

Small Mammalian Remains from the Late Holocene Deposits on Ishigaki and Yonaguni Islands, Southwestern Japan

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Yuichiro Nishioka, Ryohei Nakagawa, Shin Nunami, and Satoshi Hirasawa (2016) Small mammalian remains were newly discovered from the Late Quaternary sediments of the Yaeyama region (Ishigaki and Yonaguni Islands) in the southwestern-most part of Japan. We examined these materials based on taxonomical and chronological approaches, in order to reconstruct the past fauna in this region. Accelerator Mass Spectrometry radiocarbon dating indicates that the mammalian assemblages from Ishigaki and Yonaguni Islands are composed mainly of late Holocene fossils. The fossil assemblage from Ishigaki Island comprises five species of small mammals belonging to Soricomorpha (*Suncus murinus*), Chiroptera (*Pteropus* sp., *Hipposideros turpis*, and *Rhinolophus perditus*), and Rodentia (*Niviventer* sp.). One rodent bone, collected from the fissure sediments near Sabichi-do Cave, Ishigaki Island, is dated at 230 ± 20 yBP (ca. AD 1,700), and is considered part of the recent remain. Furthermore, the fossil assemblage from Umabana-zaki Fissure, on Yonaguni Island, is dated at $1,760 \pm 20$ yBP (ca. AD 300) and comprises three species of small mammals belonging to Chiroptera (*Pipistrellus* cf. *abramus*) and Rodentia (*Niviventer* sp. and *Mus musculus*). *Niviventer* is not currently distributed in Japan. Only domestic rats (*Rattus rattus* and *R. norvegicus*) live on Ishigaki and Yonaguni Islands at the present time. However, the fossil assemblage from Umabana-zaki Fissure is dominated completely by *Niviventer* sp. Most fossils of small mammals found from the late Holocene Ishigaki and Yonaguni Islands represented species that are currently endemic to the Yaeyama region. *Niviventer* sp. from these islands is unique because this form has never been found from neighboring regions, such as Taiwan and Miyako Islands, and because it likely existed in the late Holocene. These discoveries support the hypothesis that the Yaeyama region had been isolated zoogeographically from the continent even during the Last Glacial Maximum, when the sea level had drastically fallen.

Key words: Rodentia, Chiroptera, Soricomorpha, Quaternary, Fossil, Ryukyu.

BACKGROUND

The Ryukyu Arc is a chain of islands in southwestern Japan. These islands represent the easternmost extremity of the Indomalaya region, and are separated zoogeographically from the Palearctic, including mainland Japan (Hokkaido, Honshu, Shikoku, and Kyushu), by the Watase's line or the Tokara Gap (Fig. 1A). The Ryukyu Arc is subdivided into five groups based on distribution

of endemic species on each island: Tokara Group, Amami Group, Okinawa Group, Miyako Group, and Yaeyama Group (Motokawa 2000; Ota 2000). Paleontological examination is a usual way to elucidate the evolutionary process of terrestrial animals in these groups.

Most terrestrial mammals on the Ryukyu Islands likely migrated from the Eurasian continent to each island via land bridges during sea level lowstands of the Pliocene and Pleistocene. Some

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small mammals recently found from the Plio-Pleistocene of East China may support this faunal migration as paleontological evidence (Jin 2004; Tomida and Jin 2009; Wang et al. 2010).

Many mammal fossils from the Pleistocene Ryukyu (stratigraphic) Group have been reported over the past half-century, and they were reviewed by Otsuka and Takahashi (2000). They argued that there were three periods of faunal migration between the continent and Ryukyu Islands during the Pleistocene land connections. However, recent studies based on small mammal fossils have not supported the existence of such a long land bridge at least in the Last Glacial Maximum (Kawamura 1998, 2014; Kawamura and Nakagawa 2009, 2012; Nakagawa et al. 2012). Furthermore, living reptiles and amphibians are also peculiar to each island group due to a long-time isolation from the continent (Ota 2000, 2003; Koizumi et al. 2014).

The southwestern part of the Ryukyu Arc, or the Miyako and Yaeyama Groups, are not to be ignored in discussing the faunal relationship between the Eurasian continent and the Ryukyu

Islands, although no native species of living mammals spreads on these islands, except for a wild cat, *Prionailurus iriomotensis* (or *bengalensis*), on Iriomote Island (Motokawa 2000). Some locations on Miyako Island have yielded a great deal of terrestrial mammal fossils that are correlated with the continental fauna (Hasegawa 1985; Kaneko and Hasegawa 1995; Nakagawa et al. 2012). For example, *Microtus fortis* has been yielded commonly from the Late Pleistocene deposits on Miyako Island, but is currently distributed only in the continental region. Kawamura (2014) suggested that *M. fortis* probably migrated from the continent to Miyako Island in the Middle Pleistocene, because its fossil record is absent since the Late Pleistocene on Ishigaki Island, ca. 45 km west of Miyako Island (Kawamura and Kawamura 2013).

The Yaeyama Islands are still insufficient in quantities of fossil records. Otsuka and Hasegawa (1973) reported deer fossils from the Todoroki river basin on Ishigaki Island, but the fossil-bearing horizon was unspecified. Small mammal fossils,

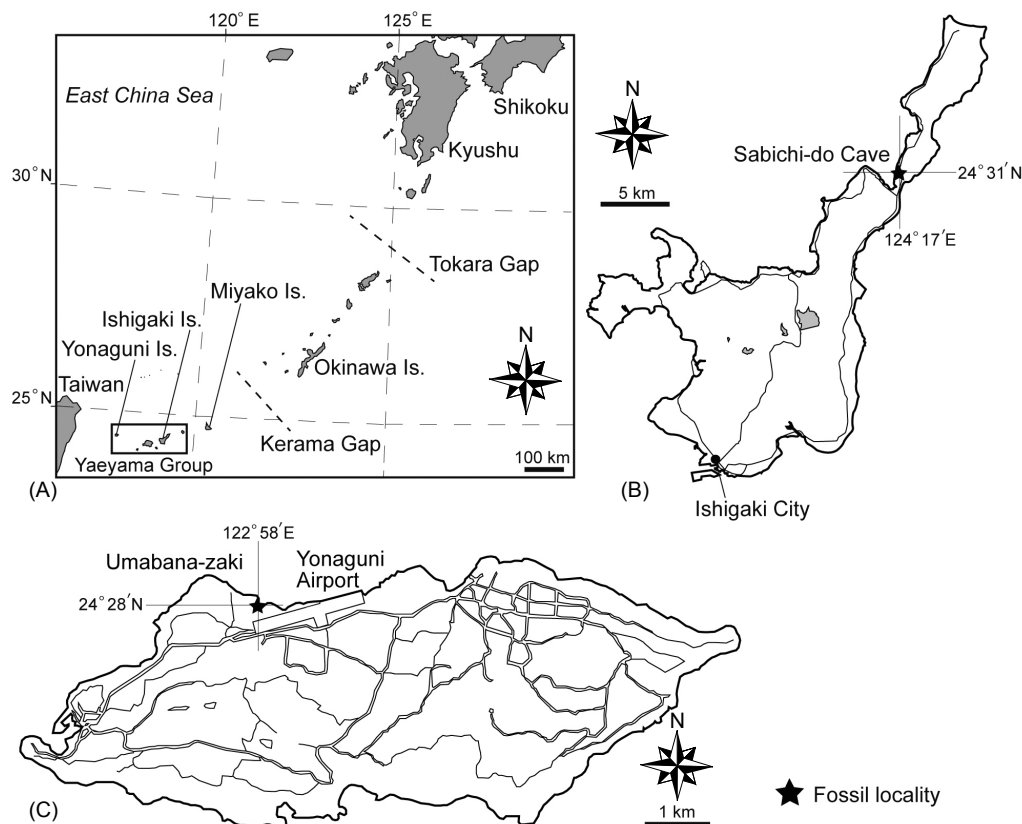


Fig. 1. Locations at which small mammal remains were collected. (A) Yaeyama Group in Ryukyu Archipelago; (B) Sabichi-do Cave, Ishigaki Island; (C) Umabana-zaki, Yonaguni Island.

including bats (*Pteropus dasymallus yayeyamae*? and *Rhinolophus cornutus*) and rats (*Rattus rattus*), were discovered with extinct deer, *Metacervulus* (= *Cervus*) *astylodon*, from fissure sediments of the Ishisuku-yama archaeological site, Ishigaki Island, although the age and morphological description of the fossils were not mentioned in detail (Hasegawa and Nohara 1978). In Yonaguni Island, Otsuka et al. (2008) reported deer fossils from the Late Pleistocene deposits, and Takahashi et al. (2008, 2014) described terrestrial turtles from the Late Pleistocene and Holocene. However, there is no fossil record of small mammals, such as rodents, to date.

