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A new subspecies of the least weasel *Mustela nivalis* (Mammalia, Carnivora) from Taiwan

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Abstract. A new subspecies of the least weasel, *Mustela nivalis* (Mammalia, Carnivora) was described from the central mountains of Taiwan. The external and skull morphology, and conventional, G-banded and C-banded karyotypes of the present subspecies were compared with those of other subspecies. This new subspecies is distinct from the other subspecies by relatively longer tail, a broad and short interorbital region, short and narrow rostrum, anteriorly positioned infraorbital foramen, well developed protocone and parastyle of the fourth upper premolars, and anterior margin of right and left upper molars located in a straight line. The number of C-blocks in chromosomes of this new subspecies is less than those for other *M. nivalis* subspecies.

Key words: karyotype, *Mustela nivalis*, new subspecies, systematics, Taiwan.

The least weasel *Mustela nivalis* Linnaeus, 1766 (Mammalia, Carnivora) has a wide distribution, covering the whole of Europe, North Africa, North America and the range from Asia Minor to northeastern Siberia, Korea and Japan (Nowak 1999; Abramov and Baryshnikov 2000; Wozencraft 2005; Fig. 1A). *Mustela nivalis* was originally described from Sweden (Wozencraft 2005); it is the smallest member of the Order Carnivora; and can be defined from the other congeneric species by the color of tail tip, the smaller size of skull, and baculum morphology (Sheffield and King 1994). This Holarctic species had been taxonomically much confused and many named forms were described by many authors as reviewed by Sheffield and King (1994), Abramov and Baryshnikov (2000), and Wozencraft (2005). Several recent studies concluded that only a larger form, *M. subpalmata* Hemprich and Ehrenberg, 1833 from Egypt could be separated from *M. nivalis* to represent a full species (Frank 1985; van Zyll de Jong 1992; Reig 1997; Abramov and Baryshnikov 2000; Wozencraft 2005). Wozencraft (2005) recognized 18 subspecies within *M. nivalis*, mostly following Abramov and Baryshnikov (2000).

Morphological variations among subspecies are exten-

sive, and the taxonomic statuses of several subspecies in East Asia have been still confused. For example, subspecies *M. n. namiyei* Kuroda 1921 distributed in northern Honshu of Japan has distinct chromosome number ($2n = 38$, versus 42 for other subspecies karyotyped) (Obara 1991). Obara (1991) suggested that *M. namiyei* may deserve full specific status based on this chromosome difference, but this view is not accepted (Abramov and Baryshnikov 2000; Wozencraft 2005).

Two subspecies of *M. nivalis* occurring in the southern China and the northern Vietnam were first described as separate species: *M. russelliana* by Thomas (1911) from Szechwan (= Sichuan), China and *M. tonkinensis* by Bjorkegren (1941) from northern Vietnam. These two subspecies are isolated from the main continuous distribution range of *M. nivalis* (Fig. 1A). As well, these two subspecies have somewhat longer tails, 39% and 41% of the head and body length for two individuals of *M. russelliana* (calculated from measurements given in Thomas [1911]) and 45% for an individual of *M. tonkinensis* (Bjorkegren 1941), distinct from the European populations with shorter tail 17.7–42.4% (ranges for 26 population means: Abramov and Baryshnikov 2000; Abramov 2006). While Corbet and Hill (1992)

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included the two forms as junior synonyms of *M. nivalis*, they mentioned that *M. russelliana* might be a distinct species and also doubted the placement of *M. tonkinensis*, which represented only by one specimen.

In addition, a population from Shaanxi Province, northwestern China, originally described as *M. aistodonnivalis* by Wu and Kao (1991) is currently considered a subspecies of *M. nivalis* by Wozencraft (2005). This subspecies also has a longer tail relative to the head and body, 38–41% for four individuals (calculated from measurements given in Wu and Kao [1991]).

As mentioned above, the several East Asian forms are likely to be much diverged and separated from *M. n. nivalis* as distinct subspecies or even as distinct species. However, currently available data is still not enough to give them full specific rank. Therefore, we consider several distinct forms as subspecies until comprehensive systematic revision will be made based on enough specimens from East Asia.

Abramov and Baryshnikov (2000) reported *Mustela nivalis* from Taiwan for the first time based on abstract by Lin and Harada (1998); and Wozencraft (2005) and Larivière and Jennings (2009) included Taiwan as distribution of *M. nivalis*. Abramov and Baryshnikov (2000) reported weasels from Taiwan as “*Mustela nivalis* subsp. n.”, but they never describe it nor give specific name. Lin and Harada (1998)’s abstract consists 138 words with title “A new species of *Mustela* from Taiwan”, but they did not give new species name in that abstract. Hosoda et al. (2000) examined mitochondrial cytochrome *b* gene sequence of several species of *Mustela* and *Martes* including a specimen from Taiwan as *M. nivalis* and they found that the Taiwan specimen is included within *M. nivalis* cluster, but they did not make any comment on its taxonomy. Duff and Lawson (2004) listed the Taiwan weasel as *Mustela formosana* with citation to Lin and Harada (1998)’s abstract, but Lin and Harada (1998) did not name the Taiwan weasel as mentioned above. Duff and Lawson (2004, p. 123) only wrote three sentences “*Mustela formosana* / Taiwan Mountain Weasel / Mountains of Taiwan”, which does not fulfill the condition in describing new species according to International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999, Article 16) as discussed by Abramov (2006).

