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Taxonomic Status of the Senkaku Mole, *Nesoscaptor uchidai*, with Special Reference to Variation in *Mogera insularis* from Taiwan (Mammalia: Insectivora)

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ABSTRACT—The taxonomic status of the Senkaku mole, *Nesoscaptor uchidai* Abe, Shiraishi et Arai, 1991 (Mammalia: Insectivora: Talpidae), described from Uotsurijima in the Senkaku Group, Ryukyu Archipelago, was re-evaluated. Morphological analyses suggest that *N. uchidai* is most similar to *Mogera insularis* from Taiwan, although several morphological characters, such as the number of premolars and the shapes of the anterior portion of the palate, zygomatic arch, auditory bulla, and coronoid process, differentiate *N. uchidai* from *M. insularis*. Therefore, we synonymize the monotypic genus *Nesoscaptor* Abe, Shiraishi et Arai, 1991 with the genus *Mogera* Pomel, 1848, and define *Mogera uchidai* (Abe, Shiraishi et Arai, 1991) as a valid species endemic to Uotsurijima. In addition, we analyzed morphological variation within *M. insularis*, such as variation in the second upper premolar pair, overall cranial size, and the breadth of the rostrum and palate. Some of this variation may be associated with topographical and environmental factors in its habitat.

INTRODUCTION

The Senkaku mole, *Nesoscaptor uchidai*, is the most recently discovered non-volant Japanese mammal. Abe *et al.* (1991) described the unique holotype from near the western coast of Uotsurijima, in the Senkaku Group of the Ryukyu Archipelago (25°44' N, 123°28' E: Fig. 1), as a new genus and species. Based on comparisons with other Eurasian talpine genera, including *Euroscaptor, Mogera*, *Parascaptor, Scaptochirus*, and *Talpa, Nesoscaptor* was diagnosed by a combination of 19 morphological characters. Of these, the dental arrangement was thought to be the most important and to differentiate the genus *Nesoscaptor* from the other talpine genera (Abe *et al.*, 1991).

The genera *Talpa* in Europe and *Euroscaptor* in Asia have primitive mammalian dentition, which consists of 44 teeth, including three pairs of incisors, one pair of canines, four pairs of premolars, and three pairs of molars in both the upper and lower jaws (Abe *et al*., 1991). The other genera have reduced dentition. *Mogera* has 42 teeth due to the loss of one lower incisor pair; *Parascaptor* has 42 due to the loss of one upper premolar pair; and *Scaptochirus* has 40 due to the loss of one upper and one lower premolar pair (Abe *et al.*, 1991; Corbet and Hill, 1992). Currently, these five genera are validated primarily by such differences in dental arrangement (e.g., Hutterer, 1993), although Corbet (1978) and Corbet and Hill (1992) questioned the taxonomic validity of dental formula in mole genera. The genus *Nesoscaptor* has no more than 38 teeth, since it lacks one pair of lower incisors and two pairs of premolars, one in the upper jaw and one in the lower, compared to the putative primitive dentition of 44 teeth (Abe *et al.*, 1991: see above).

Uotsurijima is located approximately 160 km ENE of Taiwan, and is the largest island in the Senkaku Group. It is about 3.3 km long, 1.3 km wide, 4.3 km^2 in area, and 362.0 m in maximum elevation (Abe *et al*., 1991; Ota *et al*., 1993). Abe *et al.* (1991) postulated that the ancestor of *N. uchidai* migrated to Uotsurijima from the mainland in the Miocene, when the Senkaku Group was part of the mainland, and was subsequently isolated on Uotsurijima. Subsequent authors, such as Hutterer (1993) and Abe (1994), followed the taxonomic view of Abe *et al.* (1991), and regarded both the genus *Nesoscaptor* and the species *N. uchidai* as valid. Although tentatively sup-

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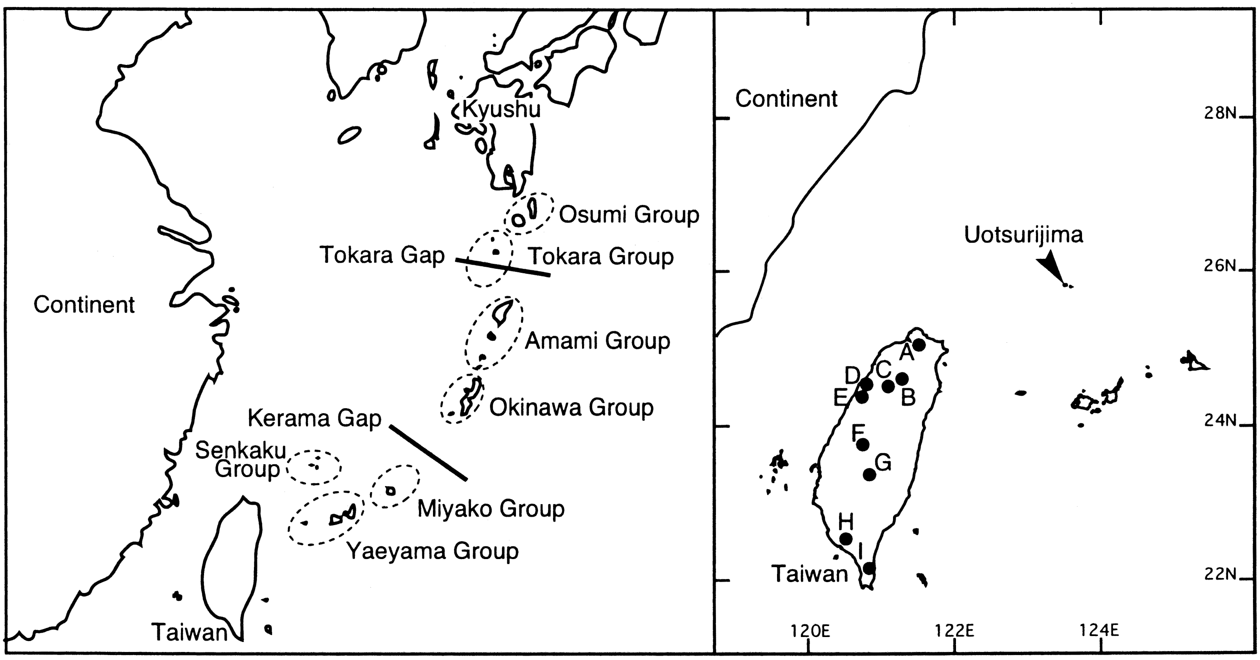