Recently, the present authors discovered Late Pleistocene and Holocene human remains from Shiraho-Saonetabaru cave site on eastern Ishigaki Island (Nakagawa et al. 2010). The sediments, from which the human remains were recovered, also contain a huge number of rodents of the genus *Niviventer* (Kawamura and Kawamura 2013). This genus is currently not distributed in Japanese Islands but in Southeast Asia, China, and Taiwan. Kawamura and Kawamura (2013) indicated that non-volant small mammals on Ishigaki Island had already formed an island fauna isolated completely from those of neighboring islands since the latest Pleistocene. Furthermore, they suggested that *Niviventer* had been the most dominant rodent on Ishigaki Island until the later Holocene.

In this study, we describe the small mammal fossils from two new fossil localities on Ishigaki and Yonaguni Islands to verify whether extinct species, such as *Niviventer*, was distributed commonly throughout these islands, and discuss the past faunal relationship between the Yaeyama Islands and the Eurasian continent.

MATERIALS AND METHODS

Fossil localities and collecting methods

Small mammal remains used in this study were found in the Quaternary deposits on Sabichi-do limestone cave located in Ibaruma, northern Ishigaki Island, and at a limestone fissure in Umabana-zaki cape, northern Yonaguni Island (Fig. 1). The limestone on Sabichi-do Cave and Umabana-zaki are formed primarily by the Upper Pleistocene of the Ryukyu Group: Ohama Formation and San-ninu-dai Formation, respectively (Yazaki 1982; Kaneko et al. 2003). The cave floor or fissures are sometimes filled with muddy sediments, containing animal remains, from the Late Pleistocene to the Recent.

At Sabichi-do Cave, small mammal remains were collected from two points. One is located on a slope near the east entrance of Sabichi-do Cave (Fig. 2B). The sediments include many bat remains, which are probably mixed with recent

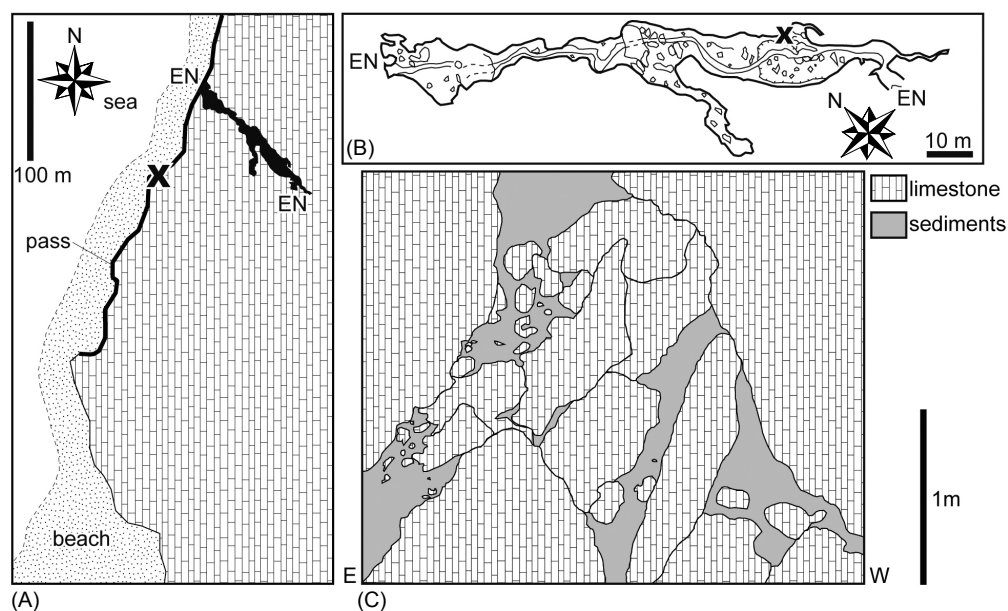


Fig. 2. Sampling points (X) at Sabichi-do Cave, Ishigaki Island. (A) Location of Sabichi Fissure; (B) Plan map of Sabichi-do Cave (after Oshiro et al. 1980); (C) East-west section of Sabichi Fissure. EN: entrance.

bones of living bats, such as *Rhinolophus perditus*. A total of 140 kg of the cave sediments were collected for extracting small mammal remains.

The other sampling point is a small fissure (called as 'Sabichi Fissure' in this study), horizontally extending from north to south, which is situated at 50 m south from the west entrance of the cave (Fig. 2A). Sabichi Fissure is filled with sediments on the floor. The wall along the fissure forms travertine, exposing deer bones and snail shells on the surface. This travertine was previously examined by Otsuka et al. (2008) to find deer fossils and obtain the fossil-bearing age. According to them, snail shells collected from the travertine indicated the Late Pleistocene ($12,360 \pm 80$ yBP) and Holocene ($3,680 \pm 30$ yBP) ages based on ^{14}C dating. In this study, a total of 420 kg fissure fillings were collected here (Fig. 2C).

The limestone fissure at Umabana-zaki, or Umabana-zaki Fissure, is exposed along the north coast on Yonaguni Island and is filled with reddish brown mud (Fig. 3). The fissure sediments were classified into seven layers by key fillings to collect samples stratigraphically. Layer 1 (ca. 40 cm thick) lies under the surface layer (Layer 0), including large-sized gravel from 10 to 40 cm diameters. Layer 2 (10–20 cm thick) contains a lot of gravel under 10 cm diameter, and small terrestrial shells (e.g., *Truncatella guerinii*). Layer 3 (10–25 cm thick)

is relatively massive, including little gravel. Layer 4 (25 cm thick) contains small gravel, as in Layer 2, but rarely includes the shells. Layer 5 (20–40 cm thick) is composed of massive and viscous mud with less gravel. Layer 6 (65 cm thick), the lowest of the collected sediments, includes large gravel with 20 cm or more diameter. A total of 865 kg of fissure fillings were collected: 15 kg from Layer 0, 100 kg from Layer 1, 20 kg from Layer 2, 20 kg from Layer 3, 90 kg from Layer 4, 320 kg from Layer 5, 180 kg from Layer 6 and 120 kg from indeterminate layers.

All collected sediments were washed and screened by using a 0.5-mm mesh, following the methods described by Kawamura (1988). After drying the residue on the mesh, all fossils were picked up. Only dental materials were used for identification and description in this study. These specimens are stored at the Mie Prefectural Museum, Tsu City, Japan, and are catalogued from MPM-Fo (Mie Prefectural Museum-Fossil) 2801 to 2954.

Comparing, measuring, and dating methods

The specimens used in this study were observed by a stereomicroscope (Nikon SMZ1000, Japan) and measured by a digital caliper on the Nikon Profile Projector V-12 (Nippon Kogaku, Japan). SEM (Scanning Electron Microscope) images were obtained by the NeoScope (model: JCM-5000, maker: JEOL Ltd., Japan), which is set up at the Mie Prefectural Museum, Japan, under the condition of a high vacuum and 10 kV accelerating voltage.

To identify the fossils, they were compared with bone specimens of living species that were collected from Ishigaki and Yonaguni Islands by the authors, and the specimens stored in the National Museum of Natural Science, Taichung (Taiwan), and in the Kyoto University Museum, Kyoto (Japan). Dental terminology and measuring method of Soricomorpha were modified after the description by Kawamura (1992, 1993), and they were also applied to Chiroptera. Tooth measurements of Chiroptera were obtained only in maximum length (antero-posterior length) and width (anterior width of upper molars and posterior width of lower molars). Dental terminology and measuring method of rodents followed the description by Kawamura (1988) (see also Figs. 4 and 5).

Absolute age of the fossil assemblages was calculated by accelerator mass spectrometry

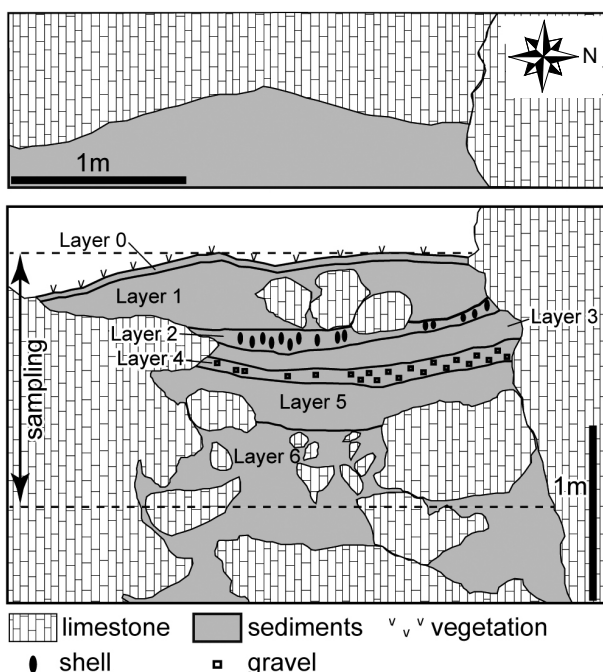


Fig. 3. Plan and section of Umabana-zaki Fissure, Yonaguni Island.