We examined morphological and karyological features of *M. nivalis* from Taiwan. Those results revealed the distinctness of Taiwan weasels from the other sub-

species of *M. nivalis*. Based on these differences, we believe that the Taiwan weasel deserves a valid subspecific status. In this paper, we describe it as a new subspecies of *M. nivalis*.

Materials and methods

Seven specimens of weasels from Taiwan examined in this study (2 males, 4 females, and 1 unknown sex) are deposited at the National Museum of Natural Science, Taichung, Taiwan (NMNS). Comparative specimens of *M. n. nivalis*, *M. n. namiyei* and *M. n. russelliana* are deposited in the Natural History Museum, London (BMNH), the National Museum of Nature and Science, Tokyo, Japan (NSMT), and the collection of Professor Yoshitaka Obara, Hirosaki University, Hirosaki, Japan (see Appendix for further details). Morphological data for *M. n. tonkinensis* and *M. n. aistodonnivalis* were taken from Bjorkegren (1941) and Wu and Kao (1991), respectively.

The following external measurements (in mm) were taken for the Taiwanese specimens by the senior author: head and body length (HB), tail length (T), hind foot length without claw (HF), and ear length (E). Tail ratio (%) was calculated by dividing T by HB. Comparative data for the tail ratio of *M. nivalis* were taken from Abramov and Baryshnikov (2000), except for those of *M. n. tonkinensis* because the value of *M. tonkinensis* in Abramov and Baryshnikov (2000) was considerably different from the original description (Bjorkegren 1941).

For all examined specimens, the following fourteen cranial measurements were taken to the nearest 0.01 mm with digital calipers (Mitsutoyo Co., Ltd): greatest length (GL), condylobasal length (CBL), zygomatic width (ZW), interorbital width (IOW), posterorbital width (POW), mastoid width (MW), palate length (PL), maxillary toothrow length (MXTL), height of braincase (HBC), breadth of rostrum (BR), length of tympanic (LT), length of mandible (LM), height of mandible (HM), and mandible toothrow length (MNLT). Definitions of these characters follow Abramov and Baryshnikov (2000). Principal component analysis (PCA) was conducted with the PRINCOMP procedure of SAS Version 6 (SAS Inst Inc 1990) based on the correlation matrix of cranial measurements. All measurements were log-transformed before PCA. Males and females were combined in each analysis due to the limited number of available specimens.

The number of vertebrae was examined for one speci-

men (NMNS 5243) by use of soft X-ray (Softex M60) and for another (NMNS 4083) by direct dissection and cleaning.

The chromosomal preparations were made from ear, tail and lung tissue cultures following Harada and Yosida (1978). Differential stainings by the G-band and C-band techniques were applied following Seabright (1971) and Sumner (1972), respectively. Comparative karyological data for *M. n. nivalis* from Hokkaido were provided by Professor Y. Obara, Hirosaki University, Japan.

Results

Mustela nivalis formosana new subspecies

Holotype: NMNS 5243, adult male collected on 22 April 2000 in a pine (*Pinus taiwanensis*) plantation forest at an elevation of 2600 m in the Tatchia area (23°38'N, 120°53'E), Yusan National Park, Chia-yi County, central Taiwan (Fig. 1B), by Zeu-Fong Su. The specimen is a stuffed skin with a complete skull.

Paratypes: One female (NMNS 4531) collected on 8 October 2000 at the same area as the holotype; 3 females (NMNS 3302, 5244, 4083) collected on 16 June 1997, 20 July 1999, and 15 August 1999, respectively, in an alpine grassland dominated by the bamboo cane (*Yushania nittakayamensis*) at an elevation of 3200 m on Mt. Eastern Houhuan (24°08'N, 120°17'E), Tarouko National Park, Nantou County, central Taiwan (Fig. 1B); one adult male (NMNS 1482) collected on 20 November 1969 at Tayuleng, 10 km N of Mt. Eastern Houhuan by a collector of the National Preventive Medicine Institute, Taipei. This specimen, originally a dried skin, was trans-

ferred to NMNS and was soaked in fluid with extracted skull. Another paratype (NMNS 5285) is a skull from a broken body of unknown sex, collected by residents at an elevation of 2300 m in Meifong, Highland Experimentation Farm of Taiwan University, 25 km of Mt. Eastern Houhuan, Nantou County, central Taiwan (date unknown).

Etymology: This new subspecies is named after the early Portuguese mariners' name for the island of Taiwan.

