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Revision of the mole genus *Mogera* (Mammalia: Lipotyphla: Talpidae) from Taiwan

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Abstract We surveyed the central mountains and southeastern region of Taiwan and collected 11 specimens of a new species of mole, genus *Mogera*. The specimens were characterized by a small body size, dark fur, a protruding snout, and a long tail; these characteristics are distinct from those of the Taiwanese lowland mole, *M. insularis* (Swinhoe, 1862). A phylogenetic study of morphological, karyological and molecular characters revealed that Taiwanese moles should be classified as two distinctive species: *M. insularis* from the northern and western lowlands and the new species from the central mountains and the east and south of Taiwan. The skull of the new species was slender and delicate compared to that of *M. insularis*. Although the karyotypes of two species were identical, the genetic distance between them was sufficient to justify considering each as a separate species. Here, we present a detailed specific description of the new species and discuss the relationship between this species and *M. insularis* based on ecological characteristics and geographic distributions.

Key words Talpidae, *Mogera*, mole, morphology, karyotype, molecular phylogeny

Introduction

Seven species of the order Lipotyphla (Insectivora) have been recorded from Taiwan to date (Hutterer, 1993). However, only one species of talpid, namely *Mogera insularis* (Swinhoe, 1862), is recognized in all taxonomic reviews (Corbet, 1978; Abe, 1995; Motokawa & Abe, 1996). *Mogera insularis* is distributed throughout Taiwan and is frequently found in agricultural and grassland regions.

Kishida (1936) was the first to note that two distinct forms of mole occurred in the lowland and mountainous areas of Taiwan, respectively. His notes lacked information about the morphology or ecology of the mole from the mountains, but he named this mole 'Yamazimogura'. Kishida's (1936) classification was not accepted by Kuroda (1940), who reviewed Kishida's (1936) work and concluded that it was unclear whether the two forms of Taiwanese mole were valid. Conversely, Kano (1940) working in the Tsugitaka (= Syneshan) Mountains described the highland species, *M. montana*, in support of Kishida's idea. However, Kano (1940) failed to specify the type specimen of *M. montana*. According to his description, this species was distributed within mountainous areas elevations greater than 700 m. However, the validity of *M. montana* was not widely accepted because the description was not sufficiently detailed.

Motokawa *et al.*'s (2001) study of variation in the Taiwanese mole revealed two forms: one with a short, thick skull and the other with a slender skull. Moles with the slender skull were collected in Nanjenshan, which is the southern limit of Pingtung Province. Motokawa *et al.* (2001) did not discuss this finding in depth and suggested that additional specimens from many localities should be examined to further elucidate variation in the Taiwanese mole.

We collected 11 moles during three expeditions (8–9 November 2001; 30 July–3 August 2002; and 11–14 March 2003) into the mountains of Taiwan (2300–2800 m elevation in Yushan National Park and Alishan National Scenic Area) and to the southernmost region of Taiwan (less than 100 m elevation in Kenting National Park) (Fig. 1). We also examined three specimens that were collected on the eastern lowlands of Taiwan (Hualien). All specimens were substantially different from *M. insularis*. Intermediate individuals were not observed. Here, we provide a detailed description of this species. In previous taxonomic reviews (e.g. Schwarz, 1948; Ellerman & Morrison-Scott, 1951; Corbet, 1978), the genus *Mogera* has been included in the synonymy of *Talpa*. Because the specific

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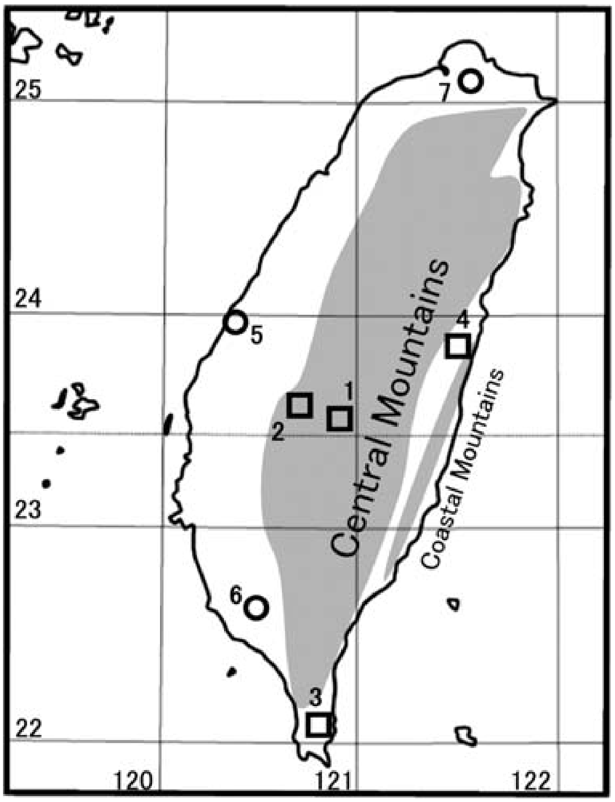

Figure 1 Collection localities of samples of *Mogera kanoana* (squares) and *M. insularis* (circles) in Taiwan. 1: Tatachia, Yushan National Park, Nantou Province; 2: Alishan National Scenic Area, Chiayi Province; 3: Manchou, Kenting National Park, Pingtung Province; 4: Tonghua University Campus, Sofong Town-ship, Hualien Province; 5: Hanpao, Chang Hua Province; 6: National Pingtung University of Science and Technology, Pingtung, Pingtung Province; 7: Shisousan, Taipei, Taipei Province.

name '*montana*' is preoccupied by the subspecies *Talpa romana montana* Cabrera, 1925, we propose a replacement name.

Materials and methods

Specimens

Eleven moles were collected in the following regions of Taiwan: Tatachia, Yushan National Park, Nantou Province; Alishan National Scenic Area in Chiayi Province; and Manchou, Kenting National Park in Pingtung Province (Fig. 1). Three additional specimens were collected on the campus of Tonghua University in Hualien Province by Mr Kun-Chie Chang. We also examined a single specimen (NSMT-M 34007; owned by Shuji Kobayashi) from the Alishan National Scenic Area, one specimen (USNM 199493; collection locality described only as 'Taiwan') in the United States National Museum of Natural History in Washington, DC, and two specimens from Shoufeng, Hualian County (AMNH 184983 and 184984) in the American Museum of Natural History, New York.

The 18 specimens described above were classified as members of the genus *Mogera* based on the presence of two incisors within the lower jaw. These specimens were compared with the following species: *M. hainana* Thomas, 1910; *M. insularis* (Swinhoe, 1862); *M. imaizumii* (Kuroda, 1957); *M. latouchei* Thomas, 1907; *M. tokudae* Kuroda, 1940 (including *M. etigo*, Yoshiyuki and Imaizumi, 1991); and *M. wogura* (Temminck, 1842) (including *M. robusta* Nehring, 1891).

Mogera hainana (from Hainan Island) and *M. latouchei* (from southern China) are usually treated as subspecies of *M. insularis* (Abe, 1995), but we considered these as separate species to directly compare geographic variation within *M. insularis*. We combined these species into an '*M. insularis* group' for comparison with our 18 specimens. All other species were considered collectively as members of a 'Japanese group'.

Specimens were deposited at the mammal collections at the National Museum of Natural Science (Taichung, Taiwan) (NMNS), the National Science Museum, Tokyo (NSMT-M), the American Museum of Natural History (AMNH), the United States National Museum of Natural History (USNM), the Siberian Zoological Museum (SZM), the Kunming Institute of Zoology (KIZ) and the Tunghai University collection (THU).

Morphological analysis

The following morphological characteristics were recorded: body mass; head and body length; tail length; forefoot length (without claw); forefoot breadth; hind foot length (without claw); and fur colour and muzzle shape. The tail ratio (%) was calculated as (tail length/head and body length) × 100.

Skull measurements (Fig. 2a–c) were used for direct comparisons and incorporated into a multivariate analysis (see below). Fifteen linear measurements were made with a digital calliper and were recorded to the nearest 0.01 mm. Skull measurements included: the greatest length of the skull; palatal length from the anterior tip of the first incisor to the posterior lip of the palate; inner length of the zygomatic arch; length of the upper tooth row; distance between the upper canine and third molar; length of the upper molars; rostral breadth at the canines; breadth between the infraorbital foramina; breadth across the upper second molars; greatest interorbital breadth; mandible length; mandible height at the coronoid process; length of the lower tooth row; distance between the lower first premolar and third molar; and length of the lower molars.

To evaluate the degree of cranial differentiation between species, skull measurements were analysed in a two-step canonical discriminant analysis using SPSS for Windows (ver. 10.0.5J; SPSS Inc., Chicago, IL). In the first step, the analysis was applied to all the aforementioned species of *Mogera* (except *M. hainana*) to identify whether the new species of mole was related to the *M. insularis* or Japanese group (*M. imaizumii*, *M. tokudae* and *M. wogura*). The second step was a more detailed analysis of the members of the *M. insularis* group. *M. hainana* was not included in either analysis because the skulls of the specimens were partially damaged. In each step, discriminant success rate was calculated for the evaluation of taxonomic validity.