(AMS) ^{14}C dating by the Paleo Labo Co. Ltd., Japan, for a rodent femur (labo number: PLD-18106, 257.1 mg) from Sabichi Fissure and a rodent coxa (labo number: PLD-18107, 315.3 mg) from Layer 5 of Umabana-zaki Fissure.

RESULTS

Fossil assemblage and age

Three fossil assemblages examined in this study are composed of small mammals belonging to Soricomorpha, Chiroptera, and Rodentia. The fissure fillings (420 kg sediments) collected from Sabichi Fissure contain few mammal fossils (only seven specimens), whereas 140 kg sediments from Sabichi-do Cave include a total of 72 specimens of chiropterans (Table 1).

The fossil assemblage from Sabichi Fissure includes *Suncus murinus*, *Pteropus* sp., *Hipposideros turpis*, and *Niviventer* sp. *Suncus murinus* and *Hipposideros turpis* currently live on Ishigaki Island (Motokawa 2009; Sano 2009a), and

Pteropus sp. probably corresponds to extant *P. dasymallus* on this island. *Niviventer* from Sabichi Fissure is never distributed in the Ryukyu Islands and all Japanese islands, although it is diversified in the east of Eurasia including Southeast Asia, China, and Taiwan at present (Corbet and Hill 1992). Furthermore, a lower molar of an extinct deer (*Cervus* sp.) is mixed with the small mammal fossils from Sabichi Fissure. This deer remain probably originated from the Late Pleistocene travertine above the fissure fillings, which recovered *Cervus astylodon* ('Ryukyu jika') (Otsuka et al. 2008).

The fossil assemblage from Sabichi-do Cave is composed of two microchiropteran species, *Hipposideros turpis* and *Rhinolophus perditus*. Both species currently inhabit Sabichi-do Cave and/or neighboring caves (e.g., North Sabichi-do Cave), based on the authors' field observations. There is another microchiropteran species, *Miniopterus fuscus*, on Ishigaki Island at present (Sano 2009b), but this species is absent in the fossil assemblages from both Sabichi-do Cave and Sabichi Fissure.

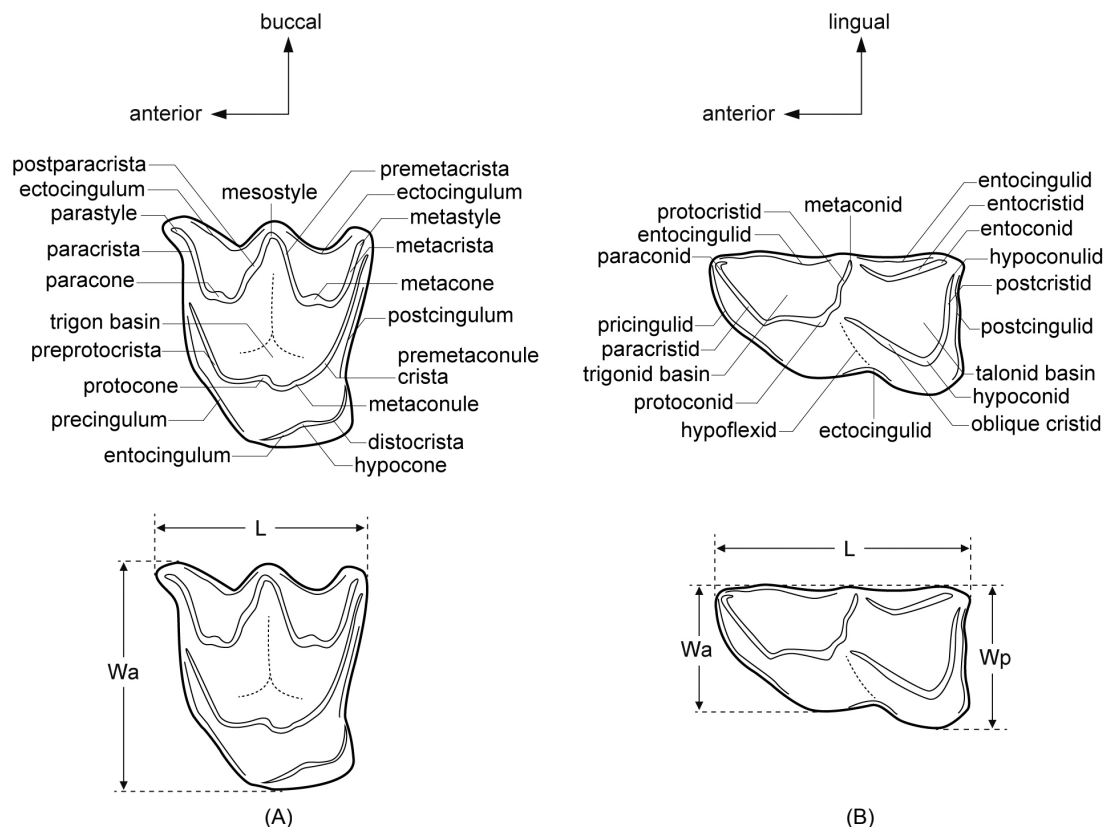


Fig. 4. Tooth terminology and measuring points of Chiroptera and Soricomorpha (after Kawamura 1992, 1993). (A) Left upper molar of Rhinolophidae; (B) Left lower molar of Soricidae.

The fossil assemblage from Umabana-zaki Fissure includes three small mammal species: *Pipistrellus cf. abramus*, *Niviventer* sp., and *Mus musculus*. *Pipistrellus cf. abramus* and *Mus musculus* are distributed widely in Eurasia, including Yonaguni Island (Iwasa 2009a; Kawai 2009). *Niviventer* has not been reported from Yonaguni Island to date, but is conspecific as the form from Sabichi Fissure, which is described in this study. *Niviventer* sp. is dominant in the fossil

assemblage (21 specimens), and most of the specimens were yielded from Layer 5 or Layer 6 of the fissure fillings. *Hipposideros turpis* and *Rhinolophus perditus* are not included in the fossil assemblage, because they are cave-habitat bats.

AMS ^{14}C dating of the rodent fossils indicated that the fossil assemblages from Sabichi Fissure and Umabana-zaki Fissure (Layer 5) comprise the late Holocene fauna: i.e., 230 ± 20 yBP (AD 1,650–1,795) and $1,760 \pm 20$ yBP (AD 240–320),