Fig. 1. Map showing the Ryukyu Archipelago (left), the type locality (Uotsurijima) of *Nesoscaptor uchidai*, and the sampling localities of *Mogera insularis* (right). A, Yangmingshan, Taipei City; B, Tsejen Village, Fuhsing County, Taoyuan Prefecture; C, Kuanwu, Taian County, Miaoli Prefecture; D, Houlung Town, Miaoli Prefecture; E, Miaoli Sanyi Houyenshan Nature Reserve, Miaoli Prefecture; F, Chushan Town, Nantou Prefecture, and Chichi Town, Nantou Prefecture, and Yuchih County, Nantou Prefecture, and Shuili County, Nantou Prefecture; G, Tatachia, Hsinyi County, Nantou Prefecture; H, Neipu County, Pingtung Prefecture; I, Mt. Nanjenshan, Manchou County, Pingtung Prefecture.

porting the validity of *Nesoscaptor* and *N. uchidai*, Nowak (1998) suggested that the genus *Nesoscaptor* was synonymous with the genus *Mogera*.

The genus *Mogera* currently consists of four species (Abe, 1995; Motokawa and Abe, 1996): *M. tokudae*, *M. imaizumii*, *M. wogura*, and *M. insularis*. Of these, the first two species are endemic to the main islands of Japan, and the third occurs in the Korean Peninsula, northeastern China, the Russian Far East, and the western part of the main islands of Japan (Abe, 1995). The fourth species is known from Taiwan, the southern part of continental China, and Hainan Island (Abe, 1995). Abe *et al.* (1991) compared *N. uchidai* with *M. tokudae*, *M. imaizumii*, and *M. wogura*, and found several major morphological differences between it and the latter species.

Recently, Motokawa (2000) pointed out the similarity in some morphometric characters between *N. uchidai* and the Taiwanese *M. insularis* using the reports of Abe *et al.* (1991) and Abe (1995). He surmised that this similarity reflected a close relationship, which corroborates the recent paleogeographical hypothesis of a land connection joining the Senkaku Group, including Uotsurijima, with Taiwan and the continent in the late Pleistocene (Ota *et al.*, 1993; Ota, 1998). To test Motokawa's (2000) prediction, we examined the holotype of *N. uchidai* and specimens of *M. insularis* from Taiwan, and analyzed their morphological variation in detail.

MATERIALS AND METHODS

We examined the holotype of *Nesoscaptor uchidai* deposited in the Zoological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka. For comparison, we also examined 26 specimens of *Mogera insularis* from nine localities in Taiwan (Fig. 1). These specimens are deposited in the National Museum of Natural Science, Taichung (NMNS), the Taiwan Endemic Species Research Institute, Chichi (TESRI), the National Pingtung Science and Technology University, Neipu (NPSTU), the National Science Museum, Tokyo (NSMT), the Osaka City University Medical School, Osaka (OCUMS), and the Zoological Collection of Kyoto University, Kyoto (KUZ) (Appendix).

The following external measurements (in mm) taken by the collectors were used for this study: head and body length (HB), tail length (T), forefoot length without claw (FFsu), forefoot length with claw (FFcu), forefoot width (FFW), hind foot length without claw (HFsu), and hind foot length with claw (HFcu). The senior author took 21 cranial measurements to the nearest 0.01 mm with digital calipers (Mitsutoyo Co., Ltd.) (Fig. 2). These included the greatest length of the skull (GLS), condylobasal length (CBL), palatal length from the anterior tip of first incisor to the posterior lip of the palate (PL), rostral length from the anterior tip of the first incisor to the anterior-most portion of the orbit in the infraorbital foramen (RL), postpalatal length from the posterior edge of the postpalatal lip to the anterior-most point on the foramen magnum (PPL), maximum length of the auditory bulla (ABL), postpalatal depth measured from a point just posterior to the posterior lip of the palate to the closest point on the cranial surface (PPD), braincase depth (BD), rostral breadth at the canines (RB), greatest interorbital breadth (IOB), zygomatic breadth (ZB), braincase breadth (BB), breadth across upper molars (BAM), distance from the first upper incisor to the third upper molar (UTR), distance from the canine to the third upper molar (CM3), distance from the fourth upper premolar to the third upper molar (P4M3), breadth across the canines (CC), mandibular length (ML), mandibular height at the coronoid process (MH), distance from the first lower incisor to the third lower molar (LTR), and distance from the first lower premolar to the third lower molar (P1M3). Braincase depth (BD) differs from that of Abe *et*