Diagnosis: Small subspecies of *Mustela nivalis* and the smallest carnivore found in Taiwan. Tail invariably long, ranging from 42% to 46% of the head and body length. Skull characterized by a broad and short interorbital region. Rostrum short and narrow and infraorbital foramen positioned anteriorly. Protocone and parastyle of the fourth upper premolars well developed. Anterior margin of right and left upper molars located in a straight line.

Description of holotype: Body weight 95.9 gram, HB 202, T 93, E 15, HF 30, GL 39.00, CBL 36.65, ZW 18.92, IOW 8.74, POW 9.40, MW 17.64, PL 14.60, MXTL 11.74, HBC 11.87, BR 8.20, LT 12.70, LM 19.32, HM 9.35, MNTL 12.60.

Body (Fig. 2) slender with short legs less than 3–4 cm, a long neck, inconspicuous ears. Muzzle short with dark and brown vibrissae, mostly 30 mm long. Chin and throat white. Remainder of ventral white with pale yellow and brown spots. Hairs on central dorsal part darker brown than body sides. Line of demarcation between the upper-brown and the lower-white colors irregular. Two color forms closely together on the middle of body. Tail and four feet all brown on both dorsal and ventral sides. Tip of tail with darker brown hairs.

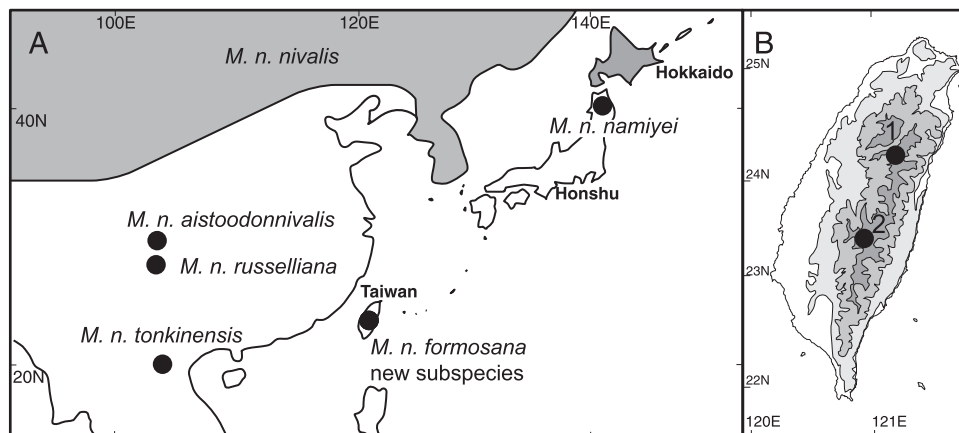
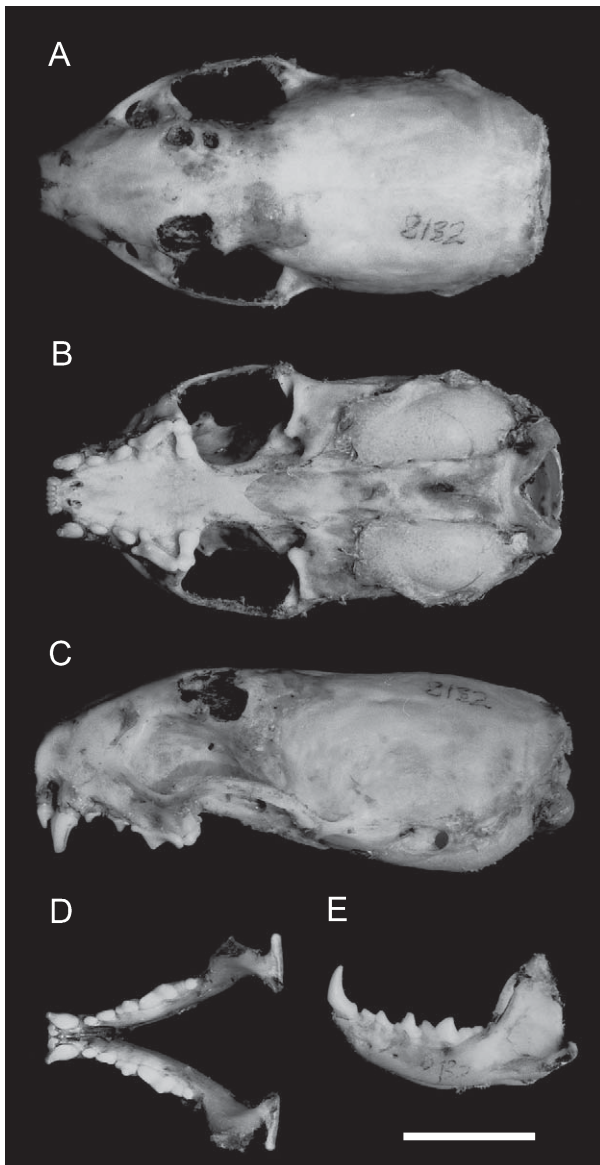


Fig. 1. Map showing *Mustela nivalis* subspecies included in the present study. A: Distribution map of *M. n. nivalis* (shaded area), *M. n. namiyei*, *M. n. russelliana*, *M. n. tonkinensis*, *M. n. aistoodonnivalis* and *M. n. formosana* new subspecies in Asia, B: Sampling localities of *M. n. formosana* in Taiwan, 1. Mt Eastern Houhuan; 2. Tatchia area. Contour lines represent 100 m, 1000 m and 2000 m in elevation.