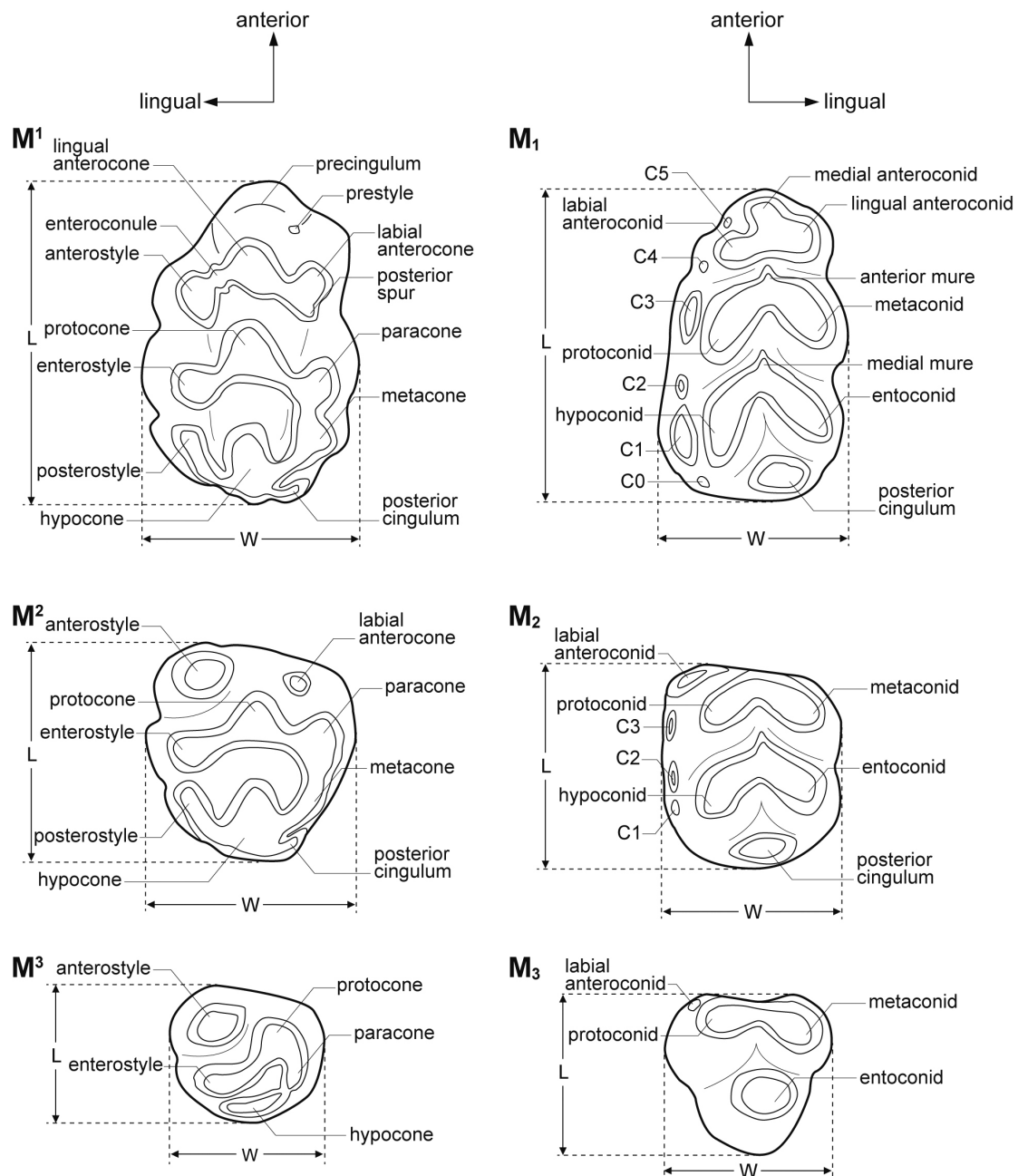


Fig. 5. Tooth terminology and measuring points of murid rodents (after Kawamura 1988).

respectively. These dates are supported by a sufficient yield of collagen for dating (12.5% and 3.17% for each sample).

Systematic paleontology

Suncus murinus Linnaeus, 1766

(Fig. 6)

Class Mammalia Linnaeus, 1758
Order Soricomorpha Gregory, 1910
Family Soricidae Fischer, 1814
Genus *Suncus* Ehrenberg, 1832

Material examined: A right mandible with I₁, M₁, M₂, and M₃ (MPM-Fo 2802); a left M₂ (MPM-Fo 2803).

Locality: Sabichi Fissure, Ishigaki Island.

Measurements: M₁ (MPM-Fo 2802): L, 2.17 mm; Wa, 1.35 mm; Wp, 1.64 mm. M₂ (MPM-Fo 2802): L, 2.01 mm; Wa, 1.39 mm; Wp, 1.50 mm. M₂ (MPM-Fo 2803): L, 1.97 mm; Wa, 1.32 mm; Wp, 1.60 mm. M₃ (MPM-Fo 2802): L, 1.47 mm; Wa, 0.85 mm.

Description: The mandible, MPM-Fo 2802, is an anterior part without posterior processes, and preserves I₁, M₁, M₂, and M₃. The buccal surface of the mandible is dissolved, exposing incisor and molar roots. The mandibular body is slender but robust dorso-ventrally. The alveolus has root sockets for I₁, lower C, P₄, M₁, M₂, and M₃. The crowns of lower C and P₄ are absent. I₁ has two distinct roots.

Molars show a typical tribosphenic pattern (W-shaped pattern) that is composed of the trigonid and talonid basins. The paraconid is

prominent, and is smaller than the protoconid and the metaconid. The main cusps on the molars are connected to each other by sharp crests (e.g., paracristid and protocristid), and surround the isosceles triangle occlusal outline of the trigonid or talonid. The hypoconid connects to the postero-buccal wall of the trigonid by an oblique crest. The postcristid, extending from the hypoconid, joins with a cingulum (or the entocingulid) at the base of the entoconid. The postcristid runs in parallel with the protocristid in occlusal view. The cingulums surround both lingual and buccal bases of the crown. The hypoconulid is absent. Each molar has

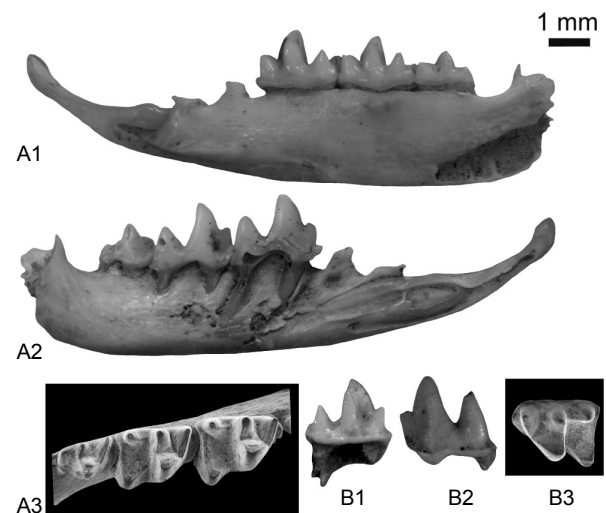


Fig. 6. *Suncus murinus* from Sabichi Fissure. (A) MPM-Fo 2802, right mandible with I₁, M₁, M₂, and M₃ (A1, lingual view; A2, buccal view; A3, occlusal view by SEM); (B) MPM-Fo 2803, left M₁ (B1, lingual view; B2, buccal view; B3, occlusal view by SEM).

Table 1. List of small mammal remains from Ishigaki and Yonaguni Islands

	Ishigaki Is.			Yonaguni Is.	
	Sabichi Fissure	Sabichi Cave	Living	Umabana-zaki	Living
Soricomorpha					
<i>Suncus murinus</i>	2	-	○	-	○
Chiroptera					
<i>Pteropus</i> sp. indet.	1	-	○	-	
<i>Hipposideros turpis</i>	3	41	○	-	○
<i>Rhinolophus perditus</i>	-	31	○	-	
<i>Pipistrellus</i> cf. <i>abramus</i>	-	-	?	1	○
Rodentia					
<i>Rattus rattus</i>	-	-	○	-	○
<i>Rattus norvegicus</i>	-	-	○	-	○
<i>Niviventer</i> sp.	1	-	-	21	-
<i>Mus musculus</i>	-	-	○	1	○

two roots.

M_2 is same basically as M_1 in terms of occlusal pattern. M_2 is smaller than M_1 , but the anterior width of the former is slightly larger than that of the latter. The M_3 talonid is much reduced, and lacks the basal cingulum on the posterior side.

Remarks: *Suncus murinus* is characterized by lower dental formula, 1.1.1.3, non-reddish tooth, large-size, and much reduced talonid of M_3 , and is distinguished from any other species of the Soricidae and Talpidae by these features (Abe 2000). *Suncus murinus* is similar in basic dental morphology with two Taiwanese soricids, *Soriculus caudatus* and *Anourosorex squamipes* (Hanamura et al. 1979, 1980). According to them, the dental size of *Suncus murinus* is intermediate between that of *Soriculus caudatus* (with smaller teeth) and *Anourosorex squamipes* (with larger teeth). M_3 of *Suncus murinus* is more reduced than that of *Soriculus caudatus*, but larger than that of *Anourosorex squamipes*. The M_1 cingulum of *Anourosorex squamipes* extends on the anterior base, whereas that of *Suncus murinus* surrounds the base from the anterior to the posterior. *Suncus murinus* from Sabichi Fissure is included in a size variation of extant species (*Suncus murinus riukiuanus* from Okinawa Island; Hanamura et al. 1979) and of those collected from Yonaguni Island in this study.

Distribution (natural): South Asia, Southeast Asia, South China, Taiwan, and Ryukyu Islands (Motokawa 2009).

Locality: Sabichi Fissure, Ishigaki Island.

Measurements: M_1 (MPM-Fo 2804): L, 5.64 mm; W, 2.92 mm.

Description: The tooth is simple like a unicuspid tooth of carnivorans. The occlusal surface shows an ellipse outline, and is composed of the prominent protoconid and the small metaconid. There is a crest along the occlusal outline. The talonid basin is broad and slightly concaved. The tooth is anchored by two robust roots.

Remarks: A lower molar of flying fox, or *Pteropus*, lacks the original tribosphenic pattern (the W-shaped pattern), which is represented by microchiropteran species. Three species of *Pteropus* are known in Japan: *P. pselaphon* on Ogasawara Islands (1000 km south of Honshu), extinct *P. loochoensis* on Okinawa Island, and *P. dasymallus* in the Ryukyu Islands (Kinjo 2009; Kinjo and Izawa 2009; Kinjo and Nakamoto 2009). Fossils of *Pteropus dasymallus* were reported from Ishigaki Island, although it has not been compared with other species (Hasegawa and Nohara 1978). Moreover, the Late Pleistocene and Holocene deposits on Miyako and Ishigaki Islands recently yielded *Pteropus* remains, but these were not identified at a species level due to a deficiency of comparisons with *P. loochoensis* and *P. pselaphon* (Nakagawa et al. 2012; Kawamura and Kawamura 2013). The lower molar from Sabichi Fissure is not different from that of living *P. dasymallus*, based on the specimens collected from the Ishigaki Island.