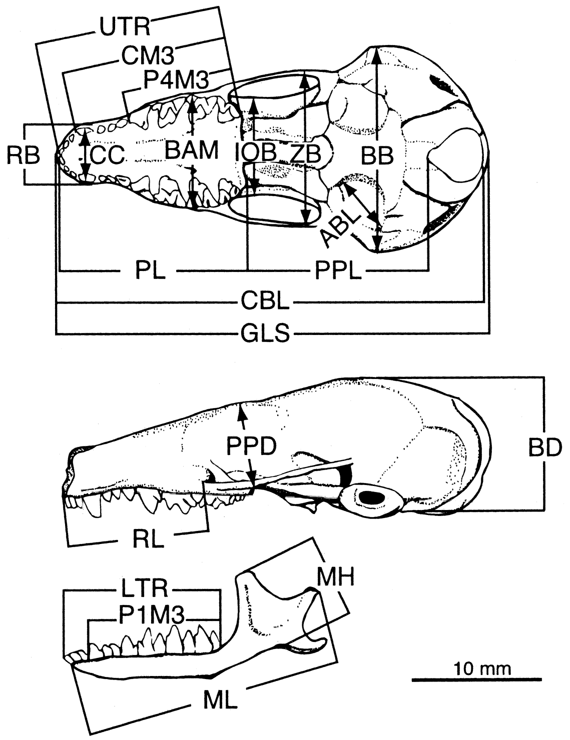

Fig. 2. Cranial and mandibular measurements used in this study. The abbreviations used for the measurements are described in the text.

al. (1991) in excluding the auditory bulla.

Principal component analysis (PCA) was carried out with the PRINCOMP procedure of SAS Version 6 (SAS Institute Inc., 1990) based on the correlation matrix of cranial measurements. Condylobasal length (CBL) was not included in the PCA, because it did not differ much from GLS (Fig. 2). PPD and ZB were also excluded from the PCA, because relevant portions of these measurements were not available in some specimens. All measurements were log-transformed before PCA. Males and females were combined in each analysis, because the sexual differences in the Japanese moles were slight (Abe, 1967) and the number of available specimens was limited. All specimens have the dentition worn slightly or moderately, and thus considered to be adult.

Table 1. External measurements of *Nesoscaptor uchidai* and *Mogera insularis* (mm). Values are given as the means ± SD, followed by the ranges, and sample sizes in *M. insularis*. See text for abbreviations used for the measurements.

Character	*N. uchidai*	*M. insularis*		
	Holotype	Mean ± SD	Range	N
HB	129.9	120.9 ± 14.73	99.5 – 151.5	13
T	12.0	12.0 ± 3.09	7.0 – 17.0	13
HFsu	16.0	15.2 ± 0.66	14.0 – 16.0	12
HFcu	—	17.7 ± 0.83	16.6 – 19.4	11
FFsu	14.0	14.0 ± 0.88	12.3 – 15.6	11
FFcu	19.2	18.2 ± 0.79	16.7 – 19.5	10
FFW	15.4	14.4 ± 0.93	12.3 – 15.6	11

Table 2. Cranial and mandibular measurements for *Nesoscaptor uchidai* and *Mogera insularis* (mm). Values are given as the means ± SD, followed by the ranges, and sample sizes in *M. insularis*. See text for abbreviations used for the measurements.

Character	*N. uchidai*	*M. insularis*		
	Holotype	Mean ± SD	Range	N
GLS	31.61	31.79 ± 0.90	30.59 – 33.72	17
CBL	30.69	31.00 ± 0.88	29.80 – 33.05	17
PL	13.01	13.16 ± 0.61	12.20 – 14.34	20
RL	9.55	9.50 ± 0.43	8.58 – 10.41	20
PPL	14.35	14.38 ± 0.70	13.15 – 15.51	17
ABL	4.72	4.93 ± 0.36	4.27 – 5.44	17
PPD	6.18	6.27 ± 0.26	5.69 – 6.64	16
BD	9.09	8.83 ± 0.44	8.16 – 9.34	18
RB	4.51	4.60 ± 0.29	3.89 – 5.12	20
IOB	7.49	7.38 ± 0.31	6.79 – 7.99	18
ZB	12.58	11.62 ± 0.94	10.22 – 12.81	14
BB	15.25	14.82 ± 0.65	13.61 – 15.80	18
BAM	8.80	8.47 ± 0.55	7.43 – 9.19	21
UTR	13.55	13.27 ± 0.61	12.34 – 14.27	21
CM3	11.99	11.69 ± 0.54	10.69 – 12.44	21
P4M3	8.42	7.65 ± 0.48	6.84 – 8.23	21
CC	3.98	4.06 ± 0.28	3.47 – 4.47	20
ML	21.00	20.67 ± 0.90	18.96 – 22.19	20
MH	6.46	6.48 ± 0.26	6.02 – 6.98	21
LTR	12.83	12.30 ± 0.63	11.03 – 13.06	22
P1M3	10.63	10.32 ± 0.54	9.06 – 10.94	22

RESULTS

The external and cranial measurements are presented in Tables 1 and 2, respectively. In most characters, values for the holotype of *N. uchidai* fell within the range for *M. insularis*. The values for *N. uchidai* were slightly larger than the maximum values for *M. insularis* in one cranial measurement (P4M3).

