae: 1 pectoral, 1 abdominal, and 1 inguinal. Two females from Kawauchi, Sumiyo, Amami-Ohshima Island were lactating in February and March (F. Yamada, in litt.).

ECOLOGY. Amami-Ohshima and Tokuno-shima islands are subtropical (mean annual temperature of 21°C). *P. furnessi* is distributed in mountainous ranges with a forest cover of 86% on Amami-Ohshima Island and 44% on Tokuno-shima Island. It occurs in coastal scarp rocks with cycads and in mountain forest with oaks. Range size as estimated by pellet counts during 1992–1994 was 334.7 km² (47% of the island) on Amami-Ohshima Island and 33.0 km² (13% of the island) on Tokuno-Shima Island (Sugimura et al. 2000; Sugimura and Yamada 2004). Range size on Amami-Ohshima Island in 1994 was 20–40% smaller than estimated in 1974 and 1977, and 1 fragmented population in the north was recorded. Range size estimated by pellet counts during 2002–2003 was 301.4 km² (42% of the island) on Amami-Ohshima Island (Sugimura and Yamada 2004).

When the islands were originally covered by dense primary forests, the Amami rabbit lived mainly in primary forest. Following deforestation of 70–90% the islands in the 1970–1980s, the Amami rabbit lives not only in primary forest but also in cut-down areas and forest edges covered by the *Miscanthus sinensis* (Sugimura et al. 2000; Suzuki 1985).

Population size, estimated by pellet counts during 1992–1994, was 2,500–6,100 on Amami-Ohshima Island and 120–300 on Tokuno-Shima Island (Sugimura et al. 2000; Sugimura and Yamada 2004). Thus, the total number of Amami rabbits was 2,600–6,400. Population size, estimated by pellet counts during 2002–2003, was 2,000–4,800 on Amami-Ohshima Island (Sugimura and Yamada 2004). Population size in 2003 on Amami-Ohshima Island was 20% lower than estimated in 1994.

The only native predator of the Amami rabbit is the crotalid snake, *Trimeresurus flavoviridis*. The introduced mongoose *Herpestes javanicus* and feral dogs also prey on the Amami rabbit in Amami-Ohshima Island (Hattori and Itoh 2000; Yamada 2002; Yamada et al. 2000).

The Amami rabbit feeds on >29 species of plants, including 12 species of herbaceous plants, including *Adenostemma lavenia*, *Carex*, *Miscanthus sinensis*, *Peucedanum japonicum*, *Mosla dianthera*, and 17 of species shrubs, including *Castanopsis sieboldii*, *Melastoma candidum*, *Rubus sieboldii*, *Styrax japonica*, *Zanthoxylum ailanthoides*, at Kawauchi, Sumiyo in Amami-Ohshima Island (F. Yamada, in litt.). Stems and twigs <10 mm diameter of herbaceous plants and <7 mm diameter of shrubs were clipped and eaten by the Amami rabbit, and the bark of stems and twigs >7 mm in diameter of shrub plants was eaten. Acorns of *Castanopsis seiboldii* fallen on the ground during autumn and winter are eaten by the Amami rabbit. The Amami rabbit eats mainly sprouts and young parts of plants, including cambium, and nuts from a wide range of plant species. The raw amount of food per day eaten by a rabbit in captivity was measured as 360 g for runners of sweet potato *Ipomoea batatas*, 120 g for sprouts and young leaves of the Japanese pampas grass *Miscanthus sinensis*, 210 g for leaves and twigs of the fig tree *Ficus erecta*, and 140 g for leaves of the sugar cane *Saccharum officinarum* (Kirino et al. 1984).