Fig. 2. Dorsal (upper) and ventral (lower) views of skins of male (holotype, NMNS 5243) and female (paratype, NMNS 4531) specimens of *M. n. formosana* new subspecies. The bar indicates 50 mm.



Skull (Fig. 3) moderate in size with 39.00 mm GL. Braincase long and oval, with weakly developed mastoid process, and lambdoid and sagittal crests. Rostrum short and narrow; BR less than POW. Zygomatic arch moderately expanded laterally, gradually increasing in width anteroposteriorly; zygomatic process moderately wide, its anterior-most points reaching at posterior border fourth upper premolar. Infraorbital foramen wide, small, its anteriormost point reaching at level of parastyle of fourth upper premolar. Interorbital region broad; postorbital constriction less developed and positioned posterior to midpoint of interorbital region; POW greater than IOW. Palate moderately wide, extending behind upper molars; posterior margin greatly concave; its width approximately equal to distance between tympanic bullae, larger than length from just behind upper molars to anterior-most point of posterior margin of palate. Tympanic bulla long, greatly inflated; distances between bullae not changing anteroposteriorly. Profile smoothly upward from rostrum to interorbital region, straight in braincase with slight concavity in anterior position of braincase.

Three pairs of upper incisors; well crowded in a straight line; first and second small, similar-sized, third twice as long as first two. Upper canine moderately large. Upper premolars three pairs (second, third and fourth); second anteroposterior length twice that of buccolingual width; third oval, distances between right

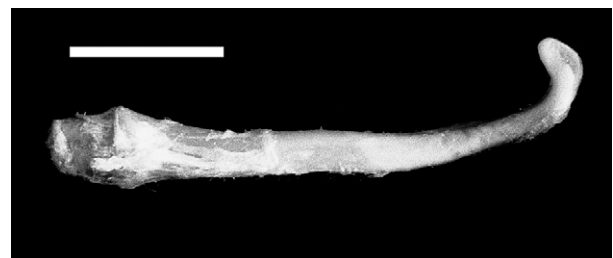
Fig. 3. Dorsal (A), ventral (B) and left lateral (C) views of cranium, and occlusal (D) and left lateral (E) views of mandible of *M. n. formosana* new subspecies (holotype, NMNS 5243). The bar indicates 10 mm.

Table 1. Cranial and mandibular measurements for *M. n. formosana* new subspecies, *M. n. nivalis*, *M. n. namiyei*, and *M. n. russelliana* (mm). Values are given as means \pm SD (upper row) and ranges (lower row) when $n \geq 3$, and as original data when $n \leq 2$. See text for abbreviations used for the measurements