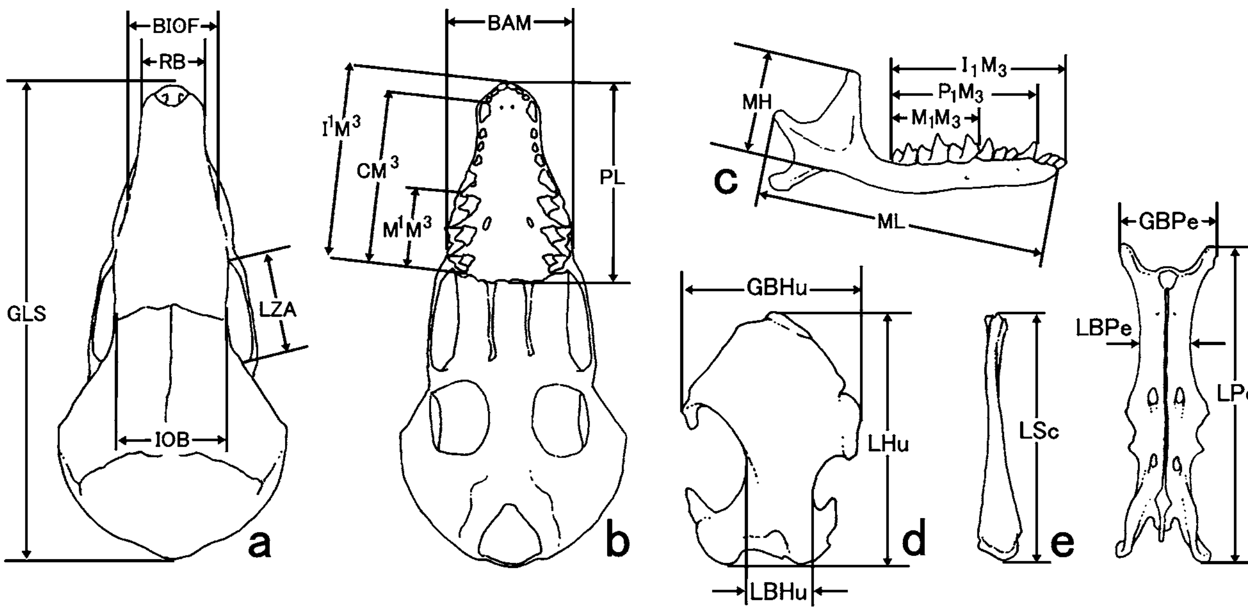

Figure 2 Measurements of skulls and postcranial skeleton used in this study. Dorsal (a) and ventral (b) views of skull are shown together with a lateral view of mandible (c), humerus (d), pelvis (e) and scapula (f). Skull measurements: GLS, greatest length of skull; PL, palatal length from the anterior tip of first incisor to the posterior lip of the palate; LZA inner length of zygomatic arch; I^1M^3, length of upper tooth row; CM^3, length between upper canine to third molar; M^1M^3, length of upper molars; RB, rostral breadth at the canines; BIOF, breadth between infraorbital foramina; BAM, breadth across upper second molars; IOB, greatest interorbital breadth; ML, mandible length; MH, mandible height at the coronoid process; I_1M_3, length of lower tooth row; P_1M_3, length between lower first premolar to third molar; and M_1M_3, length of lower molars. Humerus measurements: Lhu, length; GBHu, greatest breadth; and LBHu, least breadth. Pelvis measurements: Lpe, length; GBPe, greatest breadth; and LBPe, least breadth. Scapula measurement: LSc, length.

The postcranial skeletons (humerus, scapula and pelvis) of moles are important indicators of adaptation to an underground environment. Therefore, the following measurements were recorded and were compared among species: humerus length; greatest and smallest breadth of the humerus; pelvis length; greatest and smallest breadth of the pelvis; and scapula length (Fig. 2d–f). These data were used in a univariate analysis (see below).

Karyological analysis

Karyological data were obtained from six specimens (NMN S009312 (holotype), NSMT-M 33863–33867). Bone marrow cells were suspended sequentially with a hand-held centrifugal separator and directly prepared for chromosomal preparations in the field. Epithelial tissue samples preserved in the media were brought to the Highland Animal Experimental Station at Nagoya University in Japan and cultured for chromosome preparations. These cells were treated with a hypotonic solution (0.075 M KCl) and fixed in modified Carnoy's solution (3:1 methanol: acetic acid). Chromosomes were stained with 4% Giemsa solution. G-band was visualized by the ASG (acetic/saline/Giemsa) method of Sumner *et al.* (1971). Chromosome pairs were categorized as meta-submetacentric, subtelocentric or acrocentric according to Levan *et al.* (1964). The G-banding patterns were compared with those of *M. insularis* collected in the western lowlands of Taiwan. Chromosomes were arranged according to the karyotype of *M. insularis* published by Lin *et al.* (2002).

Molecular analysis

Genomic DNA was extracted from ethanol-reserved livers from 13 specimens of the new species (NMNS 009312 (holotype), NSMT-M 33863–33869, 33871, 33872, and THU 29, 30, and 32) and 11 specimens of *M. insularis* (NSMT-M 34008–34015, and THU 38–40) by proteinase K digestion and phenol–chloroform–isoamyl alcohol extraction. The complete mitochondrial cytochrome *b* gene (cyt*b*; 1140 bp) and partial 12S ribosomal RNA gene (12S; ~840 bp) was first amplified using the universal primer pairs L-14724 and H-15915 (Irwin *et al.*, 1991) and L-613 (Mindell *et al.*, 1991) and H-1478 (Kocher *et al.*, 1989). Secondary amplification of each product was carried out using the following primer pairs: L-14724 (Suzuki *et al.*, 1997) and H-15401 (Shinohara *et al.*, 2004) and H-15916 (Suzuki *et al.*, 2000) and L-15423 (Shinohara *et al.*, 2004) for cyt*b*; R-L613 (Yamada *et al.*, 2002) and U-H1066 (Suzuki *et al.*, 1997) and R-L 946 (Shinohara *et al.*, 2004) and U-H1478 (Suzuki *et al.*, 1997) for 12S rRNA. The second polymerase chain reaction (PCR) product of each reaction was primed using the BigDye Terminator cycle sequencing kit (ABI, Foster City, CA), and both strands sequenced directly (Model 310 or 3100; Applied Biosystems, Foster City, CA). Sequences were aligned with corresponding gene sequences from seven Eurasian talpids retrieved from the GenBank/EMBL/DDBJ database (Appendix II) using the default options in Clustal-X (Thompson *et al.*, 1997). A neighbour-joining (Saitou & Nei, 1987) tree was calculated with the Kimura two-parameter model (Kimura, 1980) using PAUP 4.0

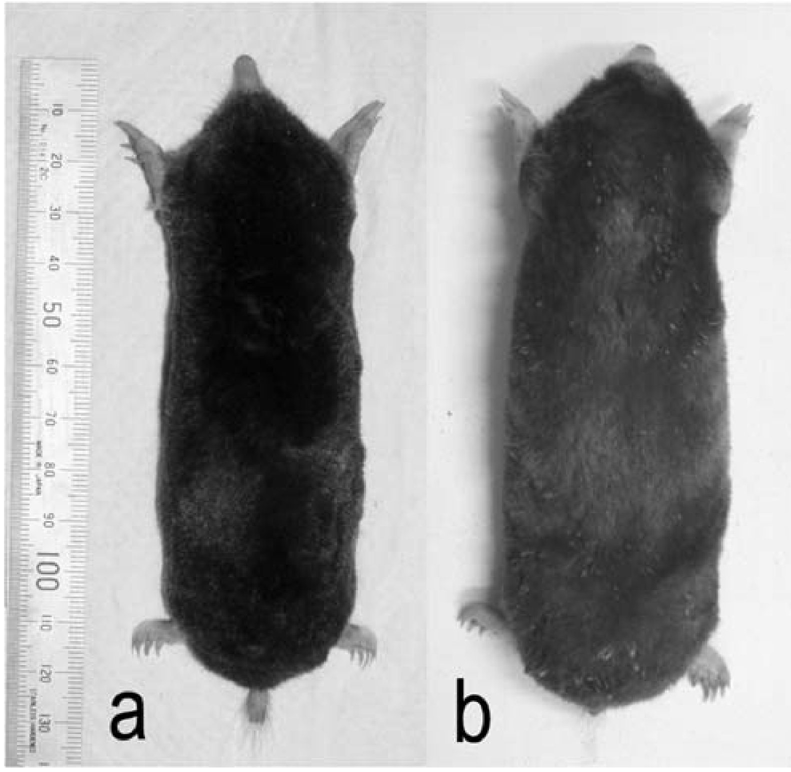

Figure 3 Dorsal views of specimens of *Mogera kanoana* (a; NSMT-M 33864) and *M. insularis* (b; NSMT-M 34013). A colour version of this figure is available as supplementary material available on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477200006002271. A hard copy has been deposited in the Biological Data Collection, General Library, Natural History Museum, London. (Email: genlib@nhm.ac.uk; www.nhm.ac.uk).

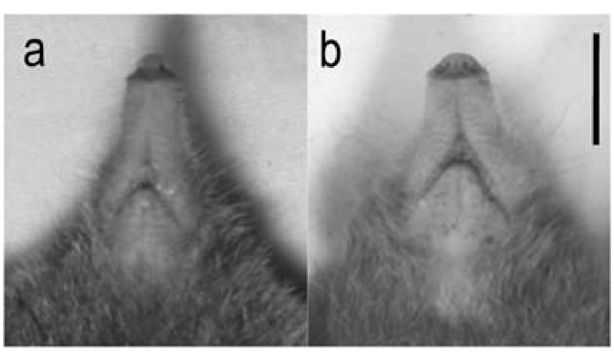

Figure 4 Ventral rostrums of *Mogera kanoana* (a: NSMT-M 33864) and *M. insularis* (b: NSMT-M 34013). Bar indicates 10 mm.

(Swofford, 2001). Statistical confidence of a particular cluster of sequences within a tree was evaluated using a bootstrap test (Felsenstein, 1985).

Results: Taxonomy

Mogera kanoana nom. nov. for *M. montana* Kano, 1940

Figs 3a, 4a, 5, 6a, b, e, f, 7a, 8

Material examined

HOLOTYPE AND TYPE LOCALITY. The holotype (NMNS 009312, field number; SIK 0583) is an adult male that was collected in Tatachia, Yushan National Park, Nantou Province, Taiwan on 1 August 2002. The holotype comprises

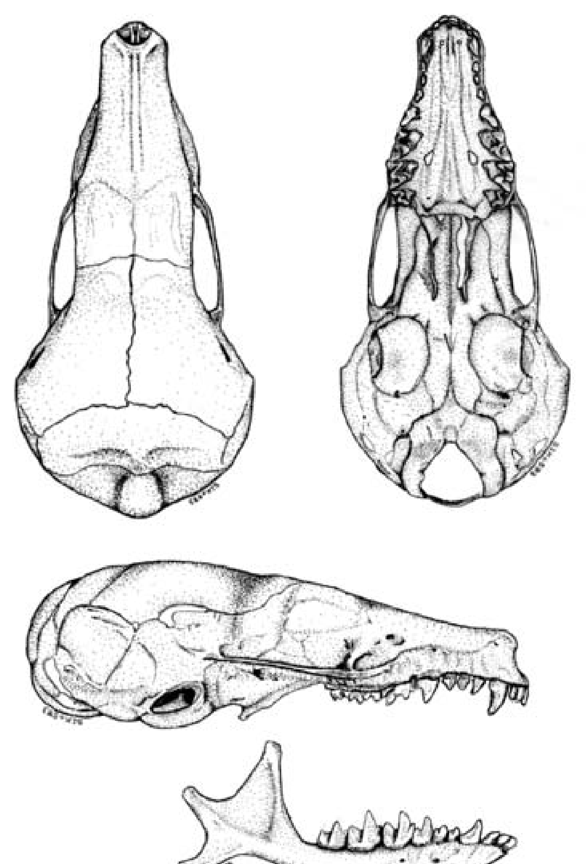

Figure 5 Skull and mandible of the holotype of *Mogera kanoana* (NMNS 009312). Bar indicates 10 mm.