Fecal pellets of the Amami rabbit are discoidal with the central part swollen. They average 7.5–14.5 mm in greatest diameter, with a mode of 11 mm (Suzuki 1985). Fresh pellets are shiny and smooth with mucous membrane coating and become nonshiny and hard when dry. Black pellets and irregular shape consist of leaves and bark of trees and ferns eaten by the rabbit, whereas brown pellets with a rounded shape consist mainly of leaves of the Japanese pampas grass *Miscanthus sinensis* (Suzuki 1985). The number of fresh pellets in a dunging of the Amami rabbit is estimated at 28.7 ± 22.1 *SD* (Sugimura et al. 2000). Pellets occur on runways along the sides of streams and loads; therefore, the number of pellets per km along a stream gives a suitable index for measuring relative abundance (Sugimura et al. 2000). The frequency of dunging per day was 7–12, and dunging occurred between 1500–0600 h, with a peak between 1900–0400 h (up to 2.4/h—Kirino 1977). Duration of a single dunging (20–30 pellets) was 10–30 min. Average daily number of pellets produced by a captive Amami rabbit is 147 (min. 62, maximum 221); $n = 3$ Amami rabbits for 30 days (Hayashi et al. 1984). The number of pellets decreased with a diet of sweet potato and runners of fig leaves and increased with a diet of pampas grass. Average, daily mass of pellets per captive Amami rabbit (average body mass; 2,130 g for 5 males and 2,180 g for 5 females) is 50.2 ± 28.6 *SE* g for males and 53.8 ± 22.8 *SE* g for females. Average, daily number of pellets for the same animals was 176.3 ± 67.4 *SE* for males and 207.7 ± 51.3 *SE* for females (Kamiya et al. 1987b).

Entrances to burrows are horizontal or slightly oblique and of round shape. They are 10–20 cm high and 12–25 cm wide (Abe 1963; Wildlife Conservation Group 1984). Tunnels follow a straight line for 30–200 cm. L-shaped tunnels follow a straight line 30–200 cm long from the entrance and then bend up at a right angle before following a straight line 60–185 cm long to a chamber (20 cm in diameter) laid with leaves (6 cm deep). Amami rabbits also use bases of trees, bases of rocks, and insides of fallen trees for burrows. The entrance, 15 cm high and 20 cm wide, in the base of a tree is slightly oblique downward, and the tunnel follows a gentle horizontal curve 80 cm long (Abe 1963). The maximum temperature (18–26°C) at 1.5 m from the entrance of the nest was 5–9°C lower than that (27–31°C) outside the nest, and the differential between maximum and minimum temperatures in a day (1.5–2.0°C) at 1.5 m from the entrance of the nest was smaller than that (8–11°C) outside the nest (Kirino 1977). Amami rabbits leave their nests at ca. 1700 h (70% from 1500 to 1800 h) and they return and enter nests at 0600 h (Kirino 1977).

Average size of home range of the Amami rabbits was 1.3 ha for 4 males and 1.0 ha for 3 females analyzed by radiotransmitters (Yamada et al. 2000). Home ranges of females did not overlap with that of each other, whereas those of males did, and male ranges overlapped those of females.

The Amami rabbit is active mainly at night. They move 100–200 m away from their burrows to feed and drop pellets in open places, such as forest roads. Burrows are usually located in small valleys covered by dense forests. Amami rabbits frequently use runways to climb up and down steep slopes from burrows and climb through mountain streams and undergrowth to open areas. An Amami rabbit swam a stream and came ashore (Kirino 1977).

Amami rabbits host 13 species of 8 genera of trombiculid mites, *Acomatacarus yosanoi*, *Ascoshcoengastia ctenacarus*, *A. noborui*, *A.* unidentified species, *Cordiseta nakayamai*, *Eltonella ichikawai*, *Gahrliepia saduski*, *Leptotrombidium kawamurai*, *L. kuroshio*, *L. pallidum burnsi*, *L. scutellare*, *Miyatrombicula okadai*, and *Walchia pentalagi*. *C. nakayamai* (restricted to Mt. Yuwan in Amami-Ohshima Island) and *W. pentalagi* are host specific to the Amami rabbit (Kamiya et al. 1987a; Suzuki 1975, 1976, 1977, 1980) and can be used to distinguish active versus inactive burrows (Suzuki 1975). *P. furnessi* hosts 5 species of 3 genera of ticks, *Amblyomma testudinarium*, *Dermacenter taiwanensis*, *Haemaphysalis formosensis*, *H. hystricis*, and *H. pentalagi*. *H. pentalagi* is host specific to *P. furnessi* (Kitaoka and Suzuki 1974).