Character	<i>M. n. formosana</i>		<i>M. n. nivalis</i>		<i>M. n. namiyei</i>		<i>M. n. russelliana</i>	
	Male $n = 2$	Female $n = 4$	Male $n = 6$	Female $n = 7$	Male $n = 5$	Female $n = 2$	Male $n = 2$	Female $n = 1$
GL	38.30, 39.00	33.72 \pm 0.22 33.48–33.97	37.53 \pm 5.06 31.03–43.01	32.21 \pm 2.19 29.67–34.69	31.66 \pm 0.44 31.27–32.27	30.18, 31.06	30.00, –	29.09
CBL	35.36, 36.65	31.88 \pm 0.45 31.21–32.23	34.90 \pm 4.53 29.02–39.49	29.47 \pm 1.76 27.39–31.56	29.47 \pm 0.35 29.05–29.74	28.01, 27.89	27.81, –	27.10
ZW	17.95, 18.92	16.31 \pm 0.52 15.80–16.78	20.20 \pm 3.63 14.67–25.85	15.52 \pm 1.60 13.90–17.36	16.80 \pm 0.34 16.19–17.00	15.26, 15.54	14.87, –	14.40
IOW	7.97, 8.74	7.00 \pm 0.24 6.69–7.25	8.41 \pm 1.33 6.24–10.00	6.77 \pm 0.53 6.04–7.44	6.86 \pm 0.18 6.56–6.98	6.31, 6.27	–, –	6.08
POW	9.51, 9.40	8.68 \pm 0.77 8.02–9.76	8.22 \pm 0.94 7.28–9.63	7.60 \pm 0.78 6.72–8.98	7.73 \pm 0.28 7.43–7.99	6.84, 7.39	–, –	5.45
MW	16.67, 17.64	14.92 \pm 0.15 14.79–15.07	17.93 \pm 2.63 13.88–22.00	14.52 \pm 1.10 13.01–15.96	15.23 \pm 0.33 14.69–15.54	14.02, 14.48	14.62, –	13.50
PL	14.62, 14.60	12.51 \pm 0.29 12.29–12.93	15.38 \pm 2.51 12.17–18.08	11.96 \pm 1.48 10.02–14.25	11.66 \pm 0.24 11.46–12.07	10.80, 10.70	10.61, –	10.28
MXTL	11.25, 11.74	10.61 \pm 0.16 10.49–10.84	12.43 \pm 1.47 10.33–14.18	10.28 \pm 1.04 9.25–11.40	10.01 \pm 0.13 9.83–10.13	9.35, 9.20	9.70, 10.07	9.32
HBC	11.21, 11.87	10.63 \pm 0.19 10.41–10.84	12.04 \pm 1.26 10.12–13.43	10.39 \pm 0.91 9.35–11.67	10.40 \pm 0.21 10.18–10.60	9.41, 9.43	10.50, –	10.14
BR	8.15, 8.20	6.96 \pm 0.17 6.74–7.14	8.96 \pm 1.36 6.37–10.07	7.07 \pm 0.67 6.21–8.05	7.85 \pm 0.16 7.75–8.14	7.46, 7.55	–, –	6.78
LT	11.53, 12.70	10.95 \pm 0.24 10.69–11.16	12.53 \pm 1.76 10.19–14.18	10.56 \pm 0.46 10.05–11.32	10.71 \pm 0.25 10.31–10.97	10.26, 10.01	9.44, –	9.39
LM	18.84, 19.32	16.89 \pm 0.06 16.83–16.95	20.02 \pm 3.05 15.38–23.20	15.70 \pm 1.38 13.87–17.33	16.70 \pm 0.35 16.32–17.02	15.44, 15.42	14.46, 14.79	14.41
HM	8.51, 9.35	7.49 \pm 0.23 7.22–7.78	9.56 \pm 1.61 6.89–11.65	7.15 \pm 0.64 6.50–7.97	7.35 \pm 0.09 7.29–7.48	6.80, 6.72	7.44, 7.29	7.07
MNTL	11.88, 12.60	10.85 \pm 0.13 10.72–11.02	13.09 \pm 2.03 10.07–15.70	10.38 \pm 1.11 9.18–11.77	10.54 \pm 0.27 10.20–10.81	9.82, 10.13	9.31, 9.32	9.10

and left gradually increasing anteroposteriorly; fourth elongate and largest, protocone moderately developed, positioned posteriorly to the posteriormost point of third premolar, its parastyle well developed, its paracone and metacone less developed. Upper molars one pair (the first); transversely elongated; its protocone, paracone, and metacone moderately developed; anterior margin of right and left sides located in a straight line. Mandible robust, its coronoid process broad. Lower incisors two pairs; both two small and similar-sized. Lower canine large, its posterior edge well curved. Lower premolars in three pairs (second, third, and fourth); second smallest; third medium sized; fourth largest. Lower molars in two pairs (first and second); first large, with well-developed protoconid and paraconid; second small, rounded.

Cervical vertebrae 7, thoracic 14, lumbar 6, sacral 3, caudal 21. Baculum (Fig. 4) 17.78 mm in length with a

**Fig. 4.** The structure of the baculum of *M. n. formosana* new subspecies (holotype, NMNS 5243). The bar indicates 5 mm.

proximal knob, a slightly tapered shaft with a deep ventral urethral groove, distal part with weakly concaved dorsally; bend of shaft not pronounced, terminal hook well developed with two developed knobs.

Variation: Sexual size dimorphism exists (Fig. 2; Table 1). The only male specimen examined in a com-

plete shape (holotype) was 21–36% longer in HB and 55–113% heavier than females. External measurements of females: NMNS 4531, body weight (= BW) 45 gram, HB 155, T 69, E 13, HF 25; NMNS 3302, BW 62, HB 160, T 68, E 15, HF 27; NMNS 4083, BW 52, HB 167, T 70, E 15, HF 25; NMNS 5244, BW 55, HB 148, T 63, E 14, HF 25. The pelage color was brighter brown on dorsum and pure white on venter in females. The holotype had an additional caudal vertebra compared to the female of NMNS 4083. Cranial characters showed no considerable variation except for size variation where males were larger than females (Table 1).

Comparisons: All specimens of this new subspecies show greater tail ratio compared with the other subspecies given by Abramov and Baryshnikov (2000): 44.8% (NMNS 4531), 42.5% (NMNS 3790), 41.9% (NMNS 4083) and 42.6% (NMNS 5244). Frank (1985) classified two ventral color patterns as the “nivalis” type with a straight demarcation line between the brown dorsal and white abdominal areas along the entire body and no pronounced spotted pattern on the ventral side, and as the “vulgaris” type with an indented demarcation line and several brown spots in both neck and trunk regions. The ventral color type of *M. n. formosana* shows the “vulgaris” type and consistence in all specimens. Even so, the brown spots are found in the trunk region only (Fig. 2).