***Pteropus* sp. indet.**
(Fig. 7)

Order Chiroptera Blumenbach, 1779
Family Pteropodidae Gray, 1921
Genus *Pteropus* Erxleben, 1777

Material examined: A left M_1 (MPM-Fo 2804).

***Hipposideros turpis* Bangs, 1901**
(Fig. 8)

Family Hipposideridae Lydekker, 1891
Genus *Hipposideros* Grey, 1831

Material examined: A right maxilla with C , P^3 , P^4 , M^1 , M^2 , and M^3 (MPM-Fo 2805); two left P^4

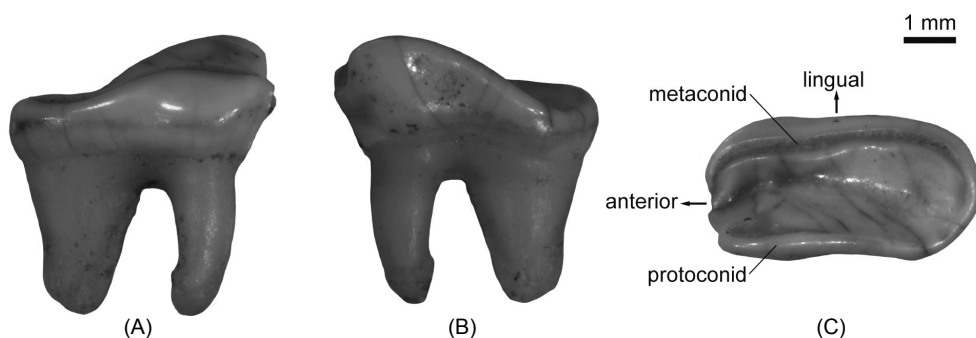


Fig. 7. *Pteropus* sp. indet. (MPM-Fo 2804, left M_1) from Sabichi Fissure. (A) lingual view; (B) buccal view; (C) occlusal view.

(MPM-Fo 2812-2813); a right P⁴ (MPM-Fo 2814); two left M¹ (MPM-Fo 2815-2816); three right M¹ (MPM-Fo 2817-2819); three left M² (MPM-Fo 2820-2822); four right M² (MPM-Fo 2823-2826); a right M¹ or M² (MPM-Fo 2827); three left M³ (MPM-Fo 2828-2830); a right M³ (MPM-Fo 2831); a left mandible with P₂, P₄, M₁, and M₂ (MPM-Fo 2832); a left mandible with M₂ and M₃ (MPM-Fo 2833); two left mandibles with M₂ (MPM-Fo 2834-2835); a left mandible with M₁ and M₂ (MPM-Fo 2836); a right mandible with P₄, M₁, and M₂ (MPM-Fo 2837); a right mandible with M₁, M₂, and M₃ (MPM-Fo 2838); a right mandible with M₂ and M₃ (MPM-Fo 2839); a left P₄ (MPM-Fo 2845); five left M₁ or M₂ (MPM-Fo 2846-2850); three right M₁ or M₂ (MPM-Fo 2851-2853); two left M₃ (MPM-Fo 2854-2855); two right M₃ (MPM-Fo 2856-2857).

Locality: Sabichi Fissure and Sabichi-do Cave, Ishigaki Island.

Measurements: See Tables 2 and 3.

Description: The maxilla (MPM-Fo 2805) preserves a canine, two premolars, and three molars (Fig. 8A). The root socket of the canine concaves dorso-ventrally. The canine is large, robust, and with a weak ridge on the buccal side and sharp keels on the anterior and posterior sides. The base of the canine is elongated antero-posteriorly, and has a distinct cingulum. The cingulum at the buccal side shows a chevron line bending almost at a right angle.

There are two upper premolars. The smaller one (usually called as P³) is situated on the buccal side behind the canine. The larger one, or P⁴, is composed of a single cusp (paracone) and has a triangular occlusal outline. The buccal surface of P⁴ also shows an equilateral triangle due to the crown height almost as long as the crown length. The basal cingulum is strong. P⁴ is in contact with

Table 2. Upper tooth measurements (in mm) of the chiropteran remains from Ishigaki and Yonaguni Islands

	C L	C W	P ³ L	P ³ W	P ⁴ L	P ⁴ W	M ¹ L	M ¹ Wa	M ² L	M ² Wa	M ³ L	M ³ Wa
<i>Hipposideros turpis</i>												
MPM-Fo 2805	2.97	1.86	0.61	0.62	1.59	1.67	2.56	2.05	2.35	2.18	1.68	1.53
<i>Rhinolophus perditus</i>												
MPM-Fo 2858	1.32	1.05	0.41	0.37	1.30	0.95	1.43	1.44	1.42	1.35	1.34	1.18
MPM-Fo 2859	-	-	-	-	1.44	1.20	1.52	1.45	-	-	-	-

Table 3. Lower tooth measurements (in mm) of the chiropteran remains from Ishigaki and Yonaguni Islands

	C L	C W	P ₂ L	P ₂ W	P ₃ L	P ₃ W	P ₄ L	P ₄ W	M ₁ L	M ₁ Wp	M ₂ L	M ₂ Wp	M ₃ L	M ₃ Wp
<i>Hipposideros turpis</i>														
MPM-Fo 2837	-	-	-	-	-	-	1.49	1.30	2.51	1.40	2.52	1.57	-	-
MPM-Fo 2838	-	-	-	-	-	-	-	-	2.74	1.49	2.68	1.59	2.29	1.43
MPM-Fo 2836	-	-	-	-	-	-	-	-	2.55	1.47	2.57	1.34	-	-
MPM-Fo 2833	-	-	-	-	-	-	-	-	-	-	2.65	1.61	2.41	1.41
MPM-Fo 2839	-	-	-	-	-	-	-	-	-	-	2.60	1.30	2.21	1.27
MPM-Fo 2834	-	-	-	-	-	-	-	-	-	-	2.69	1.55	-	-
MPM-Fo 2835	-	-	-	-	-	-	-	-	-	-	2.57	1.43	-	-
<i>Rhinolophus perditus</i>														
MPM-Fo 2883	1.00	0.87	0.57	0.59	0.21	0.22	0.91	0.84	1.55	1.02	1.34	1.07	1.32	1.04
MPM-Fo 2884	-	-	-	-	0.21	0.23	0.92	0.83	1.52	0.99	1.41	1.09	1.36	0.99
MPM-Fo 2878	-	-	-	-	-	-	0.92	0.89	-	-	-	-	-	-
MPM-Fo 2879	-	-	-	-	-	-	0.98	0.77	1.60	0.96	1.49	0.98	1.47	0.94
MPM-Fo 2885	-	-	-	-	-	-	0.99	0.84	1.47	1.04	1.43	1.10	1.37	1.05
MPM-Fo 2880	-	-	-	-	-	-	-	-	1.58	1.03	1.50	1.05	1.58	0.99
MPM-Fo 2881	-	-	-	-	-	-	-	-	1.62	1.08	1.62	0.98	-	-
MPM-Fo 2882	-	-	-	-	-	-	-	-	-	-	1.54	0.95	-	-
<i>Pipistrellus cf. abramus</i>														
MPM-Fo 2910	0.77	0.71	-	-	-	-	-	-	1.07	0.93	1.14	0.97	1.01	0.70

the canine at the antero-lingual side.

Upper molars have a W-shaped pattern with a trapezoidal occlusal outline. The crown of M¹ is composed of four main cusps (paracone, metacone, protocone, and hypocone) and three styles (parastyle, mesostyle, and metastyle). The parastyle is as large as the mesostyle in the buccal view, and the metastyle is slightly weaker than the other styles. The cristas connect main cusps and styles on the buccal side, comprising a W-shaped line. The ectocingulum is smaller than the precingulum and the postcingulum. The metacone is slightly larger than the paracone. The metaconule is absent or indistinct. The hypocone is vestigially present at the postero-lingual

corner. The entocingulum and the distocrista are strong, connecting with the precingulum and the postcingulum, respectively.

The occlusal pattern of M² is basically the same as that of M¹, although the posterior wall of M¹ bends inward strongly. The crown size of M² is slightly smaller than that of M¹. M³ is much reduced in the posterior part composed of the metacone and the hypocone. Thus, the occlusal surface of M³ shows a triangular shape. The parastyle of M³ projects more buccally than the other styles.