The body was small in both *N. uchidai* (42.7 g, 129.9 mm HB) and *M. insularis* (40.8–72.5 g [n=4], 99.5–151.5 mm HB [n=13]). The manus was relatively small in both *N. uchidai* (14.0 mm FFsu, 19.2 mm FFcu, 15.4 mm FFW) and *M. insularis* (12.3–15.6 mm FFsu [n=11], 16.7–19.5 mm FFcu [n=10], 12.3–15.6 mm FFW [n=11]). The hind foot (HFsu) was 16.0 mm in *N. uchidai* and 14.0–16.0 mm (n=12) in *M. insularis*. The tail is relatively short in both species, with T being 12.0 mm in *N. uchidai*, and 7.0–17.0 mm (n=13) in *M. insularis*, showing extreme individual variation. In both species, the nostril was directed outward, and the naked portion on the upper side of the muzzle was rectangular in outline.

The crania and mandibles of *N. uchidai* and *M. insularis* are shown in Fig. 3. There was substantial local variation in *M. insularis* (see below), and two individuals of *M. insularis* from different localities are shown in Fig. 3. The skull was small and the rostrum was short in both *N. uchidai* and *M. insularis*. The anterior portion of the palate of *N. uchidai* was shorter and narrower than that of *M. insularis*. The interorbital and palatal portions were broad in both species. There was distinct local variation in the relative breadth of the rostrum and palate in *M. insularis*. A specimen with a broad rostrum and palate and another with distinctly narrower ones are shown in Figs. 3B and 3C, respectively. The zygomatic arch curved