Oocysts of the protozoa *Eimeria* are frequent in seats of Amami rabbits (Kamiya et al. 1987a). *P. furnessi* hosts 3 species of nematodes: *Obeliscoides pentalagi* from the stomach (number of rabbits parasitized/number of rabbits, 3/3), *Heligmonella leporis* from the small intestine (3/3), and *Trichuris* from the cecum (1/3—Fukumoto et al. 1986). *O. pentalagi* is host specific to the Amami rabbit (Fukumoto 1986; Kamiya et al. 1987a). An Anoplocepalidae cestode (3/3) and a trematode, *Ogmocotyle*, were recorded (1/3) in the small intestine (Kamiya et al. 1987a). Dung of the Amami rabbit harbors 16 species of fungi, which kill nematodes, rotifers, and microscopic animals (Glockling 1998; Glockling and Yamada 1997; Zare and Gams 2001).

HUSBANDRY. In the Elementary and Secondary School of Yamato Village, runners of sweet potato were the main diet for the rabbit, and *Miscanthus sinensis*, *Asplenium antiquum*, some fruits and vegetables were sometimes provided (Kirino 1977). In the Kagoshima Hirakawa Zoo, the diet was sweet potatoes, apples, and commercial pellets for rabbits; leaves of the fig *Ficus erecta*, akebi *Akebia quinata*, and other species, were seasonally supplemented (Sako et al. 1991). In feeding trials, 70 kinds of wild plants were eaten by *P. funessi*. Some Amami rabbits died due to infection by a tapeworm, *Cysticercus pisiformis*, carried by wild plants. At the Central Institute for Experimental Animals, grasses and weed were supplied just after introduction from the field, after which commercial pellets for rabbits (CR-3, CLEA Japan Inc.) and for pikas (CIEA-117) were the main diet, supplemented with sweet potato and apple (Matsuzaki et al. 1989).

The enclosure at the Elementary and Secondary School of Yamato Village was 184 m^2, with walls 2.5 m height composed of 1.5 m of concrete and 1 m of wire netting (Kirino 1977). To prevent the rabbits from escaping through tunnels, a wall of concrete 0.77 m deep was buried underground. Rocks and mounds were provided. Trees (cycad, Japanese banana *Musa basjoo*) were planted, and a pond was made for water. In the Kagoshima Hirakawa Zoo, the primary enclosure is 159 m^2, with a wall of 2.2 m height composed of 1.2 m of concrete and the other 1 m of wire netting. A secondary enclosure is 120 m^2. The primary enclosure has several oaks and pine. Captivity facilities have feeding and drinking posts. In the Central Institute for Experimental Animals, rabbits were reared in a laboratory (Matsuzaki et al. 1989). The animal room was kept at a temperature of 22 ± 2°C and a humidity of 55% ± 5%. Air was changed 10–15 times per hour with fresh air. Lights were on 0600–2000 h. Ten rabbits (5 males and 5 females) were in reproduction cages (CLEA Japan, Inc., Model CR-II), 75 cm wide, 50 cm deep, and 35 cm high. Each cage was divided into 2 parts by a partition with an opening to pass through. One part of the cage was covered by an aluminum plate to keep it dark and was laid with dry grass for a nest; the other part was for food, water, and toileting.

Insect nets were used to capture Amami rabbits in the enclosures of the Kagoshima Hirakawa Zoo when the animals were out of their burrows. To restrain an animal, the flabby skin from neck to back of the rabbit was held by the right hand, and the hind limbs held by the left hand. Juveniles were moved to a secondary enclosure to prevent parents from attacking them at the age of independence of the juvenile.

BEHAVIOR. The Amami rabbit has a vocalization like pikas *Ochotona* (Kawamichi 1981), and beats the ground with the hind limbs (F. Yamada, in litt.). At dusk, Amami rabbits appear at the entrances of their burrows before they become active and make calls that can be heard loud and clear in small valleys. A mother vocalizes to attract its offspring when she approaches the nursing burrow. Vocalizations and beating the ground occur when humans enter the habitat. A vocalization usually consists of 3–4 calls like 'puyi, puyi, puyi' (frequency, 6–12 KHz; length, 0.4–0.6 s; interval, 0.4–0.6 s—F. Yamada, in litt.). When captured, both sexes of Amami rabbits often call 'puyi', 'puy', and 'pii'; males also call 'qwa', 'gwa', 'qui', 'qwau', 'wiiq', and 'quyic' and females call 'kii' and 'quyi' (Kirino 1977) upon capture. Three captive rabbits called strongly in response to sounds of ca. 15–16 KHz, whereas they ran away from sounds of lower and higher frequencies (Kirino 1977). The number of vocalizations per h from the same 3 captive Amami rabbits was 3–30, with peaks at 2000 and 0300 h in August and 3–24 with peaks at 1900–2300 and 0300 h in October.