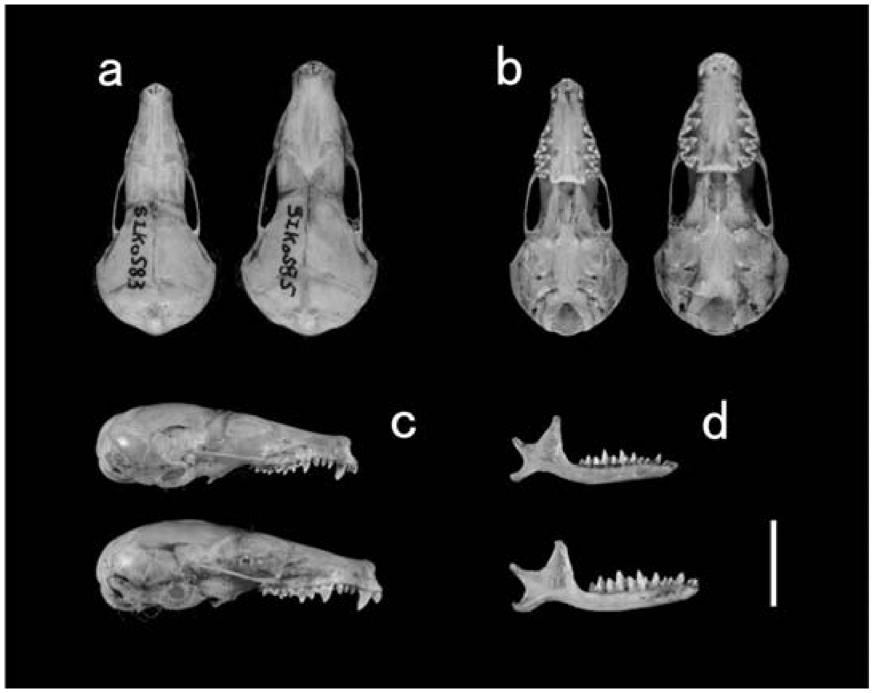

Figure 6 Dorsal (a) and ventral (b) and right lateral (c) views of cranium, and right lateral view of the mandible (d) of *Mogera kanoana* (holotype, field number SIK 0583) and *M. insularis* (NSMT-M 34013, field number SIK 0585). *Mogera kanoana* is arranged to the left of a, b and at the top of c, d for direct comparisons of skulls. Bar indicates 10 mm. A colour version of this figure is available as supplementary material available on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477200006002271. A hard copy has been deposited in the Biological Data Collection, General Library, Natural History Museum, London. (Email: genlib@nhm.ac.uk; www.nhm.ac.uk).

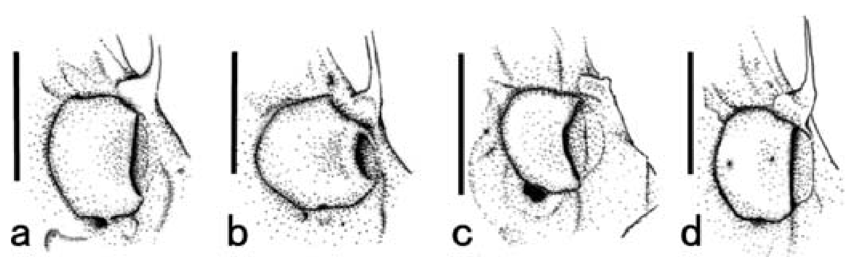

Figure 7 Auditory bulla of *Mogera kanoana* (a: holotype), *M. insularis* (b: NSMT-M 34013), *M. latouchei* (c: USNM252190) and *M. imaizumii* (d: NSMT-M 34016). Bars indicate 5 mm.

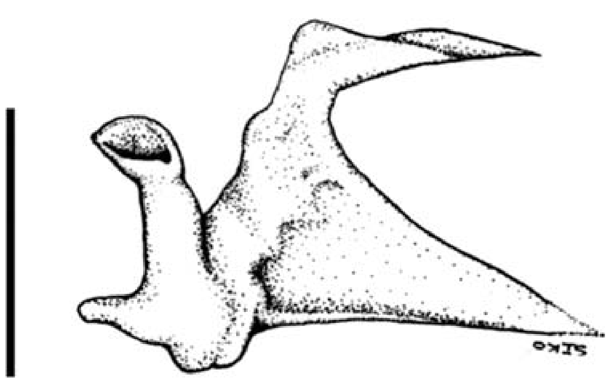

Figure 8 Ventral view of malleus – incus complex of *Mogera kanoana* (holotype). Bar indicates 1 mm.

a stuffed skin, cranium, mandible, and near-complete skeleton. The holotype was deposited at the National Museum of Natural Science (Taichung, Taiwan).

REFERRED SPECIMENS. The paratypes (NSMT-M 33863 and 33864) collected in the type locality on 8 November 2001 and on 2 August 2002, respectively, were young adult males. One female (NSMT-M 33865) and two male (NSMT-M 33866 and 33867) paratypes werecollected in Kenting National Park, Pingtung Province from 6–8 August, 2002. Five paratypes (NSMT-M 33868–33872; two males and three females) and additional one female paratype (NSMT-M 34007) were collected in the Alishan National Scenic Area, Chiayi Province, on 11–14 March 2003 and 24 July 1988, respectively. The external morphological and skull dimensions of these specimens are presented in Table 1. Paratypes were deposited at the National Science Museum, Tokyo (Tokyo, Japan).

For other material, see Appendix 1.

Diagnosis

Small *Mogera* endemic to the southeastern part of Taiwan characterized by the dark fur colour, long tail and protruding snout. Skull with long slender palate and small molars.

			Measurements[a]							
Specimen No.	Sex	Date	BW	H&B	T	FFL	FFB	HF	Testis	Tail ratio
NMNS009312	♂	2002.08.01	35.0	114.5	10.0	14.0	14.0	14.5	6.31 × 3.98	8.73%
NSMT-M33863	♂	2001.11.08	36.0	121.5	12.0	15.0	15.5	14.5	5.99 × 3.31	9.88%
NSMT-M33864	♂	2002.08.02	41.0	124.5	10.5	15.0	15.0	15.0	15.07 × 8.48	8.43%
NSMT-M33865	♀	2002.08.06	47.0	130.5	11.0	14.5	14.5	14.5		8.43%
NSMT-M33866	♂	2002.08.07	59.0	125.5	8.5	16.0	15.5	15.0	11.77 × 5.95	6.77%
NSMT-M33867	♂	2002.08.08	55.0	133.5	10.0	15.0	15.5	14.5	12.07 × 6.36	7.49%
NSMT-M33868	♂	2003.03.12	30.1	117.0	12.5	13.0	13.5	14.0	4.19 × 2.04	10.68%
NSMT-M33869	♀	2003.03.12	40.5	120.5	12.0	13.5	13.5	13.5		9.96%
NSMT-M33870	♂	2003.03.13	43.5	124.5	11.5	14.0	13.5	14.0	13.66 × 8.65	9.24%
NSMT-M33871	♀	2003.03.13	23.5	113.0	10.5	14.0	14.0	14.0		9.29%
NSMT-M33872	♀	2003.03.13	28.4	116.0	13.5	14.0	13.5	13.5		11.64%

Table 1 External measurements of the type specimens of *Mogera kanoana* collected in three expeditions in Taiwan.

[a] BW, body weight (g); F&B, head and body length (mm); T, tail length (mm); FFL, fore foot length without claw (mm); FFB, fore foot breadth (mm); HF, hind foot length without claw (mm); Testis, long × short diameters (mm). Tail ratio calculated as T/(head-body length) × 100.

Description of holotype

The body of *M. kanoana* is smaller than *M. insularis* (Fig. 3a). The fur is dense and velvety black – a characteristic common in the genus *Talpa*, but not *Mogera*. The chest and abdomen is not coated by secretions. The tail is short and is covered by long hairs. External measurements were as follows: head and body length, 114.5 mm; tail length, 10.0 mm; forefoot length (without claw), 14.0 mm; forefoot breadth, 14.0 mm; and hind foot length (without claw), 14.5 mm. The tail to head and body ratio (8.7%) is slightly greater than that of *M. insularis* (mean = 6.9%; n = 6). Compared with *M. insularis*, the snout is long and slender, the median pad of the rhinarium protrudes forward and the nostrils open sideways (Fig. 4a).

The skull of *M. kanoana* is small (Fig. 5 and 6), with the greatest length being 29.06 mm. The palate is relatively short and narrow, especially in the rostrum. The outline of the rostrum is not strongly constricted, and bends ventrally in the anterior position of the fourth premolar in the side view. The zygomatic arch is curved laterally. The vertical opening of the auditory bulla is wide and the entotympanic bone is incomplete (Fig. 7a). The middle ear bones (malleus and incus) resemble the usual *Mogera* pattern (Fig. 8), with the malleus having an obvious apophysis orbicularis. The breadth of the foramen magnum is wide relative to the longitudinal length. The posterior border of the infraorbital foramen lies above the metastyle of M2.

The dental formula is I 3/2, C 1/1, P 4/4, M 3/3 = 42. The row of upper incisors projects slightly forward and is V-shaped. The pair of upper first incisors is clearly larger than the other teeth. The upper first to third premolars are well spaced and are not as cramped as in *M. insularis*. The upper fourth premolar is sharp and narrow and is missing the mesial cingulum cusp. The upper molars are rather small and the hypocones are not developed, giving these teeth a triangular shape. The mesostyles of the first to third molars are not well divided. The lower tooth row has two incisors, derived via the removal of the third incisor from the fundamental formula. The lower premolars are largest in P1. In the following three premolars, P2 is slightly larger than P3 but both are much smaller than P4. Thus the tips of the second to fourth premolars are not arranged linearly. The two main cusps on the lower molars are prominent, but the distal cusp is much lower than the mesial cusp.

The vertebral formula is 7 cervical + 13 thoracic + 6 lumbar + 6 sacral bones. The caudal bones were not counted. The humerus is typical shape, but slender (Fig. 9a, b) compared with other species of the genus *Mogera*. The ratio of the greatest breadth to length was 71.2%. The scapula at 20.26 mm is shorter than in other *Mogera* species. The ratio of the scapula to the greatest length of the skull was 66.12%. The pelvis is very slender and is similar to the general *Mogera* form with two pairs of sciatic foramina (Fig. 9e, f). The frontal and caudal foramina are smaller than in other *Mogera* species.