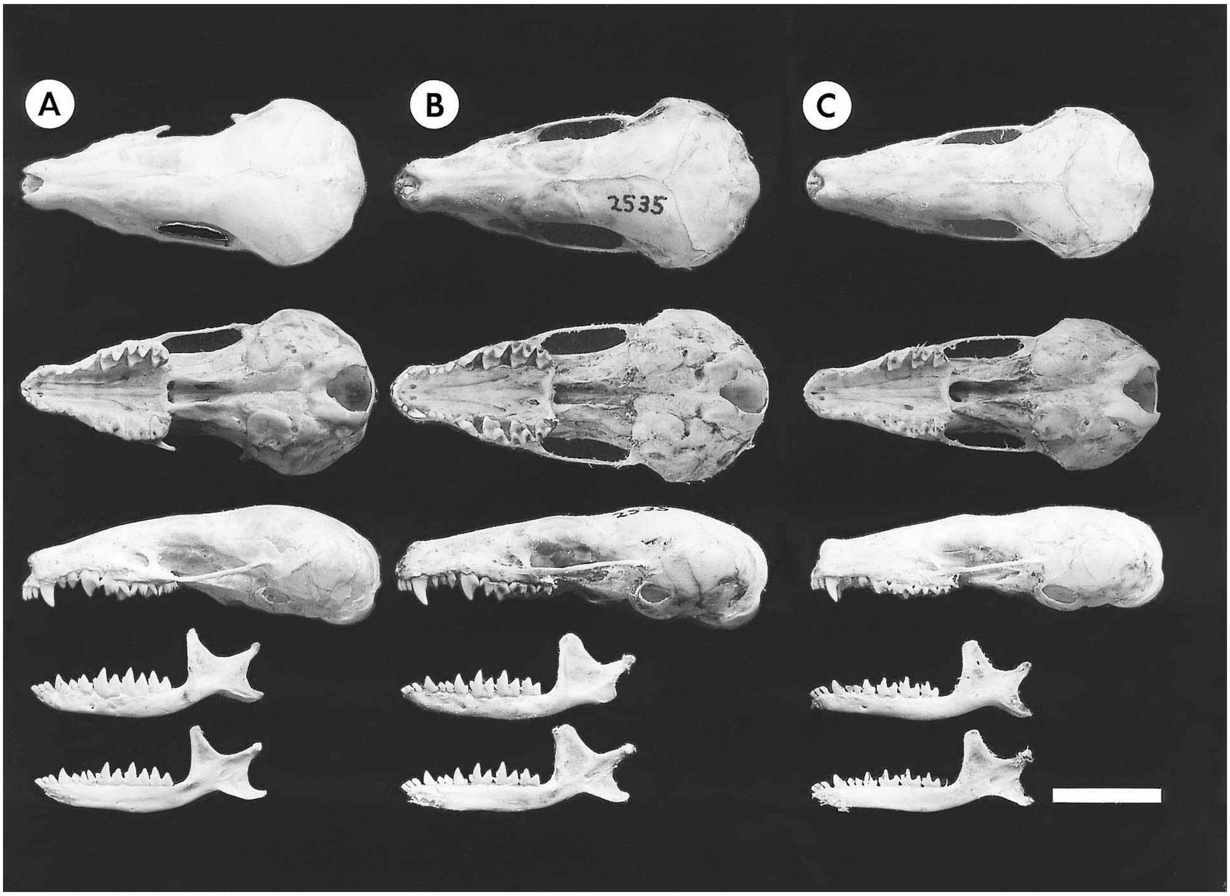

Fig. 3. Dorsal, ventral, and left lateral views of the cranium, and lateral and lingual views of the mandible (from top to bottom) of *Nesoscaptor uchidai* (A, holotype) and *Mogera insularis* (B, KUZ M2535; and C, KUZ M3362). The bar indicates 10 mm.

in *N. uchidai*, but was straight in *M. insularis* (see lateral views in Fig. 3). The anterior margin of the zygomatic arch reached to the level of the second upper molar (see the ventral view in Fig. 3A) in *N. uchidai*. In *M. insularis*, it also reached to a similar level in some individuals (Fig. 3B), but only to the level of the third upper molar in the remaining specimens (Fig. 3C).

The upper incisor row projected forward in both species. It clearly projected in *N. uchidai* (see the ventral view in Fig. 3A) and the specimens of *M. insularis* with a narrow rostrum (Fig. 3C), whereas in specimens of *M. insularis* with a broad rostrum, the degree of projection was lower (Fig. 3B). The first upper incisor was well developed in both species, but its size relative to the second upper incisor was variable within *M. insularis*. Most specimens of *M. insularis* had four upper premolar pairs, while *N. uchidai* had three. Of 23 specimens of *M. insularis* examined, 22 specimens had 42 or fewer teeth due to complete or partial loss of some after eruption. In the latter case, the roots or other remaining portions of teeth were located in their normal positions. Excluding these variants, we recognized numerical variation in dentition in only one specimen; a specimen from Mt. Nanjenshan (KUZ M3362, Fig. 3C) lacked two teeth, most likely corresponding to the second upper premolars on both sides, judging from the position of the existing teeth. In this specimen, the dental space existed between the first and third upper premolars, but the roots or other remaining portions of teeth were not found. The upper molars were very large in *N. uchidai* and *M. insularis*. The length of their row clearly exceeded the distance from the canine to the last premolar in *N. uchidai*, and it was equal to or slightly smaller than the latter distance in *M. insularis*. The degree of lingual development of the last upper premolar (= the fourth upper premolar) in *N. uchidai* was different on the right and left sides: it was more developed on the left side than on the right. In *N. uchidai*, the tympanic bulla was large, roundish, and flat, with its posterior tip extending backwards beyond the line connecting the mastoid processes. On the other hand, the tympanic bulla of *M. insularis* was similar to that of *N. uchidai* in the ventral view, but it was not flattened or well developed ventrally (see the lateral view of Fig. 3).

The mandibles of *N. uchidai* and *M. insularis* were slender, and their general appearances were similar. There were three large lower incisor-like teeth in both species. In *N. uchidai*, there were three lower premolars: the first was caniniform, the second was the smallest, and the third was relatively large and bore two roots. On the other hand, *M. insularis* had four lower premolars: the first was caniniform, the second and third were small, and the fourth was relatively large, unicuspid, and had two roots. Size comparison suggested that the missing teeth of *N. uchidai* correspond to the second lower premolars of *M. insularis*. There was some morphological variation between the right and left fourth lower premolars in *N. uchidai*; the right was characterized by two clearly developed main cusps, whereas the left only had one main cusp (Fig. 3). The lower molars were large, and the length of their row exceeded the distance between the first lower incisor and the fourth lower premolar in both *N. uchidai* and *M. insularis*. The third lower molar was more developed in *N. uchidai* than in *M. insularis*. The shape of the coronoid process was quite different between the two species; it was narrow and slender in *N. uchidai*, whereas it was broad and robust in *M. insularis*. The size and shape of the humerus were similar in *N. uchidai* and *M. insularis*.

Table 3. Eigenvectors of the principal component analysis (PCA) based on 18 morphometric characters of *Nesoscaptor uchidai* and *Mogera insularis*. See text for abbreviations used for the measurements.

Character	PRIN1	PRIN2
GLS	0.212	0.393
PL	0.246	0.078
RL	0.063	0.530
PPL	–0.014	0.408
ABL	0.153	–0.095
BD	0.251	–0.128
RB	0.251	–0.134
IOB	0.203	–0.233
BB	0.265	–0.103
BAM	0.267	–0.133
UTR	0.277	0.061
CM3	0.285	–0.027
P4M3	0.270	–0.155
CC	0.262	0.043
ML	0.283	0.126
MH	0.128	0.467
LTR	0.284	–0.006
P1M3	0.285	–0.045
Proportion	0.623	0.103
Cumulative proportion	0.623	0.726