Amami rabbits can climb up by plunging its long nails into logs inclined at 70 degrees (Kirino 1977).

The Amami rabbit is coprophagous in captivity (Matsuzaki et al. 1989).

GENETICS. The karyotype of *Pentalagus furnessi* has a diploid number of 46 and a fundamental number (including the X chromosome) of 80 (Harada et al. 1985). The 23 pairs of chromosomes consist of 10 pairs of meta-submetacentric chromosomes, 8 pairs of subtelocentric chromosomes, and 5 pairs of acrocentric chromosomes. The X chromosome might be a biarmed pair (Harada et al. 1985). A homologue of chromosome 1 in *Oryctolagus* may exist in *P. furnessi* (Van der Loo et al. 1981). The arms of chromosome pairs 1 and 2 in *P. furnessi* are separate acrocentric chromosomes in other leporids. *P. furnessi* (2n = 46) is differentiated by the Robertsonian fusion of 2 chromosomes from the ancestral species (Harada et al. 1985).

Nucleotide sequences of mitochondria 12S ribosomal RNA (rRNA) and cytochrome *b* (cyt *b*) genes of *P. furnessi* are in the DDBJ, EMBL, and GenBank databases with the accession numbers AB058603–AB058609 and AB058614 (Yamada et al. 2002). Molecular data suggest no phylogenetic relationship between *Pentalagus* and *Pronolagus* (Matthee et al. 2004; Yamada et al. 2002).

CONSERVATION STATUS. The Amami rabbit was designated a natural monument of Japan in 1921 (Uchida 1920) and upgraded to a special natural monument of Japan in 1963 by the government. Since the designation, hunting and capture of the Amami rabbit has been prohibited. The Amami rabbit was listed as an endangered species, EN A2b, B1+2bce, C1, by the International Union for the Conservation of Nature and Natural Resources (2000) and ranked as an endangered species, EN(IB), by the government (Ministry of the Environment 2002).

Impact of habitat loss is severe for the Amami rabbit because extensive logging operations on the 2 islands reduced the area of old forests to <10–30% of its 1980 extent (Sugimura et al. 2000). Furthermore, the impact of invasive predators, such as feral dogs and cats and mongooses, on the Amami rabbit also occurs on both islands.

The Lagomorph Specialist Group of the International Union for the Conservation of Nature and Natural Resources proposed conservation action for *Pentalagus furnessi* (Chapman et al. 1990). In Amami-Ohshima Island, the Amami Wildlife Conservation Center of the Ministry of the Environment was established in 1999. The Amami rabbit was designated under the Endangered Species Act by the Ministry of the Environment (2004). A program of mongoose eradication was restarted in 2005 by the Ministry of the Environment to protect the Amami rabbit and other native species (Yamada 2002; Yamada and Sugimura 2004).

REMARKS. Other common names for *Pentalagus furnessi* are Liu Kiu rabbit and Ryukyu rabbit (Corbet 1994; Ellerman and Morrison-Scott 1951; Nowak 1999; Stone 1900). We are grateful to Y. Tomida of the National Science Museum, Tokyo, M. Harada at Osaka City University, H. Suzuki at Hokkaido University, H. Suzuki at Nagasaki University, T. Sako at the Kagoshima Hirakawa Zoo, S. Abe at the Ministry of the Environment, and N. Kawaji, H. Satoh, and K. Sugimura at the Forestry and Forest Products Research Institute for reviewing an early draft of the manuscript. H. Endo and H. Namikawa at the National Science Museum, Tokyo, and S. Hattori at the University of Tokyo helped measure crania.

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