Variation

The specimens collected in Kenting National Park (NSMT-M 33865–33867) and Hualien (THU 29, 30, 32) had brown fur that was darker than that of *M. insularis*. The variations in external measurements are presented in Table 1. Specimens from the mountain (NMNS 009312, NSMT-M 33863 and 33864, NSMT-M 33868–33872) and the eastern lowlands (Hualien; THU 29, 30, 32) were similar in external size and skull characters. However, specimens from the southernmost population (Kenting; NSMT-M 33865–33867) were larger and possessed an enlarged dorsal interorbital portion of the skull (the palate was elevated in the lateral view). Among the different populations, the scapulae of the specimens from the southernmost population were the longest. The pelvis of specimen NSMT-M 33865 (at the sciatic bones) was remarkably narrower than that of any other specimen. Three

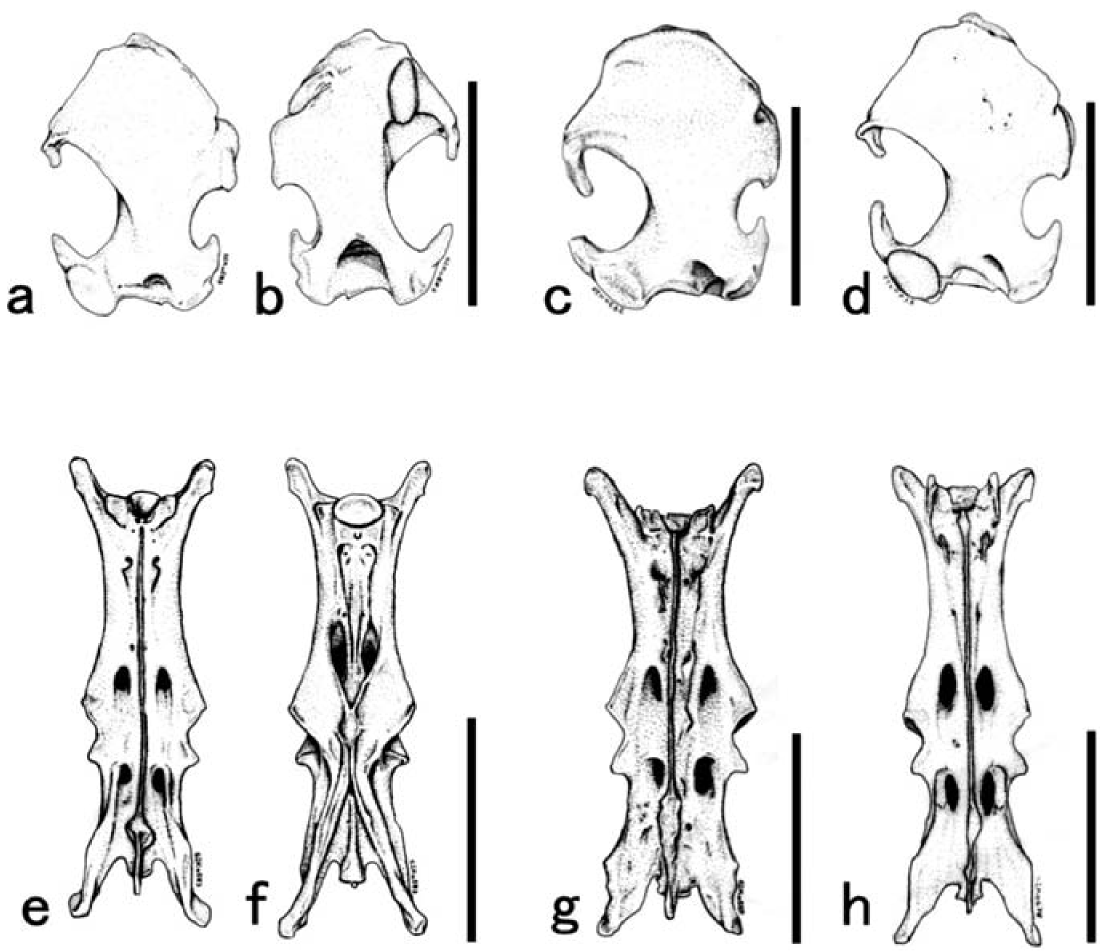

Figure 9 Humerus and pelvis of *Mogera kanoana* (a, e: dorsal; b, f; ventral; holotype), *M. insularis* (c, g: dorsal; NSMT-M 34013) and *M. imaizumii* (d, h: dorsal; NSMT-M 34016). Bars indicate 10 mm.

geographic populations of *M. kanoana* were identified: type I from the Tatachia (type locality; NMNS 009312, NSMT-M 33863 and 33864) and Alishan mountain (NSMT-M 33868–33872); type II from the eastern lowlands (Hualien; THU 29, 30, 32); and type III from the southern Kenting region (NSMT-M 33865–33867). Morphological characteristics of these populations are summarized in Table 2.

Ecological notes

Three *M. kanoana* were collected in a high, mountainous habitat (~2800 m above sea level). The holotype (NMNS 009312) was captured in a tunnel that crossed a trail that led to the top of a mountain. In the forest within Yushan National Park, there were many small tunnels that may have been constructed by *M. kanoana*. The main habitat is broadleaf forests. This

	M. kanoana			
Character	**Type I**	**Type II**	**Type III**	***M. insularis***
Locality	Tatachia, Alishan	Hualien	Kenting	Northern to western Plains
Body size	small	small	medium	medium to large
Fur color	black	dark brownish-grey	dark brownish-grey	pale brownish-grey
Tail	short	short	short	almost hidden by fur
Rhinarium	protruding	protruding	protruding	round
Forehead skull shape	smooth-arched	smooth-arched	round	round and very broad
Breadth of rostrum	slender	slender	medium	broad
Breadth of palate	slender	slender	slender	broad
Scapula	short		long	long

Table 2 Variation among three morphotype of *Mogera kanoana* with comparisons to *M. insularis*.

habitat is similar to that of other *Mogera* species, but *M. kanoana* also enters gardens and constructs tunnels around flowerbeds. Two reference specimens (NSMT-M 33863 and 33864) were caught there. These habitats are similar to that of other *Mogera* species. In the AlishanNational Scenic Area, there were many tunnels within wasabi fields and gardens and lawns at some sightseeing locations. In gardens and lawns, *M. kanoana* constructed small mounds and surface tunnels that resembled those of other *Talpa* or *Mogera* species. We caught two specimens (NSMT-M 33871 and 33872) and found three dead specimens (NSMT-M 33868–33870) in the gardens and lawns of the Alishan National Scenic Area.

In the lowlands of Kenting National Park, *M. kanoana* was not encountered in rice fields or in other agricultural areas in the vicinity of human dwellings. However, we collected several specimens (NSMT-M 33865–33867) from a small farm at the foot of a mountain. In Kenting National Park, most farm areas were inhabited by large rats, and there were many large tunnels. These rats may compete with or (most probably) prey upon moles. Several specimens of *M. kanoana* (THU29, 30, and 32) were collected on the campus of Tonghua University, Hualien county (K. Chang, Tunghai University, pers. obs.).

Paratypes NSMT-M 33865 and 33871 were pregnant females, each with three foetuses. These females were caught in August (Kenting) and March (Alishan), respectively, leading us to surmise that these months may be the breeding seasons of *M. kanoana* in two different elevations.

Comparisons with other *Mogera* species

Mogera kanoana is a member of the genus *Mogera* because it possesses two incisors in the lower jaw. The external appearance of syntypes of *M. insularis* that are preserved in the British Museum of Natural History and the Leiden Natural History Museum exhibit brownish fur and a short, thick snout. Although we could not examine the skulls of these syntypes, the appearance matched that of the Taiwanese lowland mole, *M. insularis* and were distinct from *M. kanoana*. A long slender snout and a protruded rhinal pad further distinguished *M. kanoana* from *M. insularis* and the Japanese *Mogera* species.

To validate the new species designation for *M. kanoana*, we examined the collections at the United States National Museum of Natural History in Washington, DC, and the American Museum of Natural History in New York. Collectively, these institutions housed 40 specimens of *M. insularis* from Taiwan, 10 specimens of *M. latouchei* and four specimens of *M. hainana*. According to the description of Thomas (1907), *M. latouchei* is characterized by a black fur and a slender snout with a protruding rhinal pad. These external characters are similar those of *M. kanoana*. The fur colouration of *M. hainana* is much lighter than that of *M. kanoana* and similar to that of *M. insularis* and the Japanese *Mogera*.

Table 3 summarizes the external measurements of the *Mogera* species that we examined. *Mogera kanoana* was the smallest species, except for *M. latouchei*. The tail of *M. kanoana* was slightly longer than that of *M. insularis* and *M. hainana*, but was much shorter than that of *M. latouchei* and the Japanese *Mogera*. The relatively small body mass of *M. kanoana* versus the head and body length was indicative of the slenderness of this species.

The skull of *M. latouchei* was relatively small, but its outline was similar to that of *M. kanoana*: it possesses a long and slender rostrum, a narrow brain case, and a weak zygomatic arch. These characters are noticeably different from those of *M. insularis*. The opening of the auditory bulla of *M. kanoana* was similar to the Japanese species of *Mogera*, and appeared to be intermediate between *M. latouchei* and *M. insularis* (Fig. 7). The middle ear bones (malleus and incus) of *M. kanoana* were similar in shape to those of the Japanese species of *Mogera*, but were different from those of *M. insularis* in that the malleus was longer than the incus and the malleus had an obvious apophysis orbicularis.

The vertebral formula of *M. kanoana* was the same as that of *M. insularis*, but differed from that of the Japanese species of *Mogera*, which possess 14 thoracic bones. The humerus of *M. kanoana* was more slender than those of the other *Mogera* species examined, except that of *M. uchidai* (as reported by Abe *et al.* 1991) (Fig. 9a–d). The ratio of humerus breadth to length in *M. kanoana* (average: 71.2%) was intermediate to that of *M. uchidai* (67.1%) and the remaining *Mogera* species (72–73%), and was substantially smaller than that of *M. insularis* (75.4%; Table 4). The pelvis of *M. kanoana* was similar to the Japanese species of *Mogera*, but was more slender than that of *M. insularis* (Fig. 9e–h).

Skull morphometrics

Table 5 shows the mean skull measurements of the various *Mogera* species and these measurements relative to greatest length of the skull in each species. The skull size of *M. kanoana* was between intermediate to those of *M. latouchei* and *M. insularis*. The skulls of the Japanese species of *Mogera* were much larger than any of those within the *M. insularis* group.