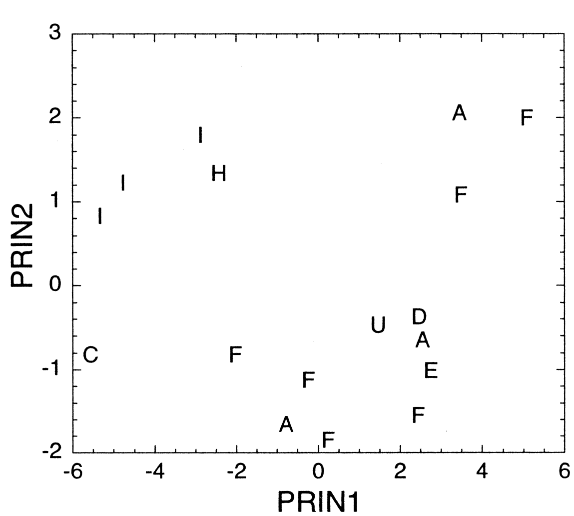

Fig. 4. Scatter plots of the scores on the first and second principal component axes based on 18 morphometric characters of *Nesoscaptor uchidai* (U) and *Mogera insularis* (A-I, see Fig. 1 for localities).

Eighteen cranial morphometric characters of *N. uchidai* and *M. insularis* were subjected to PCA. The first and second principal component axes explained 62.3 and 10.3% of the total variation, respectively (Table 3). In the first axis, all variables except for PPL showed positive loadings. In the second axis, RL, MH, and PPL had relatively large positive loadings. Individual scores for the first and second principal component variables (PC1 and PC2) are plotted in Fig. 4.

In this ordination, the plot of the holotype of *N. uchidai* fell within the range of *M. insularis* (Fig. 4). Four specimens from the southern part of Taiwan (Neipu and Mt. Nanjenshan; H and I) were distinguished from the other samples by small PC1 and large PC2 scores. The plots of specimens from the northern (Yangmingshan, Houlung Town, and Miaoli Sanyi Houyenshan Nature Reserve; A, D, and E) and central parts of Taiwan (Chushan Town, Chichi Town, and Yuchih County; F) largely overlapped. A specimen from Kuanwu (C) had the smallest PC1 score (–5.55). Kuanwu is approximately 2,000 m above sea level, whereas the elevations of the localities of the other specimens were less than 1,000 m. Six specimens from central Taiwan (F) were collected from localities within 40 km of each other. PC1 scores of these specimens was variable. In descending order, it was largest in a specimen from Teshanli (about 200 m in altitude) (5.12), followed by one from Chushan (about 200 m), two from the Taiwan Endemic Species Research Institute at Chichi (about 300 m), one from Neiliao (about 500 m), and one from Lienhuachi (about 800 m) (–2.00).

DISCUSSION

Morphological variation in *M. insularis*

Mogera insularis was originally described from Formosa (=Taiwan) by Swinhoe (1862), and is currently regarded as a valid species (Hutterer, 1993; Abe, 1995; Nowak, 1999). Two forms from continental China (*M. latouchei*) and Hainan Island (*M. hainana*) are often included in *M. insularis*, but their taxonomic relationships remain controversial (Hutterer, 1993; Abe, 1995; Nowak, 1999). The Taiwanese *M. insularis* may be diverged from the continental and Hainanese forms, because the former has a larger GLS as described by Allen (1938) and Abe (1995).

In his study on the zoogeography of Taiwan, Kano (1940) listed two *Mogera* species, *M. insularis* and *M. montana*, as occurring in Taiwan. The latter species bore the authorship "Kishida", but it was never actually described by Kishida or any other author. Thus, *Mogera montana* should be regarded as *nomen nudum*. Kano (1940) believed that *M. insularis* and "*M. montana*" occur at altitudes of less than 600 m and more than 900 m, respectively. Currently, it is believed that there is only one species, *M. insularis*, and it occurs from near sea level (e.g., Houlung Town) to the high mountains, such as Kuanwu (about 2,000 m) and Tatachia (about 2,500 m).

It is believed that a number of environmental factors gave rise to the morphological variation in the Japanese *Mogera* (Abe, 1967, 1997). The actual local variation in some morphological characters was documented for *M. wogura* in detail. According to Abe (1967, 1997), mountain populations of this species, often referred to as the small local form, are characterized by a smaller body and a relatively narrow rostrum compared to lowland populations. Such variation is thought to have been caused by the lower availability and greater fragmentation of mountain habitats (Abe, 1967, 1997).

The geomorphology of Taiwan is much more diverse than that of Japan, and mountains, valleys, and rivers may fragment the habitat of *M. insularis*. In this study, the first principal component score of *M. insularis*, obviously largely reflecting the overall cranial size, tended to be small in samples from montane localities and large in lowland samples. In specimens from central Taiwan, PC1 seems to decrease with an increase in the elevation of the sampling locality, although the sample size (six specimens from five localities) was not large enough to obtain any conclusion with certainty. Among the specimens used in the PCA, the Kuanwu specimen, which was collected from the highest locality (ca. 2,000 m), had the smallest PC1 score. Therefore, the overall size variation (as expressed in PC1) may be similar to that in the Japanese *M. wogura*; presumably it is affected by the effective habitat area among localities. Future detailed analyses of the local variation of *M. insularis* in Taiwan should be carried out, using more specimens from more localities, including both lowlands and mountains.