The cranial measurements of *M. n. formosana*, *M. n. nivalis*, *M. n. namiyei*, and *M. n. russelliana* are given in Table 1. Cranial size of *M. n. formosana* is similar to those of *M. n. nivalis* and *M. n. tonkinensis* (GL = 37.3 mm in male holotype: Bjorkegren 1941), while greater than those of *M. n. namiyei*, *M. n. russelliana* and *M. n. aistoodonnivalis* (GL = 33.3 mm in one male and 27.7–32.0 mm in three females: Wu and Kao 1991). The zygomatic arch is well expanded laterally in *M. n. nivalis*, *M. n. namiyei*, and *M. n. tonkinensis*, moderately expanded in *M. n. formosana* and *M. n. aistoodonnivalis* and less expanded in *M. n. russelliana*. *Mustela n. formosana* is characterized from the others by its broad interorbital region and less developed constriction with POW greater than IOW, in contrast to POW smaller than IOW in the remaining subspecies. The palatal region is expanded posteriorly to the tooththrow, the concavity of its posterior margin is deep in *M. n. formosana* and *M. n. russelliana*, while slight or none in *M. n. nivalis*, *M. n. namiyei*, *M. n. aistoodonnivalis* and *M. n. tonkinensis*. Inner margins of the tympanic bulla is parallel-sided in *M. n. formosana*, *M. n. russelliana* and *M. n. aistoodonnivalis*, while it is not parallel-sided and diverges posteri-

Table 2. Eigenvectors of the first and second principal component axes (PC1 and PC2) based on 14 morphometric characters of *M. n. formosana* new subspecies, *M. n. nivalis*, *M. n. namiyei*, and *M. n. russelliana*. See text for abbreviations used for the measurements

Character	PC1	PC2
GL	0.281	0.096
CBL	0.279	0.121
ZW	0.278	-0.101
IOW	0.274	0.025
POW	0.149	0.879
MW	0.280	-0.086
PL	0.279	0.023
MXTL	0.279	-0.023
HBC	0.258	0.110
BR	0.245	-0.384
LT	0.267	-0.080
LM	0.281	-0.071
HM	0.282	-0.112
MNTL	0.281	-0.028
Eigenvalue	12.108	0.890
Difference	11.219	0.596
Proportion	0.865	0.064

orly so that the distance between their anterior inner margins is less than that of the posterior one in *M. n. nivalis*, *M. n. namiyei* and *M. n. tonkinensis*. Protocone of the upper fourth premolar is well distinguished in *M. n. formosana*, *M. n. russelliana* and *M. n. aistoodonnivalis* compared to *M. n. nivalis*, *M. n. namiyei* and *M. n. tonkinensis*. Its anterior margin is posterior to the third premolar in *M. n. formosana*, *M. n. nivalis*, *M. n. namiyei*, *M. n. aistoodonnivalis* and *M. n. tonkinensis*, whereas it is elongated and exceeds the level of the posteriormost point of the third upper premolar in *M. n. russelliana*. The anterobuccal and anterolingual margins of the upper first molar are located anteriorly at a similar level in *M. n. formosana*, *M. n. russelliana* and *M. n. aistoodonnivalis*, although the anterobuccal margin is located more anteriorly than the anterolingual margin in *M. n. nivalis*, *M. n. namiyei* and *M. n. tonkinensis*.

In PCA, the first and second principal component axes explained 86.5 and 6.4% of the total variation, respectively (Table 2). All variables showed positive loadings in the first axis. In the second axis, POW (positive) and BR (negative) had relatively large loadings in order. Individual scores for the first and second principal components (PC1 and PC2) are plotted in Fig. 5. The value of PC2 was greater in *M. n. formosana* than in other subspecies with a slight range overlap only with *M. n. nivalis*. In PC1, *M. n. formosana* was greater than *M. n.*

Table 3. Chromosomal comparison of *M. n. formosana* new subspecies, *M. n. nivalis* and *M. n. namiyei*

Species	2n	FN	Autosomal pair			X	Y	C-blocks	Reference
			M-SM	ST	A				
<i>M. n. formosana</i> (Taiwan)	42	66	11	2	7	SM	M	3	This study
<i>M. n. nivalis</i> (Europe)	42	70	12	3	5	M	SM	6	Zima and Grafodatskij (1985)
<i>M. n. nivalis</i>	42	70	13	4	3	SM	M	–	Wurster-Hill (1973)
<i>M. n. nivalis</i> (Japan)	42	74	14	3	3	M	SM	7	Obara (1991)
<i>M. n. namiyei</i> (Japan)	38	66	13	2	3	M	SM	5	Obara (1982, 1985, 1991)
<i>M. n. boccamela</i> (Bulgaria)	42	80	16	4	0	SM	SM	–	Peshev et al. (1985)

M, metacentric; SM, submetacentric, A, acrocentric.