The discriminant functions of the first three vectors had eigenvalues >1.0 (Table 6), which is considered to be a good indicator of total skull variation. Table 7 shows the results of the canonical discriminant analysis. *Mogera imaizumii* and *M. wogura* were less distinguishable than the other species of *Mogera*, which could be clearly identified. Each group was discriminated in the total success rate of 94.1%. In the two-dimensional plot of the first two vectors of the canonical discriminant analysis (Fig. 10), *M. tokudae* was separated from a group containing *M. imaizumii* and *M. wogura*. The *M. insularis* group was distinguishable from the Japanese group by a different direction of vector 1. Within the *M. insularis* group, *M. insularis* and *M. latouchei* were not clearly discernible, but *M. kanoana* was separated from this grouping by vector 2 (Fig. 10).

A second canonical discriminant analysis using *M. insularis*, *M. latouchei* and the three morphotypes of *M. kanoana* was carried out to elucidate relationships within the *M. insularis* group (Tables 8 and 9). Eigenvalues of the first and second vectors were >1.0 and each group were discriminated in the total success rate of 95.2%. The three dimensional plot (Fig. 11) clearly separated the three species, however the three morphotypes of *M. kanoana* were not distinguishable.

Species		Mean values of external measurements[a]						
		BW	HB	T	FFL	FFW	HF	Tail Ratio
Mogera kanoana (n = 11)	Mean	39.91	121.91	11.09	14.36	14.36	14.27	9.14%
	Range	23.5–59.0	113.0–133.5	8.5–13.5	13.0–16.0	13.5–15.5	13.5–15.0	6.7–13.0%
	SD	10.93	6.56	1.39	0.84	0.87	0.52	1.39%
M. insularis (n = 6)	Mean	56.86	128.50	9.13	15.38	16.25	15.69	7.08%
	Range	42.0–72.5	112.0–134.0	6.5–11.5	14.0–16.0	15.5–17.5	15.5–16.0	5.8–8.8%
	SD	10.53	6.98	1.69	0.79	0.71	0.26	1.15%
M. latouchei[b] (n = 5)	Mean	–	99.20	17.80	–	–	13.90	18.11%
	Range	–	87.0–115.0	15.0–20.0	–	–	13.5–14.0	14.2–18.1%
	SD	–	11.19	2.17	–	–	0.22	2.84%
M. hainana[b] (n = 4)	Mean	–	125.25	10.00	–	–	12.75	7.96%
	Range	–	120.0–134.0	9.0–12.0	–	–	8.0–18.0	9.00–18.1%
	SD	–	5.36	1.22	–	–	3.70	0.68%
M. imaizumii (n = 13)	Mean	77.68	134.88	17.65	17.85	19.54	18.15	13.12%
	Range	58.5–109.1	124.5–145.5	14.0–20.0	16.0–19.5	17.5–22.0	16.5–20.0	10.4–15.1%
	SD	14.85	6.34	1.76	0.97	1.57	0.97	1.48%
M. minor (n = 28)	Mean	53.61	119.82	15.02	15.75	17.00	16.11	12.57%
	Range	40.3–67.6	109.5–130.9	8.5–18.5	10.5–17.5	15.0–18.5	14.5–19.0	6.9–16.3%
	SD	7.49	5.91	2.20	1.25	0.79	0.94	1.95%
M. wogura (n = 75)	Mean	126.98	160.21	19.76	21.05	22.63	20.58	40.11%
	Range	90.1–170.0	139.0–180.0	14.0–28.0	19.0–24.0	20.0–25.5	19.0–23.0	38.7–41.7%
	SD	18.39	9.83	2.27	0.99	1.13	0.87	78.22%
M. tokudae (Echigo P.) (n = 7)	Mean	141.55	167.21	26.93	21.79	24.36	22.50	16.11%
	Range	131.0–161.5	159.0–172.0	24.0–29.5	21.5–22.5	24.0–25.5	22.0–23.0	14.1–17.5%
	SD	13.01	4.63	2.15	0.39	0.56	0.50	1.34%
M. tokudae (Sado Isl.) (n = 4)	Mean	103.88	149.53	25.78	19.48	21.78	20.80	17.40%
	Range	82.5–120.5	137.0–163.0	23.0–27.5	18.5–20.4	20.5–23.1	20.0–21.5	14.0–20.0%
	SD	16.37	12.25	2.04	0.88	1.23	0.81	2.72%

Table 3 Comparisons of external measurements among *Mogera* species. Values are mean, range (min-max), and standard deviation (SD).

[a] BW, body weight (g); F&B, head and body length (mm); T, tail length (mm); FFL, fore foot length without claw (mm); FFB, fore foot breadth (mm); HF, hind foot length without claw (mm); Testis, long × short diameters (mm). Tail ratio calculated as T/(head-body length)X100.
[b] Data from the collection of the American Museum of Natural History, New York.

Species		GBHu/LHu[a]	LBHu/Lhu[a]	LHu/GLS[a]	LHu/GLS[a]	GBPe/LPe[a]
M. kanoana Type I (n = 6)	Mean	69.47	25.43	40.09	65.79	15.75
	Range	68.03–71.24	23.56–27.11	38.69–41.02	64.11–64.17	15.07–16.53
	SD	1.23	1.35	0.77	1.10	0.49
M. kanoana Type III (n = 3)	Mean	69.83	26.07	41.84	72.22	14.18
	Range	68.44–71.10	25.76–26.39	40.27–42.88	70.23–73.46	13.73–14.85
	SD	1.33	0.31	1.38	1.74	0.59
M. insularis (n = 6)	Mean	74.83	29.58	42.36	71.07	16.67
	Range	72.09–77.56	28.37–30.96	40.96–43.89	69.63–73.28	15.41–18.94
	SD	1.89	0.97	1.05	1.56	1.21
M. wogura (n = 6)	Mean	73.14	28.10	45.57	72.06	14.38
	Range	68.94–76.52	27.03–28.96	44.05–46.86	70.28–73.69	13.12–15.34
	SD	2.32	1.04	0.92	3.34	0.80

Table 4 Comparison of humerus, scapula and pelvis relative to LHu (humerus length), GLS (greatest length of skull), and LPe (least breadth of pelvis) from *Mogera kanoana* (from mountain (Type I) and Kenting population (Type III)), *M. insularis* and *M. wogura*. Values are per cent mean and range (min-max), and per cent standard deviation (SD).

[a] Humerus measurements: Lhu, length; GBHu, greatest breadth; and LBHu, least breadth. Pelvis measurements: LPe, length; GBPe, greatest breadth; and LBPe, least breadth. Scapula measurement: LSc, length.

A)

Species	N	Mean measurements[a]														
		GLS	PL	LZA	I^1M^3	CM^3	M^1M^3	RB	BIoF	BAM	IOB	ML	MH	I_1M_3	P_1M_3	M_1M_3
Mogera kanoana	16	30.42	11.79	7.43	11.96	10.60	5.13	4.07	5.86	7.74	6.97	18.98	6.17	11.10	9.26	5.48
M. insularis	41	31.89	12.93	8.58	13.28	11.82	6.08	4.66	6.40	8.86	7.35	20.78	6.34	12.42	10.37	6.46
M. latouchei	6	28.17	11.30	7.00	11.51	10.25	5.12	3.77	5.86	7.34	6.78	17.77	5.78	10.78	9.14	5.57
M. imaizumii (NE Japan)	44	35.11	13.81	9.73	14.42	13.10	6.52	4.60	6.27	9.32	7.80	22.39	7.18	13.60	11.57	7.15
M. imaizumii (SW Japan)	27	31.87	12.36	7.57	12.87	11.49	5.64	4.03	5.75	8.15	7.40	19.77	6.38	12.08	10.20	6.19
M. wogura (Japan)	67	38.16	15.28	10.08	15.74	14.38	7.05	5.16	6.61	9.96	8.23	24.56	7.90	14.75	12.64	7.67
M. wogura (Russia)	7	42.94	17.06	12.84	17.29	15.90	7.42	6.22	7.58	11.09	8.96	28.50	9.11	16.40	13.82	8.21
M. tokudae (Echigo Plain)	17	41.51	17.80	10.72	18.36	16.60	8.36	5.59	7.37	11.52	8.74	27.21	9.12	17.33	14.78	9.06
M. tokudae (Sado Isl.)	13	38.93	16.69	10.22	17.34	15.75	7.90	5.09	6.88	10.65	8.39	25.55	8.67	16.36	13.94	8.53

B)

Species	Relative measurements (%)[a]														
	GLS	PL	LZA	I^1M^3	CM^3	M^1M^3	RB	BIoF	BAM	IOB	ML	MH	I_1M_3	P_1M_3	M_1M_3
Mogera kanoana		38.70	24.40	39.30	34.80	16.90	13.40	19.30	25.40	22.90	62.40	20.30	36.50	30.40	18.00
M. insularis		40.50	26.90	41.70	37.10	19.10	14.60	20.10	27.80	23.00	65.20	19.90	39.00	32.50	20.30
M. latouchei		40.10	24.90	40.80	36.40	18.20	13.40	20.80	26.10	24.10	63.10	20.50	38.20	32.40	19.80
M. imaizumii (NE Japan)		39.30	27.70	41.10	37.30	18.60	13.10	17.80	26.60	22.20	63.80	20.50	38.70	33.00	20.40
M. imaizumii (SW Japan)		38.80	23.80	40.40	36.10	17.70	12.60	18.00	25.60	23.20	62.10	20.00	37.90	32.00	19.40
M. wogura (Japan)		40.00	26.40	41.20	37.70	18.50	13.50	17.30	26.10	21.60	64.40	20.70	38.70	33.10	20.10
M. wogura (Russia)		39.70	29.90	40.30	37.00	17.30	14.50	17.70	25.80	20.90	66.40	21.20	38.20	32.20	19.10
M. tokudae (Echigo Plain)		42.90	25.80	44.20	40.00	20.20	13.50	17.80	27.80	21.00	65.60	22.00	41.80	35.60	21.80
M. tokudae (Sado Isl.)		42.90	26.30	44.50	40.50	20.30	13.10	17.70	27.40	21.60	65.70	22.30	42.00	35.80	21.90

Table 5 Comparisons of *Mogera* skulls: A) mean values and B) measurements relative to greatest skull length.

[a]Skull measurements: GLS, greatest length of skull; PL, palatal length from the anterior tip of first incisor to the posterior lip of the palate; LZA inner length of zygomatic arch; I^1M^3, length of upper tooth row; CM^3, length between upper canine to third molar; M^1M^3, length of upper molars; RB, rostral breadth at the canines; BIOF, breadth between infraorbital foramens; BAM, breadth across upper second molars; IOB, greatest interorbital breadth; ML, mandibler length; MH, mandibler height at the coronoid process; I_1M_3, length of lower tooth row; P_1M_3, length between lower first premolar to third molar; and M_1M_3, length of lower molars.