Taxonomic status of *Nesoscaptor uchidai*

The present results indicate that *N. uchidai* substantially resembles *M. insularis* morphologically. On the other hand, *N. uchidai* is diverged from the other *Mogera* species (*M. wogura*, *M. imaizumii*, and *M. tokudae*) in several important morphological characters as shown by previous authors (Abe *et al.*, 1991; Motokawa, 2000). These results suggest that *N. uchidai* is more closely related to *M. insularis* than to the remaining *Mogera* species.

Most of the diagnostic characters for the genus *Nesoscaptor* and the species *N. uchidai* (Abe *et al.*, 1991) were actually shared by *M. insularis*. Moreover, both univariate and multivariate analyses also indicate that most external and cranial measurements in the holotype of *N. uchidai* fell within the range of variation of the corresponding measurements in *M. insularis*. The major difference between the two species is the number of premolars. The holotype of *N. uchidai* lacked four teeth (one premolar pair in both the upper and lower jaws) compared to *M. insularis*. This numerical reduction of premolars in *N. uchidai* may have been caused by the decrease in palate size, especially in the anterior portion. The difference between UTR and P4M3, representing the distance between the first upper incisor and the fourth upper premolar (the size of the anterior portion of the palate), is 5.13 in the holotype of *N. uchidai*. This value is distinctly smaller than the corresponding values in *M. insularis* (5.17–6.24). In the lateral view, the space for unicuspid premolars between the upper canine and the fourth upper premolar is much smaller in the holotype of *N. uchidai* than in *M. insularis*, as shown in Fig. 3. There are three unicuspid premolars in *M. insularis*, but only two (the first and the third) in the holotype of *N. uchidai*. Since intraspecific variation in tooth number is sometimes observed in other *Mogera* species (2.8% in the three species from Japan and the Korean Peninsula [Abe *et al.*, 1991], 4.3% in *M. insularis* [this study]) and the available material of *N. uchidai* is limited to the holotype, it is uncertain whether the reduced tooth condition (total 38) observed in this specimen is a reliable diagnostic feature for defining the genus *Nesoscaptor*. Thus, we do not consider the tooth number as the valid diagnostic character of the genus *Nesoscaptor*.

Nesoscaptor uchidai and *M. insularis* are also distinguished by some morphological differences, such as in the zygomatic arch, auditory bulla, and coronoid process (Table 4). These characters may be variable among species of same genus in the talpine moles. For example, *Euroscaptor mizura* has the curved zygomatic arch, and narrow and slender coronoid process (Abe *et al.*, 1991). On the other hand, the congeneric *E. klossi* has the straight zygomatic arch, and broad and robust coronoid process (Yoshiyuki, 1988).

We could not find the vertebrata of the holotype specimen of *N. uchidai*. *Nesoscaptor uchidai* is known to be different in the number of sacral vertebrata (7 bones) from the genera *Euroscaptor* (5) and *Mogera* (6) (Abe *et al.*, 1991). We have examined this condition in five specimens of *M. insularis*, and found the individual variation. Four have six sacral bones, but the one (NMNS 1942) has seven sacral bones, which is similar to *N. uchidai*. Therefore, the validity of this character in mole taxonomy needs verification.

We could not examine one of the diagnostic characters for the genus *Nesoscaptor* and the species *N. uchidai* proposed by Abe *et al*. (1991). Abe *et al*. (1991) said that the ear bones of *N. uchidai* were similar to those of the genera *Euroscaptor* and *Mogera*. *Nesoscaptor uchidai* has malleus with small apophysis orbicularis as in *M. tokudae* and *E. mizura*, different from *M. wogura*, *M. imaizumii*, and *M. insularis* having malleus with well developped apophysis orbicularis (Abe *et al*., 1991; Abe, 1995). This character is different between *N. uchidai* and *M. insularis*, but it does not help distinguish *Nesoscaptor* from *Mogera*.

The Senkaku Group is located on the southeastern margin of the East China Continental Shelf northwest of the Okinawa Trough. Therefore, the geohistory, fauna, and flora

Table 4. Morphological comparison between *Nesoscaptor uchidai* and *Mogera insularis*.

Character	*Nesoscaptor uchidai*	*Mogera insularis*
Upper premolars	three, missing the second	four
Lower premolars	three, missing the second	four
Zygomatic arch	curved	straight
Auditory bulla	flattened	ventrally developed
Coronoid process	narrow and slender	broad and robust

of the Senkaku Group are assumed or known to be distinct from those of the other Ryukyu islands (Ota *et al*., 1993). Abe *et al*. (1991) discussed how *N. uchidai* migrated to Uotsurijima and has been isolated there since the Miocene. However, that scenario is discordant with the current paleogeographical view and the high level of morphological similarity between *N. uchidai* and *M. insularis*. During the late Pleistocene, the global land area is thought to have been much larger than that at present because of sea level lowering as a result of continental glaciation (Fairbanks, 1989). During this period, several islands of the Senkaku Group, including Uotsurijima, are thought to have been connected to the continent and to Taiwan (Ota *et al*., 1993). Therefore, these islands have not been isolated from those land masses for more than 15,000 years, since the post glacier rise in sea levels (Ota *et al*., 1993).