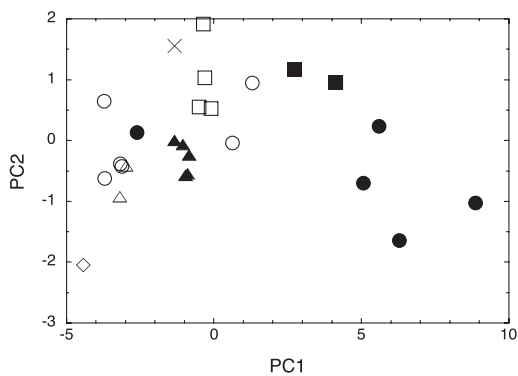


Fig. 5. Two-dimensional plots of the first against the second principal component scores of 14 skull morphometric characters in *M. n. formosana* (square), *M. n. nivalis* (circle), *M. n. namiyei* (triangle), and *M. n. russelliana* (diamond). Open symbols, female; closed symbols, male; cross, unknown sex of *M. n. formosana*.

namiyei and *M. n. russelliana*.

Karyotype: The conventional, G-banded, and C-banded karyotypes were obtained from one male (NMNS 5243, holotype) and three female (NMNS 3302, 5244, 4083 paratypes) specimens of *M. n. formosana* (Fig. 6). *Mustela n. formosana* had 20 autosomal pairs including 11 large-to-small metacentric or submetacentric pairs gradually decreasing in size (nos. 1–11), two medium subtelo-centric pairs (nos. 12 and 13), and 7 medium-to-small acrocentric pairs gradually decreasing in size (nos. 14–20). In each element of pair no. 18, a distinct secondary constriction was observed. The X chromosome was a medium-sized submetacentric element, whereas the Y chromosome was the smallest metacentric one. Thus, the diploid chromosome number (2n) and total number of autosomal arms (FN) were 42 and 66, respectively. Constitutive heterochromatin was found in the centromeric region of most chromosome pairs, and it was also detected in short arms of three metacentric or submetacentric pairs (nos. 1, 2, and 5) as large blocks (C-blocks) (Fig. 6C).

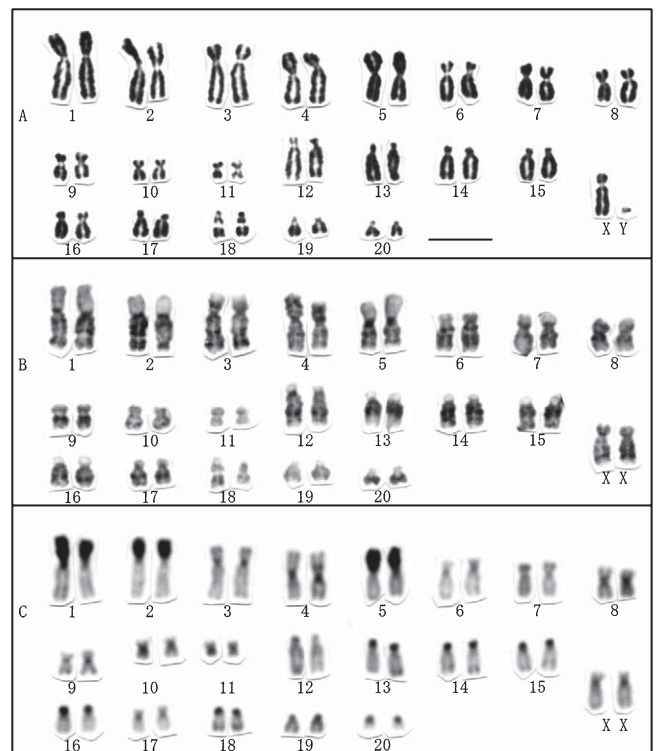


Fig. 6. Conventional (A, holotype, NMNS 5243), G-banded (B, paratype, NMNS 3302), and C-banded (C, paratype, NMNS 5244) karyotypes of *M. n. formosana* new subspecies.

The karyotype of *M. n. formosana* differs from that of *M. n. namiyei* in the diploid chromosome number (42, versus 38; Table 3; Obara 1982, 1985, 1991). It differs from karyotypes of *M. n. nivalis* and *M. n. boccamela* in the fundamental number (66, versus 70–74, versus 80; Table 3, Wurster-Hill 1973; Zima and Grafodatskij 1985; Peshev et al. 1985; Obara 1991). Comparisons of banded karyotypes of *M. n. formosana* with those of *M. n. nivalis* from Hokkaido, Japan, revealed that the homologous G-bands were well detected between them (data not shown). The C-banded karyotype of *M. n. nivalis* possessed C-blocks in seven pairs (Obara 1991),

while that of *M. n. formosana* had C-blocks in only three pairs (Fig. 6). The larger FN in *M. n. nivalis* may be attributable to heterochromatic arms with additional C-blocks.

Genetics: Mitochondrial cytochrome b gene data reported 0.006–0.012 pairwise distance between *M. n. formosana* and other subspecies (Saarma and Tumanov 2006).

Distribution: The subspecies is confined to the high mountain areas on the island of Taiwan.