The mandibles (MPM-Fo 2832 and 3838) preserve cheek teeth, P₄ to M₂ and M₁ to M₃, respectively (Figs. 8B-C). The mandibular body is robust, with a large mental foramen below the

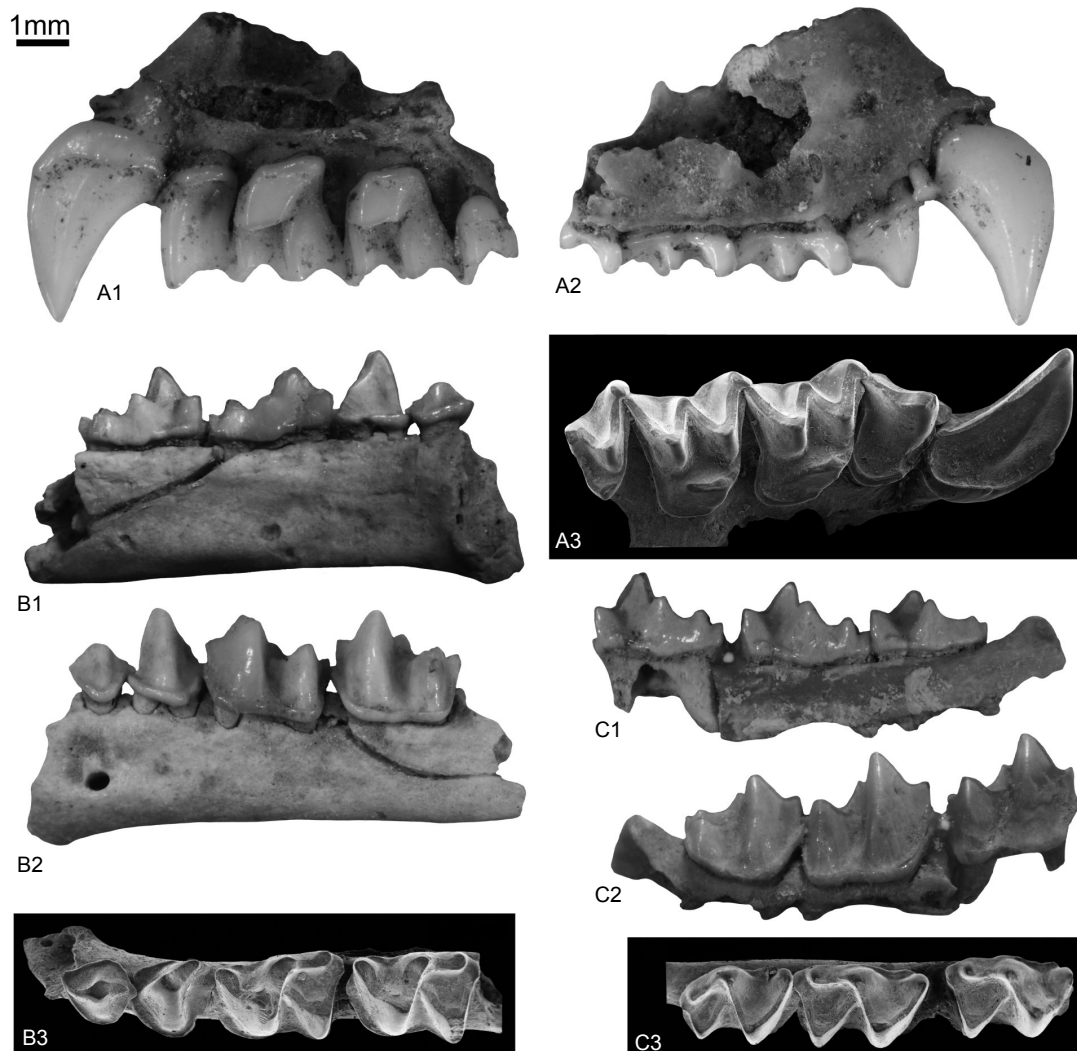


Fig. 8. *Hipposideros turpis* from Sabichi Fissure and Sabichi-do Cave. (A) MPM-Fo 2805, right maxilla with C, P³, P⁴, M¹, M², and M³ (A1, lingual view; A2, buccal view; A3, occlusal view by SEM). (B) MPM-Fo 2832, left mandible with P₂, P₄, M₁, and M₂ (B1, lingual view; B2, buccal view; B3, occlusal view by SEM). (C) MPM-Fo2883, right mandible with M₁, M₂, and M₃ (C1, lingual view; C2, buccal view; C3, occlusal view by SEM).

anterior of P₂, and curves downward at the mental protuberance between the canine and P₂.

P₂ is relatively large, and has a diamond occlusal outline. The basal cingulum is prominent on both lingual and buccal sides, and shows a sharp V-letter in the buccal view. P₂ has a single root. P₃ is absent (no alveolus). P₄ develops sharply as a canine, and has a triangular occlusal outline. The basal cingulum of P₄ bends at a right angle along the cervical line. P₄ has two roots.

The lower molars have the W-shaped occlusal pattern: each trigonid and talonid basin shows an isosceles triangle outline. The trigonid is almost as wide as the talonid. The entoconid is isolated from the hypoconulid by a gap between the postcrisid and the entocristid. The oblique cristid, extending from the hypoconid, runs onto the half point between the protoconid and the metaconid. The hypoflexid is very deep. The basal cingulums are strong on the anterior, posterior and buccal sides, and it is unbroken by the hypoflexid. A lingual cingulum (or entocingulid) is indistinct or absent. There are two roots on each molar.

The tooth pattern of M₂ is basically the same as that of M₁. M₂ has an interfacet at the anterior of the prisingulid for connecting with the hypoconulid of M₁. The crown size of M₂ is larger than that of M₁. M₃ reduces its posterior part, or lacks its postero-lingual region. The hypoconid of M₃ is considerably smaller than that of M₁ or M₂.

Remarks: *Hipposideros turpis* is a relatively large microchiropteran species with the dental formula, 1.1.2.3/2.1.2.3. This species is characterized by the upper canine overhanging anteriorly, tiny P₃, strongly reduced M₃ and M₃, no P₃, and large P₄ with two roots (Abe 2000). Hirasawa et al. (2008) described a *Hipposideros* remain found from Miyako Island, with a detailed comparison with the other chiropterans. They mentioned some minor differences in lower cheek teeth between the Miyako form (*Hipposideros* sp.) and *H. turpis* living on Ishigaki Island: e.g., P₂ of the former expands more buccally than that of the latter. This difference supports the finding that the specimen, MPM-Fo 2832 (Fig. 8B), from Sabichi-do Cave is similar to *H. turpis* living on Ishigaki Island rather than the Miyako form described by Hirasawa et al. (2008).

Distribution: Ishigaki, Iriomote, Hateruma, and Yonaguni Islands (Sano 2009a).

***Rhinolophus perditus* Andersen, 1918** (Figs. 9 and 10A-C)

Family Rhinolophidae Gray, 1825
Genus *Rhinolophus* Lacepede, 1799

Material examined: A skull with C, P⁴, M¹, M², and M³ (MPM-Fo 2858); a left maxilla with P⁴ and M¹ (MPM-Fo 2859); a left P⁴ (MPM-Fo 2867); a left M¹ (MPM-Fo 2868); four right M¹ (MPM-Fo 2869-2872); two left M² (MPM-Fo 2873-2874); two right M² (MPM-Fo 2875-2876); a right M³ (MPM-Fo 2877); a left mandible with P₄, M₁, M₂, and M₃ (MPM-Fo 2879); a left mandible with P₄ (MPM-Fo 2878); a left mandible with M₁, M₂, and M₃ (MPM-Fo 2880); a left mandible with M₁ and M₂ (MPM-Fo 2881); a left mandible with M₂ (MPM-Fo 2882); a right mandible with C, P₂, P₃, P₄, M₁, M₂, and M₃ (MPM-Fo 2883); a right mandible with P₃, P₄, M₁, M₂, and M₃ (MPM-Fo 2884); a right mandible with P₄, M₁, M₂, and M₃ (MPM-Fo 2885); a left P₄ (MPM-Fo 2888); two right P₄ (MPM-Fo 2889-2890); six left M₁ or M₂ (MPM-Fo 2891-2896); a right M₁ or M₂ (MPM-Fo 2897).

Locality: Sabichi-do Cave, Ishigaki Island.

Measurements: See Tables 2 and 3.

Description: MPM-Fo 2858 is an anterior part of skull, and preserves the nasal bone, orbitals, frontal bone, and maxilla with teeth (Fig. 9). The skull is slender: the brain-case is antero-posteriorly long. The nasal bone at the nose-leaf region projects strongly upward, like a rhino-horn. The interval between left and right canines is broad. The frontal bone is narrow laterally and becomes depressed deeply (frontal depression) due to large and converging orbitals. The brain-case has a sharp sagittal crest, extending from the frontal depression to the posterior end. The zygomatic arches are thick dorso-ventrally, and curve as an S-letter in the lateral view. The infraorbital foramen is large, whereas a bridge over this foramen is very slender. The choana is broad laterally. The anterior end of the choana is situated as far as the metacone of M². There is a small notch at the center of the palatine. The premaxilla and incisors are broken.