The ancestor of *N. uchidai* may have migrated to Uotsurijima in the late Pleistocene via the expanded portion of the southeastern continent, which included Taiwan, and then been isolated on Uotsurijima since then. Based on the current paleogeographical view and the distribution of extant terrestrial vertebrates (Ota, 1998, 2000; Motokawa, 2000), the central Ryukyus (the Amami and Okinawa Groups) are thought to have been isolated from the continent and Taiwan since the Pliocene, and the southern Ryukyus (the Miyako and Yaeyama Groups) since the middle Pleistocene. Therefore, migration of the ancestor of *N. uchidai* to the central and southern Ryukyus in the late Pleistocene may have been prevented by collapse of the preceding land bridge.

Another mammalian species from Uotsurijima, the striped field mouse, *Apodemus agrarius*, (Shiraishi and Arai, 1980), also occurs on the continent and in Taiwan. The Uotsurijima population shows slight morphological and karyological differences from populations in the latter two areas (Shiraishi and Arai, 1980; Motokawa, 2000). Abe *et al*. (1991) suggested that *A. agrarius* colonized Uotsurijima in the late Pleistocene. The population size and effective habitat area of these two small mammals native to Uotsurijima must be much smaller than those in Taiwan, because Uotsurijima is a much smaller island (4.3 km^2). The small population size may have accelerated differentiation between *N. uchidai* and *M. insularis*, and between the populations of *A. agrarius* from Uotsurijima and Taiwan over a short period of time ($<$15,000 years).

Based on molecular data, Tsuchiya *et al*. (2000) argued that the four *Mogera* species are monophyletic, and that the *M. insularis* lineage diverged from the remaining species in the Tertiary. The present results may show that the *M. insularis* lineage was split into two species, *M. insularis* and *N. uchidai*, in the late Pleistocene. Thus, the phylogenetic position of *N. uchidai* suggests that the genus *Nesoscaptor* should be included within the genus *Mogera* as a junior synonym.

Mogera uchidai (Abe, Shiraishi et Arai, 1991)

Nesoscaptor uchidai Abe, Shiraishi et Arai, 1991: 53; Hutterer, 1993: 126; Abe, 1994: 33; Nowak, 1999: 236.

Holotype: Young adult female deposited in the Zoological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka; collected from a grassy field at the western coast of Uotsurijima, in the Senkaku Group of the Ryukyu Archipelago, by Satoshi Shiraishi and Shusei Arai on 2 June 1979 (Abe *et al*., 1991).

Diagnosis: A small species of *Mogera*; tail relatively short; nostrils directed outward; rostrum of skull short and narrow; interorbital portion broad and long; palatal portion very broad; upper incisor rows projected forward; upper and lower molars large; lower incisor-like teeth three and large; the coronoid process slender and narrow.

Distribution: Uotsurijima, in the Senkaku Group of the Ryukyu Archipelago. This species is represented only by the holotype.

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APPENDIX

Specimens of *Mogera insularis* from Taiwan examined in this study.
They are deposited with the numbers given in parentheses. See text for abbreviation of acronyms. The asterisk shows specimens included in PCA.
Yangmingshan, Taipei City (NMNS 808*, sex unknown); Erhtsuping, Yangmingshan National Park, Taipei City (NMNS 798*, female); Sozan, Taipei Gun (=Yangmingshan, Taipei City; NSMT M13931*, female); Tsejen Village, Fuhsing County, Taoyuan Prefecture (NMNS 1771, female); Kuanwu, Taian County, Miaoli Prefecture (KUZ M3364*, male); Road Tachuang, Houlung Town, Miaoli Prefecture (NMNS 497*, male); Miaoli Sanyi Houyenshan Nature Reserve, Miaoli Prefecture (KUZ M3386*, female); Teshanli, Chushan Town, Nantou Prefecture (NMNS 809*, male); Neiliao, Chushan Town, Nantou Prefecture (KUZ M1651*, sex unknown); Chushan, Chushan Town, Nantou Prefecture (KUZ M2535*, female; KUZ M2536, female); Kankeng Stream, Chushan Town, Nantou Prefecture (TESRI T0050, male); Kuilin, Chushan Town, Nantou Prefecture (NMNS 1772, male; NMNS 1778, female); Taiwan Endemic Species Research Institute, Chichi Town, Nantou Prefecture (NMNS 1190*, sex unknown; TESRI T0219*, male; OCUMS 6964, male); Tayuankang, Chichi Town, Nantou Prefecture (OCUMS 6962, male); Luku, Luku County, Nantou Prefecture (OCUMS 6963, female); Lienhuachi, Yuchih County, Nantou Prefecture (NMNS 1942*, male); Shuili, Shuili County, Nantou Prefecture (TESRI T0049, female); Tatachia, Hsinyi County, Nantou Prefecture (KUZ M3363, male); National Pingtung Science and Technology University, Neipu County, Pingtung Prefecture (NPSTU SQ00504*, sex unknown); Mt. Nanjenshan, Manchou County, Pingtung Prefecture (KUZ M3362, male; KUZ M 3365, female; KUZ M3366, male).