Character[a]	Vector 1	Vector 2	Vector 3	Vector 4	Vector 5	Vector 6
GLS	0.0134	−2.3690	−0.8188	−0.0970	−0.1006	−0.7676
PL	−0.2894	0.9815	0.6531	0.5711	−1.5630	−0.5237
LZA	−0.2380	0.0017	0.3097	0.5065	0.8300	0.1211
I^1M^3	0.3423	3.2008	−0.5966	1.6225	2.0535	−5.1167
CM^3	−0.0110	−1.7215	−0.6544	−1.0679	−1.8958	3.6098
M^1M^3	−0.2509	1.5900	−0.5210	−3.1131	−0.5492	−2.7442
RB	−1.9085	−0.0282	3.5748	−1.2467	−1.1309	1.0056
BIOF	−1.8766	1.7492	0.3131	2.3359	−1.3034	2.8799
BAM	0.8380	0.1300	−0.4179	−1.3379	0.9417	−2.3468
IOB	1.1737	−0.7700	0.0241	−0.9045	1.3420	1.0071
ML	−1.1245	0.5453	1.6335	−0.5722	0.0695	−0.0627
MH	1.7657	0.0561	−0.9899	2.9233	−0.0522	−0.0825
I_1M_3	0.1099	0.6637	0.4236	1.9503	4.8749	1.1142
P_1M_3	2.5895	−0.2796	−0.6210	−1.7390	−4.5577	2.9225
M_1M_3	0.5569	0.0006	0.3439	−0.1884	0.1096	2.9709
Eigenvalue	10.8927	4.8841	2.2533	0.6506	0.3007	0.2033
Cumulative	56.7783	82.2368	93.9821	97.3731	98.9403	100

Table 6 Eigenvectors, eigenvalues and cumulative proportions for vectors 1–6 resulting from canonical discriminant analysis of skull measurements of six *Mogera* species: *M. tokudae* (MTO), *M. imaizumii* (MIM), *M. wogura* (MWO), *M. insularis* (MIN), *M. latouchei* (MLA) and *M. kanoana* (MKA).

[a]GLS, greatest length of skull; PL, palatal length from the anterior tip of first incisor to the posterior lip of the palate; LZA inner length of zygomatic arch; I^1M^3, length of upper tooth row; CM^3, length between upper canine to third molar; M^1M^3, length of upper molars; RB, rostral breadth at the canines; BIOF, breadth between infraorbital foramens; BAM, breadth across upper second molars; IOB, greatest interorbital breadth; ML, mandibler length; MH, mandibler height at the coronoid process; I_1M_3, length of lower tooth row; P_1M_3, length between lower first premolar to third molar; and M_1M_3, length of lower molars.

			MWO				
Species	***MTO***	***MIM***	**(Japan)**	**(Russia)**	***MIN***	***MLA***	***MKA***
M. tokudae	30						
M. imaizumii		66	4				1
M. wogura (Japan)		8	59				
M. wogura (Russia)				7			
M. insularis					41		
M. latouchei						6	
M. kanoana						1	15

Table 7 Canonical discriminant analysis results comparing skull measurements of six species of *Mogera*: *M. tokudae* (MTO), *M. imaizumii* (MIM), *M. wogura* (MWO), *M. insularis* (MIN), *M. latouchei* (MLA) and *M. kanoana* (MKA).

Karyology

The diploid chromosome number of all *M. kanoana* specimens examined was 2n = 32 (Table 2), matching that of *M. insularis* (Lin *et al.*, 2002). The autosomalcomplement of chromosomes comprised nine meta-submetacentric pairs, including one pair of secondary constriction-bearing chromosomes, four subtelocentric pairs and two acrocentric pairs. Sex chromosomes comprised medium-sized metacentric X and minute Y chromosomes, as is the case in other talpids. The G-banding patterns of each chromosome were identical to those of *M. insularis* (Fig. 12). Thus the new species of mole had no chromosomal characters that were distinct from *M. insularis*.

MtDNA phylogeny

We determined the complete mitochondrial cyt*b* (1140 bp) and partial 12S rRNA (about 840 bp) gene sequences from 13 and 11 specimens of *M. kanoana* and *M. insularis*, respectively. These sequences have been deposited in the DNA database (GenBank/EMBL/DDBJ) under accession Nos. AB181609–181656 (see also Appendix II in detail). No insertions or deletions (indels) were found in cyt*b*, but two indels were found in the 12S alignment. Each indel comprised a single nucleotide and was not consistent with species. The final alignment length of 12S was 830–831 bp. Of the newly determined sequences, 126 and 28 nucleotides were parsimony informative

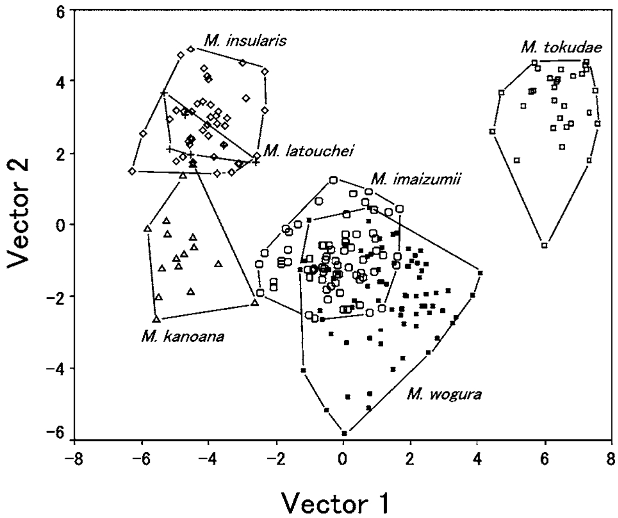

Figure 10 Two-dimensional plot of first and second vectors of canonical discriminate analysis of the species *Mogera tokudae* (open square), *M. imaizumii* (open circle), *M. wogura* (closed square), *M. insularis* (open diamond), *M. latouchei* (cross) and *M. kanoana* (open triangle).

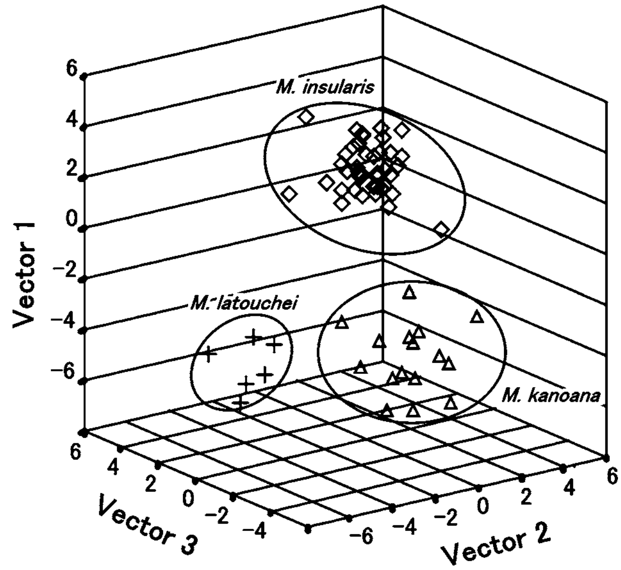

Figure 11 Three-dimensional plot of the first-third vectors of canonical discriminate analysis of species in the *Mogera insularis* group: *M. insularis*, *M. latouchei* and *M. kanoana*. Symbols as Fig. 10.

Character[a]	Vector 1	Vector 2	Vector 3
GLS	−1.4630	2.2539	−0.1415
PL	0.0966	−0.1976	1.6812
LZA	2.2868	−0.9801	−0.4863
I^1M^3	−3.2109	−0.7012	1.5877
CM^3	1.2177	−1.2290	−1.5078
M^1M^3	1.7028	0.5024	−1.7861
RB	1.2028	−0.5625	−2.2075
BIOF	−0.7469	−3.7222	3.8262
BAM	2.2478	1.5990	−1.4744
IOB	0.0659	−0.3682	0.9684
ML	0.4866	1.2338	−0.8998
MH	−0.9844	0.9231	−1.1702
I_1M_3	4.4086	0.6376	−1.6095
P_1M_3	−0.3333	−3.0130	5.9614
M_1M_3	−0.8908	−0.6345	−1.2810
Eigenvalue	13.7374	3.1952	1.4045
Cumulative	74.9158	92.3405	100

Table 8 Eigenvectors, eigenvalues and cumulative proportions for vectors 1–3 resulting from canonical discriminant analysis of skull measurements of the *insularis*-group: *M. insularis*, *M. latouchei* and *M. kanoana*.

[a]GLS, greatest length of skull; PL, palatal length from the anterior tip of first incisor to the posterior lip of the palate; LZA inner length of zygomatic arch; I^1M^3, length of upper tooth row; CM^3, length between upper canine to third molar; M^1M^3, length of upper molars; RB, rostral breadth at the canines; BIOF, breadth between infraorbital foramens; BAM, breadth across upper second molars; IOB, greatest interorbital breadth; ML, mandibler length; MH, mandibler height at the coronoid process; I_1M_3, length of lower tooth row; P_1M_3, length between lower first premolar to third molar; and M_1M_3, length of lower molars.

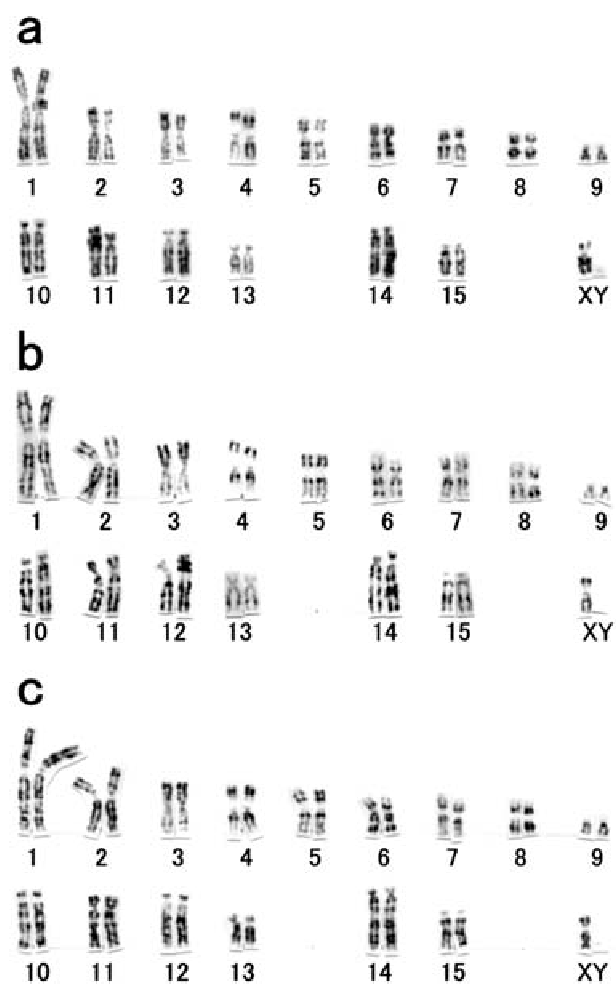

Figure 12 The G-banded karyotypes of *M. insularis* (a) and *M. kanoana* from two populations: Tatachia (b) and Kenting (c).