The maxilla has a canine, two premolars (a small alveolus and a large tooth), and three molars in each side. The premolar alveolus behind the canine is small but distinct. The other premolar (P⁴) forms a quadrate occlusal outline. The paracone of P⁴ is sharp, and has a crista extending to the lingual side. The upper molars are similar basically with those of *Hipposideros turpis* described in

this study in terms of occlusal patterns. M^1 has a trapezoidal occlusal outline with a cingulum on the postero-lingual side, while M^2 has a triangular one because the postero-lingual cingulum is very weak. The posterior of M^3 is reduced but somewhat prominent relative to that of *H. turpis*. M^3 almost lacks the postero-lingual cingulum.

The mandibles, MPM-Fo 2880, 2883, and 2884, are well preserved (Fig. 10A-C). The mandibular body is slender and straight. The mental protuberance, with a straight symphysis, is prominently developed below the canine. The mental foramen is situated directly below P_2 . The ramus is dorso-ventrally low: the coronoid process reaches as high as the protoconid of M_1 . The tip of the coronoid process is rounded, approaching to M_3 . The angular process is robust and short.

The lower canine is very sharp and straight, and has a triangular occlusal outline. The crown is surrounded by the basal cingulum on the anterior and lateral surfaces. There are six postcanine teeth (three premolars and three molars). P_2 is unicuspidated, low-crowned, and with the basal cingulum. The occlusal outline shows an equilateral triangle shape. Very small P_3 is present on the buccal side. P_4 is pointed as a canine. The protoconid extends two sharp cristids to the posterior. The basal cingulum of P_4 bends as a V-letter line in the buccal view. The anterior point of P_4 is adjacent to the posterior of P_2 . Each P_2 and P_3 has a single root, and P_4 has two roots.

The occlusal structures of lower molars are similar to those of *Hipposideros turpis* represented by a W-shaped occlusal pattern. M_1 or M_2 has the

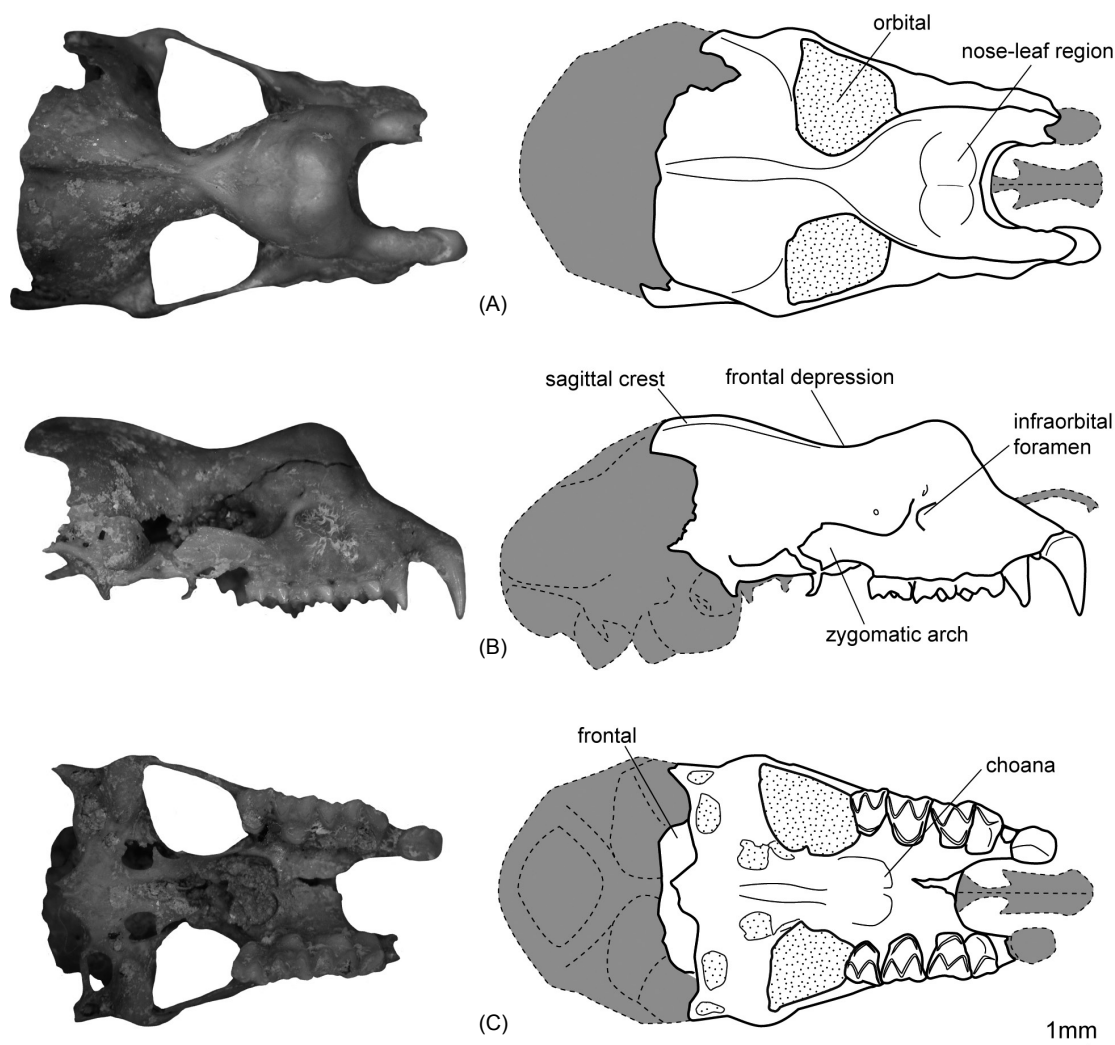


Fig. 9. *Rhinolophus perditus* (MPM-Fo 2858, skull) from Sabichi-do Cave with its schematic drawings and terminology. (A) ventral view; (B) lateral view; (C) dorsal view.

trigonid bucco-lingually narrower than the talonid. M_3 trigonid and talonid are almost the same in width. The basal cingulums are strong, except on the lingual side. M_1 is almost as large as M_2 , but the protoconid of the former is slightly higher than that of the latter. M_3 is smaller than M_1 or M_2 , but relatively less reduced than M_3 of *H. turpis*. Each molar has two roots.

Remarks: *Rhinolophus*, belonging to Rhinolophidae, is characterized by horseshoe-shaped nose (or nose-leaf), and this feature reflects to their nasal bones: *Rhinolophus* has a horn-like ridge on the nasal bone, as the skull (MPM-Fo 2858) referred in this study. The dental formula of *Rhinolophus* (1.1.2.3/2.1.3.3) is unique in having P_3 . The mandible of *Rhinolophus* is relatively slender and flat, with small processes on the ramus. These features distinguish *Rhinolophus* from the other genera of microchiropterans (Abe 2000).

There are three species of *Rhinolophus* (*R. cornutus*, *R. pumilus*, and *R. perditus*) in the Ryukyu area (or the south of Tokara Gap), and only *R. perditus* is distributed on Ishigaki Island at the present time. Morphological difference among these species have been discussed in previous studies (e.g., Yoshiyuki 1989; Abe 2000; Hirasawa et al. 2006), but their dental features are similar to one another. *Rhinolophus perditus* is usually larger than the other species in the maximum length of the skull, and has a relatively large upper premolar (P^3) behind the canine. The tooth row (from upper canine to M^3) of *R. perditus* is also larger than that of *R. cornutus* or *R. pumilus* (Yoshiyuki 1989). Based on these differences, all remains of *Rhinolophus* from Sabichi-do Cave are similar to *R. perditus* rather than *R. cornutus* and *R. pumilus*.

A possible extinct species of *Rhinolophus* was reported from Miyako Island. This species was originally described as *R. cornutus miyakonis* (Kuroda 1924), and later classified into a subspecies of *R. pumilus* (Yoshiyuki 1989) or an independent species on Miyako Island (Maeda 2001). Hirasawa et al. (2006) preliminarily discussed, based on paleontological analysis, that lower teeth of the *Rhinolophus* species on Miyako Island could not be distinguished from those of the other species. However, the dental morphology of the fossil specimens from Sabichi-do Cave fit exactly to that of living *R. perditus*, comparing with the recent remains collected from Ishigaki Island.

Distribution: Ishigaki, Iriomote, Kohama, and Taketomi Islands (Sano and Armstrong 2009).