Ecological remarks: Occurrence of *Mustela n. formosana* is apparently restricted to open forests and grasslands above 2300 m in elevation. These habitats are characterized by a cool and dry climate year round, large rock outcrops, and woody vegetation dominated by *Yushania nittakayamensis* and sparse distribution of the coniferous trees, *Pinus morrisions*, *Pinus taiwanensis* or *Abies kawakamii*. Trapping data indicate that *M. n. formosana* is uncommon even in these habitats. In 1500 trap nights at Mt. Eastern Houhuan 3000–3400 m in elevation, only three specimens were obtained from June–August. All these specimens were taken in Sherman traps baited with fresh pork.

Discussion

Extensive individual and geographic variation exists in many characters in relation to gender, age, and season, including pelage color, position of the demarcation line between brown and white fur, molt patterns, dentition, lengths of tail and hind foot, relative skull measurements, and body size in *M. nivalis* (see King 1989; Abramov and Baryshnikov 2000). Even so, the isolated forms of *M. n. russelliana*, *M. n. tonkinensis* and *M. n. formosana* are obviously different from *M. n. nivalis* in the size and shape of skulls and ratios of the tail length to the head and body length. Therefore, we consider that we unambiguously identified the above subspecies as being distinct from *M. n. nivalis*. On the other hand, C-blocks in chromosomes of *M. nivalis* are thought to have increased in the course of *M. nivalis* evolution (Obara 1991). This suggests that *M. n. formosana* karyotype possesses the primitive characters of fewer C-blocks than *M. n. nivalis* and *M. n. boccamela* karyotypes (Table 3; Mandahl and Fredga 1980; Obara 1982, 1985, 1991; Zima and Grafodatskij 1985; Peshev et al. 1985; Zima and Cenevova 2002).

The discovery of *M. nivalis* from Taiwan seems interesting from a biogeographic viewpoint, because *M.*

nivalis has a circumpolar distribution (e.g., Abramov and Baryshnikov 2000) with a gap between Taiwan and the remainder of its distribution. Therefore, we suggest that this new subspecies is a relict form from the period when *M. nivalis* had a much wider distribution during one of the peaks of the Pleistocene glaciations. During the periods of cold climate, the common ancestor of *M. nivalis* possibly invaded and colonized Taiwan as refugia and then it was isolated in the highlands when the glaciers retreated. The similar interpretation are suggested also in some endemic species that are distributed in the highlands of Taiwan such as the Formosan salamander (*Hynobius* spp.), the land-locked-salmon (*Oncorhynchus masou formosanus*), the Mikado pheasant (*Syrnaticus mikado*), and Kikuchi's vole (*Microtus kikuchii*) (Kano 1940).

According to the theory of allopatric speciation, if a species is separated into two geographic isolates, then the isolated populations over time are bound to develop genetic differences including reproductive isolation (Mayr 1970; Searle 1996). Mayr and O'Hara (1986) also pointed out that allopatric speciation has probably been an important process in the diversification of small mammals in connection with the alternating glacial and interglacial periods. Pleistocene climatic changes may have resulted in dramatic fluctuations in the distribution of the ancestor of *M. nivalis* causing a once-continuous range to split into a number of small isolates within refugia of suitable habitat, especially in the northern fringes of subtropical areas. Under these circumstances, the populations in the separate refugia could have evolved into distinct subspecies, i.e., *M. n. russelliana*, *M. n. tonkinensis*, *M. n. namiyei* and *M. n. formosana*. This view is consistent with the genetic viewpoint of Hosoda et al. (2000) who suggested that *M. nivalis* from Taiwan (*M. n. formosana* in this paper) and Honshu of Japan (*M. n. namiyei* in this paper) had been diverged from *M. n. nivalis* through the alternating glacial and interglacial periods in the Pleistocene.

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Appendix

Comparative specimens examined

Five males (C, I, F, G, E) and two females (D, H) of *M. n. namiyei* from Aomori, Japan (Yoshitaka Obara collection). Two females (A, B) of *M. n. nivalis* from Hokkaido, Japan (Yoshitaka Obara collection). One male (NSMT M17146) of *M. n. nivalis* from Hokkaido, Japan. One unknown sex (NSMT M21751) of *M. n. nivalis* from Seoul, Korea. Six males (BMNH 73.393 from England, 6.4.1.37 from France, 78.32 from Iran, 14.5.10.67 and 14.5.10.68 from Djarkent, Kazakhstan, 47.371 from Afghanistan) and five females (BMNH 73.395 from England, 19.7.1977 from France, 78.31 from Iran, 1938.4.14 from the vicinity of Leningrad, Russia, 14.11.1.14 from Alzamai, Russia) and three unknown sex specimens (BMNH 38.4.14.18 from District of Tornsk, Russia, 14.5.10.69 from Djarkent, Kazakhstan, 28.10.24.9 from West Siberia, Russia) of *M. n. nivalis* in Eurasia. Two males (BMNH 11.2.1.85, 11.2.1.84) and one female (BMNH 11.2.1.87) of *M. n. russelliana* from Sichuan, China.