	MIN			*MKA*		
Species	**Taipei**	**Taichung**	***MLA***	**type I**	**type II**	**type III**
M. insularis (Taipei)	26					
M. insularis (Taichung)	1	14				
M. latouchei			6			
M. kanoana Type I				5	1	1
M. kanoana Type II					3	
M. kanoana Type III					1	5

Table 9 Canonical discriminant analysis results comparing skull measurements of the *Mogera insularis* group: *M. insularis* (MIN), *M. latouchei* (MLA) and *M. kanoana* (MKA). Three populations of *M. kanoana* were included: mountain (Type I), Hualien (Type II) and Kenting (Type III).

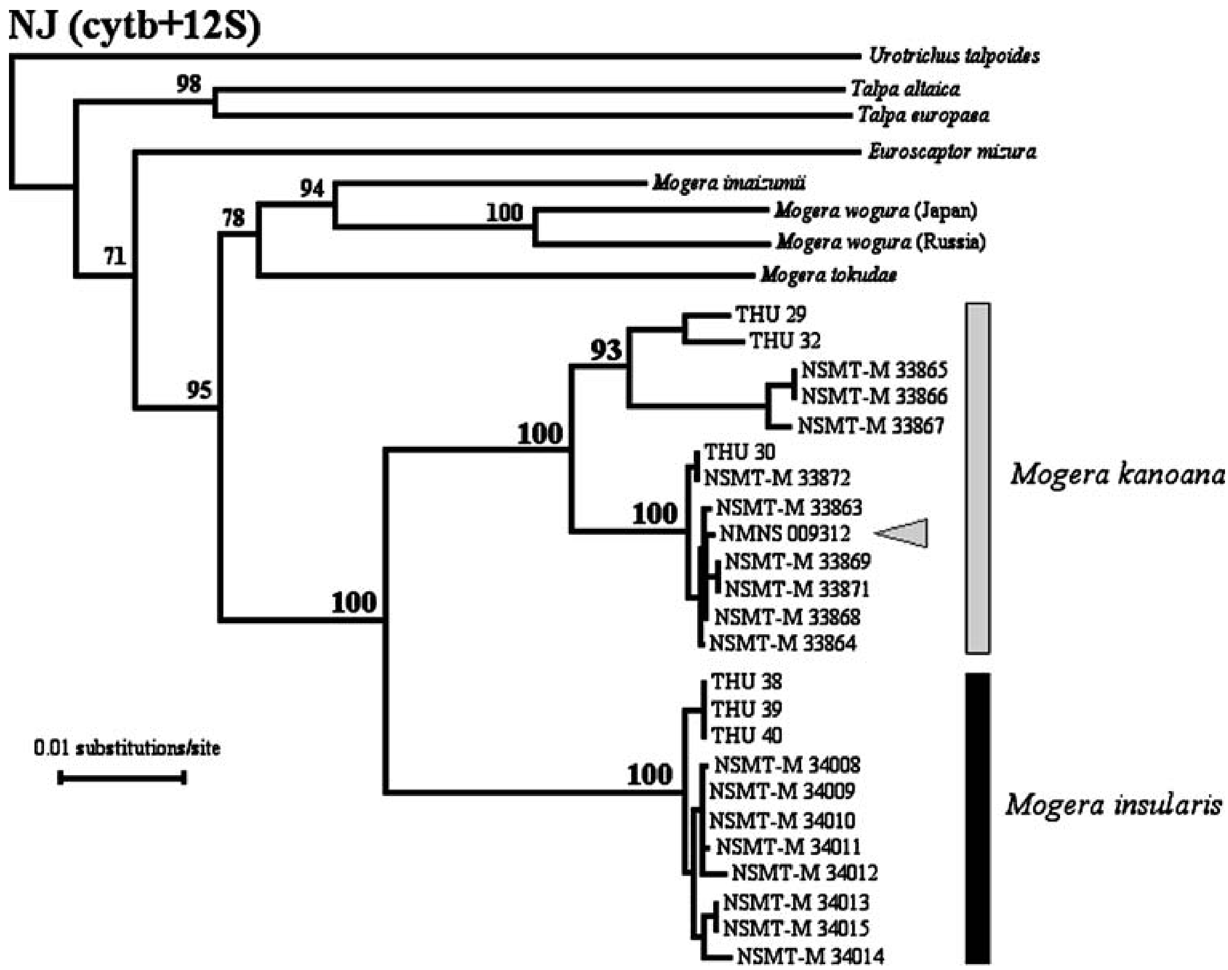

Figure 13 Neighbour joining tree constructed from the mitochondrial cytochrome *b* and 12S rRNA genes of nine talpid species. The greater Japanese shrew-mole, *Urotrichus talpoides*, was used as an outgroup. Numbers at nodes are bootstrap values (percentages of 1000 replications). Arrowhead indicates the *M. kanoana* holotype (NMNS 009312).

characters, and 11 and 7 nucleotides were parsimony uninformative changes in the cyt*b* and 12S dataset, respectively. Unfortunately, we were unable to obtain DNA from any Chinese *Mogera* species, but we were able to compare the DNA sequences of *M. kanoana* with the GenBank/EMBL/DDBJ database DNA sequences of seven Japanese and Eurasian talpids (see Appendix II). Our neighbour-joining tree (Fig. 13) indicated that *M. kanoana* and *M. insularis* were grouped with high bootstrap support (100%). The genetic distance between these two species for cyt*b* and 12S was 7.5% and 2.7%, respectively (Table 10). Notably, these *p* distances were greater than the intraspecific variation within *M. wogura* populations (cyt*b*, 5.3%; 12S, 1.9%) and only slightly smaller than interspecific variation between *M. wogura* and *M. imaizumii* (cyt*b*, 8.3%; 12S, 3.0%).

Species	M. tokudae	M. imaizumii	M. wogura (Japan)	M. wogura (Russia)	M. insularis	M. kanoana
M. tokudae	–	0.098	0.103	0.110	0.115	0.114
M. imaizumii	**0.037**	–	0.082	0.083	0.078	0.081
M. wogura (Japan)	**0.042**	**0.032**	–	0.053	0.090	0.091
M. wogura (Russia)	**0.042**	**0.029**	**0.019**	–	0.088	0.093
M. insularis	**0.039**	**0.039**	**0.039**	**0.038**	–	0.075
M. kanoana	**0.040**	**0.040**	**0.046**	**0.046**	**0.027**	–

Table 10 Molecular "*p*" distances for the mitochondria cytochrome *b* gene (normal type) and partial 12S rRNA genes (bold type) among five *Mogera* species.

Distribution

The newly designated species is distributed in the type locality, Mt. Alishan (Chiayi Province), Sofong (Hualian Province) and the Kenting National Park (Pingtung Province; see Fig. 1). The locality of specimen USNM199493 (in the United States National Museum of Natural History) was listed only as 'Formosa'.

Etymology

The specific name '*kanoana*' is dedicated to the late Dr Tadao Kano in recognition of his comprehensive studies of the nature and folklore of Taiwan and for his foresight regarding the existence of a second species of Taiwanese mole.

Discussion

Within the genus *Mogera*, classifications within the *M. insularis* group have been confounded by the presence of three isolated populations. Following the description of *M. insularis*, two additional species were described from the southern continental region of the People's Republic of China (*M. latouchei*, Thomas 1907) and Hainan Island (*M. hainana*, Thomas 1910), respectively. Thomas' description was based on fur colour, tail ratio and body size relative to *M. insularis*. However, Ellerman and Morrison-Scott (1951) treated these three species as a subspecies of *T. micrura*. In the latest taxonomic revision, Corbet & Hill (1991) and Hutterer (1993) failed to find any distinct characters that identified the Taiwanese species, *M. insularis*. These authors considered *M. latouchei* and *M. hainana* to be isolated populations of *M. insularis*.

The type locality of *M. insularis* is Taiwan Island. In the original description of *M. insularis*, Swinhoe (1862) did not specify the holotype or any details about the type locality. The syntypes of *M. insularis* include four individuals, two each of which are in the British Museum of Natural History (Jones, 1975) and the Leiden Natural History Museum (Jentink, 1888). The specimens in Leiden were collected in Tamsui ('Tamsuy' on the labels and in the original description by Swinhoe, 1862) between December 1861 and May 1862. We believe that these notes were written after the original description by Swinhoe (1862). We were not able to conduct a field survey in Tamsui to examine other specimens, but we nevertheless believed that the name '*M. insularis*' should be given to the mole (which we examined) that is distributed in the western lowlands, ranging from Taipei to Pingtung, because Tamsui is located ~10 km northwest of Taipei, where we examined the specimens. Therefore, specimens we collected from the central mountains and southeastern lowlands of Taiwan correspond to another species, *M. kanoana*.

We used morphological, chromosomal and molecular analyses to examine the classification and diversity of *Mogera* spp. in Taiwan. Morphological analyses clearly showed that *M. kanoana* is distinct from other species within the *M. insularis* group (Fig. 11). However, there were no differences between the chromosomes of the new species and those of *M. insularis* (Fig. 12). It is generally accepted that karyotype differentiation can produce postmating isolation. However, our analysis suggests that karyotype differentiation did not play an important role in the speciation of *M. kanoana* and *M. insularis*.

Additional support for the new species designation of *M. kanoana* is provided by our molecular phylogenetic analysis (Fig. 13), which clearly divided *M. kanoana* and *M. insularis* into two distinct lineages with high (100%) bootstrap support. The genetic distance between *M. kanoana* and *M. insularis* was expressed relative to that between two distinct species of Japanese mole, *M. imaizumii* and *M. wogura* (Table 10). It is important to take into account geographic variation when examining genetic variation between the Taiwanese moles. For example, *M. wogura* collected in Japan and Russia had a *p* value of 0.053, which is smaller than that of the Taiwanese forms (0.075). Notably, the continental (Russian) population of *M. wogura* is different from the Japanese population based on karyological features caused by three pericentric inversions (Kawada *et al.* 2001). Historically, the continental *M. wogura* (aligned by Abe, 1995) was described as an independent species, *M. robusta* (Nehring, 1891). Furthermore, our discriminant results of the Russian population of *M. wogura* (*M. robusta*) in the present study indicated that these animals were relatively more distinguishable from other species of *Mogera* than between *M. wogura* and *M. imaizumii* (Table 6). Therefore, it is important to re-examine the morphological characteristics of *M. wogura* to identify the variation within each population.

The characters of the skull of *M. kanoana* appear to be more primitive than those of *M. insularis*. In fact, the morphology of the ear bones, the tympanic bone and the postcranial skeleton of *M. kanoana* had features that were more similar to those of the Japanese species (e.g. the existence of an apophysis orbicularis and a slender humerus and pelvis).

Specis (population)	2n[a]	NFa[a]	References
M. tokudae (Sado)	36	60	Kawada *et al.* (2001)
M. tokudae (Echigo)	36	54	Kawada *et al.* (2001)
M. imaizumii	36	54	Kawada *et al.* (2001)
M. wogura (Japan)	36	52	Kawada *et al.* (2001)
M. wogura (Russia)	36	58	Kawada *et al.* (2001)
M. insularis	32	58	Lin *et al.* (2002)
M. kanoana	32	58	Present study

Table 11 Karyological data of five *Mogera* species.

[a] 2n: diploid chromosome number, NFa: autosomal arm number.

Therefore, it would appear that some of the morphological features of *M. insularis* are derived characters specialized for their lowland habitat.

The diploid chromosome number and G-banding pattern of *M. kanoana* were indistinguishable from that of *M. insularis* (Tateishi, 1938; Lin *et al.* 2002). The diploid chromosome number of most talpid species is 34 or 36 (Reumer & Meylan, 1986; Tsuchiya, 1988; Kawada *et al.*, 2002; summarized in Table 11), while a chromosome number of 32 distinguishes Taiwanese species from other talpids (although the chromosome number of *M. latouchei* is unknown). Therefore, it is likely that the ancestor of Taiwanese moles had a diploid chromosome number of 32, and that this ancestor then speciated into the two species that are now found on Taiwan Island. The morphological similarity between *M. kanoana* and *M. latouchei* suggests that the slender shape of these species is the ancestral state. In fact, this trait is common to most Japanese species (Abe, 1995).

Molecular data provides further support for our classification of *M. kanoana* as a discrete species. In the present study, specimens of *M. insularis* were collected over a wide geographic range, from Taipei to Pingtung, yet variation between these specimens was less than the variation between three local populations of *M. kanoana* (Fig. 13). This suggests the distribution of *M. insularis* expanded rapidly over a short period, and that *M. kanoana* might have become isolated in three relic populations. The geography of Taiwan includes wide plains along the west coast, which most populations of moles inhabit, and narrow valleys within the eastern lowlands; the Central Mountains lie between these two low-altitude areas (Fig. 1). Although the island is only ~36 000 km in diameter, there is dramatic variation in elevation, which varies from 0 to 3998 m above sea level (National Geographic, 1999). In addition, the mountains are extremely steep and rocky, which acts as a barrier against animal dispersion. These geographic conditions might have promoted the speciation of moles on the island, and hindered historical collections (and characterizations) of *M. kanoana*.

The geographic borders of the distributions of *M. insularis* and *M. kanoana* within Taiwan are unknown. At present, one population of *M. kanoana* is located in the mountainous central area of the island and there are at least two populations in the lowlands. The Central Mountains stretch from the northern to the southern tip of the island, and are presumably also within the distribution of *M. kanoana*.

Based on the distribution of populations of *M. insularis* and *M. kanoana*, we estimate that the border that separates these species may be the western edge of the Central Mountains. Furthermore, the distribution of *M. kanoana* in eastern lowlands does not support the notion that habitat affects the size or morphology of moles in Taiwan, as proposed previously by Abe (1996) for Japanese moles. Therefore, we conclude that the two types of moles observed in Taiwan do not result from intraspecific variation; rather, *M. insularis* and *M. kanoana* represent distinct species.

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Appendix 1. Additional material examined in museums

For comparison with *Mogera kanoana*, we examined the following specimens in the United States National Museum of Natural History, Washington DC (USNM), American Museum of Natural History, New York (AMNH), Siberian Zoological Museum, Novosibirsk (SZM), National Science Museum, Tokyo (NSMT-M) and the senior author's collection (SIK).

M. hainana (N = 6)

AMNH 59913–59918

M. imaizumii (N = 71)

NMST-M 3356, 4643, 4709, 4712–4714, 4717, 4898, 4900–4902, 4970, 4972, 5350, 5574, 5579, 5764, 18476–18478, 18481, 18530, 18531, 18958–18960, 18962, 18991, 18992, 18995–18997, 19104, 19105, 19127, 19129, 19130, 19132, 19133, 19190, 19210, 34016, SIK 0046, 0096, 0097, 0114, 0131, 0132, 0139, 0141, 0143, 0146, 0157, 0165, 0168, 0188, 0192, 0193, 0218, 0220, 0239, 0243, 0314, 0319, 0331, 0379, 0382, 0385–0387, 0393

M. insularis (N = 57)

USNM 294139, 294140, 308863, 330020 – 330047, 332832 - 332837, 332839, 332840, 332842, AMNH 183146, 183147, 183178, 184537 – 184539, 184983, 184984, NMST-M 13931, 34008 – 34015

M. latouchei (N = 13)

USNM 241571, 252190, AMNH 38363, 44633–44636, 84805, 84807 – 84811

M. tokudae (N = 29)

NMST-M 13209, 13574, 13575, 13577, 13580, 14482, 15644–15646, 17057, 17318, 17319, 27267, 27268, 28716, 28717, 29385, 29391, 29392, 29394, 29398, 29402, 29405, 29406, 29408, SIK0109–0112

M. wogura (N = 73)

SZM 7525, 7529, 7530, 7533, 19902, 25323, 31722, NMST-M 1334, 2615, 2618, 2620, 2623, 2766, 2834, 2835, 2836, 2840, 2909, 3546, 3554, 4723, 4725, 4784, 5745, 5747, 5749, 5750, 5754, 5854, 9183. 14091, 14129, 18487, 18489, 18508, 18511, 27884, 28197, 29995, SIK 0059, 0064–0066, 0069, 0071, 0084, 0093, 0098, 0099, 0101–0104, 0113, 0129, 0130, 0134, 0135, 0153, 0155, 0159, 0162–0164, 0166, 0167, 0235, 0236, 0315–0317, 0320, 0327

Appendix 2. Accession numbers of gene sequences used in this study

Source of data: 1, present study; 2, Tsuchiya *et al*. (2000); 3, Shinohara *et al*. (2004); 4, Shinohara *et al*. (2003); 5, Murphy *et al*. (2001); 6, Mouchaty *et al*. (2000).

M. kanoana: cyt*b*; AB181620–181632 (ref. 1), 12S; AB181644-181656 (ref. 1). *M. insularis*: cyt*b*; AB181609-181619 (ref. 1), 12S; AB181633-181643 (ref. 1). *M. wogura* (Japan): cyt*b*; AB037623 (ref. 2), 12S; AB106237 (ref. 3). *M. wogura* (Russia): cyt*b*; AB037646 (ref. 2), 12S; AB106238 (ref. 3). *M. imaizumii*: cyt*b*; AB037609 (ref. 2), 12S; AB106236 (ref. 3). *M. tokudae*: cyt*b*; AB037607 (ref. 1), 12S; AB106235 (ref. 3). *E. mizura*: cyt*b*; AB037604 (ref. 1), 12S; AB106233 (ref. 3). *U. talpoides*: cyt*b*; AB076833 (ref. 4), 12S; AB106239 (ref. 3). *T. altaica*: cyt*b*; AB037602 (ref. 1), 12S; AY012100 (ref. 5). *T. europaea*: cyt*b* + 12S; AY19192 (ref. 6).

Appendix 3. Measurements of skulls of the type specimens used in this study

	Measurements														
Specimen No.	GLS	PL	LZA	I^1M^3	CM^3	M^1M^3	RB	BIoF	BAM	IOB	ML	MH	I_1M_3	P_1M_3	M_1M_3
NMNS009312	29.06	11.22	7.00	11.38	9.91	4.65	3.73	5.55	7.40	6.62	17.73	6.07	10.70	8.71	5.22
NSMT-M33863	30.64	11.94	7.60	12.08	10.69	5.09	3.91	5.74	7.83	6.72	19.15	5.88	11.24	9.40	5.63
NSMT-M33864	30.67	11.66	7.47	11.94	10.85	5.03	3.95	5.73	7.89	6.77	19.01	6.72	11.19	9.63	5.16
NSMT-M33865	29.39	11.46	7.15	11.44	10.17	5.06	3.75	5.57	7.35	6.57	18.35	6.09	10.87	9.02	5.53
NSMT-M33866	29.18	11.38	6.96	11.24	9.99	4.86	3.76	5.74	7.45	6.78	17.72	5.99	10.48	8.71	5.14
NSMT-M33867	29.62	11.36	7.53	11.54	10.20	5.05	3.99	5.51	7.76	6.83	18.28	5.85	10.65	8.92	5.41
NSMT-M33870	31.71	12.09	7.97	12.50	10.98	5.54	4.43	6.35	7.84	6.94	19.95	6.51	11.59	9.59	5.84
NSMT-M33871	30.44	11.94	7.37	12.06	10.64	4.99	4.25	6.26	8.16	7.22	19.16	5.94	11.28	9.41	5.66
NSMT-M33872	31.02	12.39	7.88	12.55	11.15	5.81	4.29	6.10	8.08	6.76	19.66	6.55	11.64	9.71	5.91

Appendix 4. Measurements of the postcranial skeletons of the type specimens used in this study

	Measurements					
Specimen No.	**LHu**	**GBHu**	**LBHu**	**LSc**	**LPe**	**BPe**
NMNS009312	11.65	8.30	3.06	19.33	20.18	3.14
NSMT-M33863	12.39	8.74	3.26	20.26	20.87	3.28
NSMT-M33864	12.58	8.74	3.07	20.60	21.75	3.39
NSMT-M33865	11.78	8.14	2.94	19.36	20.30	3.06
NSMT-M33866	11.73	7.98	3.18	18.96	19.66	3.25
NSMT-M33867	11.46	7.84	2.70	18.99	19.43	3.11
NSMT-M33870	12.90	8.83	3.36	22.36	22.64	3.16
NSMT-M33871	12.77	9.08	3.29	22.27	22.43	3.08
NSMT-M33872	13.30	9.30	3.51	22.64	23.30	3.46