***Pipistrellus cf. abramus* Temminck, 1840** (Fig. 10D)

Family Vespertilionidae Gray, 1821
Genus *Pipistrellus* Kaup, 1829

Material examined: A right mandible with C, M_1 , M_2 , and M_3 (MPM-Fo 2910).

Locality: Indeterminate layer, Umabana-zaki Fissure, Yonaguni Island.

Measurements: See Table 3.

Description: The mandible (MPM-Fo 2910) is smaller and deeper than that of *Rhinolophus*. The body is dorso-ventrally deep at the anterior relative to the posterior. The mental protuberance projects strongly toward the ventral side. A large mental foramen is situated below the canine. The ramus is deep dorso-ventrally, and has a large triangular-shaped fossa with distinct masseteric crests.

The mandible preserves a canine and three molars. There are three small root sockets for incisors at the anterior of the canine. Although all premolars are broken, three alveoli are present between the canine and M_1 . The first (anterior) alveolus forms a large socket, and is separated from the second alveolus. The second and third alveoli belong to a single premolar (P_4) because they are adjacent to each other. A tiny premolar represented by *Rhinolophus* species is absent. As a result, the mandible has a dental formula 3.1.2.3.

The lower canine forms as a claw and has an additional small cusp (a stylid) on the posterior side. The protoconid is moderately worn. The posterior stylid connects with the protoconid by a sharp cristid. The basal cingulum is sharp, as a V-letter line, in the buccal view. The tooth is anchored by a robust root.

The molars have the W-shaped occlusal pattern similar to those of *Hipposideros turpis* or of *Rhinolophus perditus*. The talonid basin is slightly larger than the trigonid basin. The hypoconid is prominent and approaches the buccal side. The entoconid is isolated from the hypoconulid by a gap. The hypoflexid is deep, forming a V-letter gap on the buccal side. The basal cingulum is strong on the anterior, buccal and posterior sides. The cingulum (entocingulid) on the lingual side is indistinct or absent. The crown size of M_2 is slightly larger than that of M_1 . M_3 is reduced relative to M_1 and M_2 . M_3 is characterized by the relatively small paraconid and wide hypoflexid. Each molar has two roots.

Remarks: *Pipistrellus abramus* has the lower dental formula, 3.1.2.3, without P_3 , but shares

many dental characteristics with the other genera of the Vespertilionidae (Yoshiyuki 1989). This family is one of great diversified bats in Japan, including 10 genera: *Myotis*, *Pipistrellus*, *Eptesicus*, *Nyctalus*, *Vespertilio*, *Barbastella*, *Plecotus*, *Miniopterus*, *Murina*, and *Tadarida*. Among these, *Myotis*, *Nyctalus*, *Vespertilio*, *Plecotus*, and *Miniopterus* are different from *Pipistrellus*, in having two or three premolars single-rooted (Abe 2000). The mandibular symphysis of *Pipistrellus* is short and straight (not drawing an arc). This feature distinguishes *Pipistrellus* from *Eptesicus*, *Barbastella*, *Murina*, and *Tadarida*, based on the illustrations of vespertilionid mandibles (Abe 2000). The mental foramen below the canine is

also diagnostic for *Pipistrellus abramus*, which is different from many other chiropterans (Abe 2000).

Pipistrellus abramus is currently distributed in East Asia, including Yonaguni Island (Kawai 2009). MPM-Fo 2910 is not different basically from *P. abramus* living in Japan, but the canine paraconid of the former is somewhat stronger than that of the latter. Some researchers consider that *P. abramus* in Japan is isolated from the continental species, *P. javanicus* (e.g., Yoshiyuki 1989; Volleth et al. 2001), but the difference between them is probably not clear at least in dental morphology.

Distribution: Southeast Asia, South Russia, Korea, China, Taiwan, and Japan (Honshu, Shikoku, Kyushu, Ryukyu Islands) (Kawai 2009).

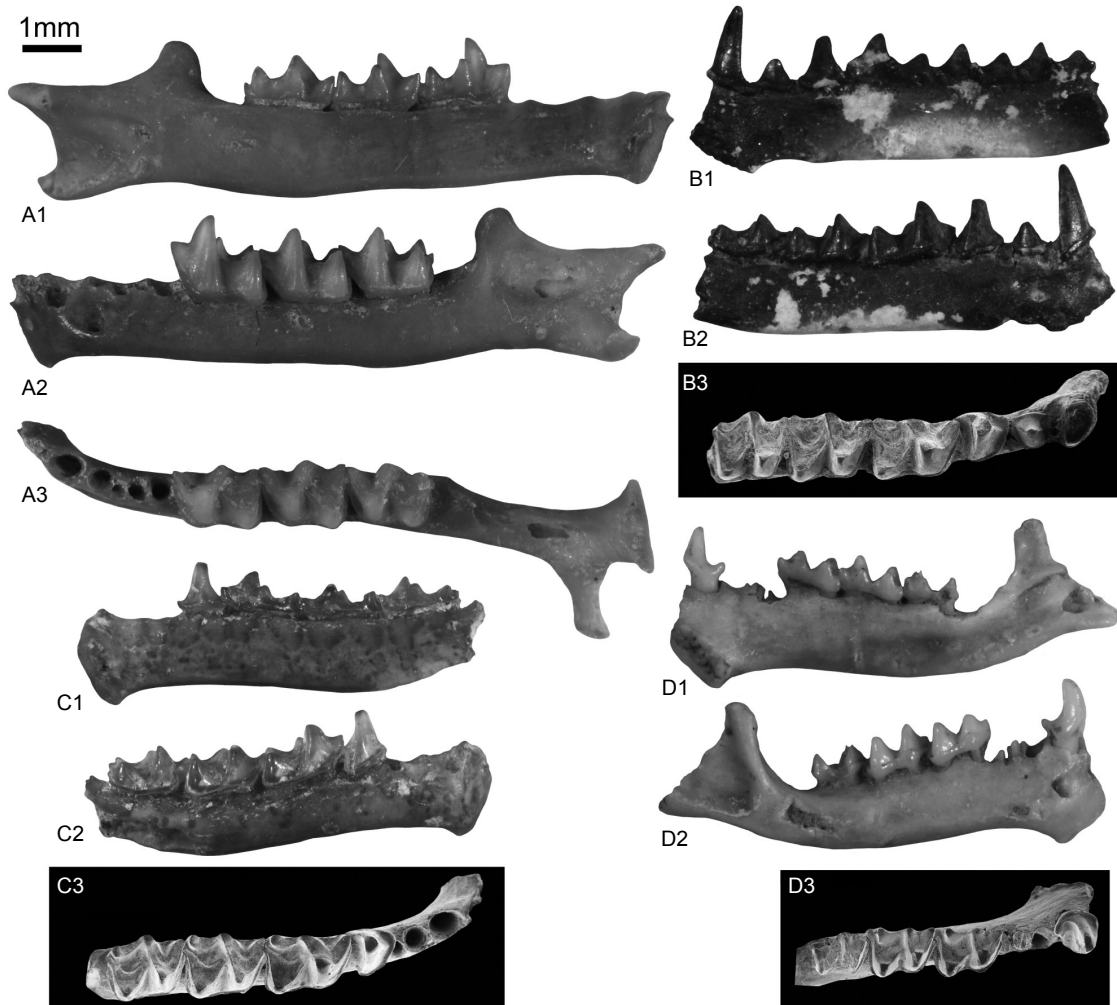


Fig. 10. *Rhinolophus perditus* (A–C) from Sabichi-do Cave and *Pipistrellus* cf. *abramus* (D) from Umabana-zaki Fissure. (A) MPM-Fo 2880, left mandible with M₁, M₂, and M₃ (A1, lingual view; A2, buccal view; A3, occlusal view). (B) MPM-Fo 2883, right mandible with C, P₂, P₃, P₄, M₁, M₂, and M₃ (B1, lingual view; B2, buccal view; B3, occlusal view by SEM). (C) MPM-Fo 2884, right mandible with P₄, M₁, M₂, and M₃ (C1, lingual view; C2, buccal view; C3, occlusal view by SEM). (D) MPM-Fo 2884, right mandible with C, M₁, M₂, and M₃ (D1, lingual view; D2, buccal view; D3, occlusal view by SEM).

***Niviventer* sp. indet.**
(Figs. 11A, C-J and 12)

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Genus *Niviventer* Marshall, 1976

Material examined: A left maxilla (MPM-Fo 2913); three left M¹ (MPM-Fo 2915-2917); two left M² (MPM-Fo 2918-2919); a right M² (MPM-Fo 2920); a left M³ (MPM-Fo 2921); a right mandible with M₁ and M₂ (MPM-Fo 2922); six left M₁ (MPM-Fo 2902, 2923-2927); four right M₁ (MPM-Fo 2928-2931); a left M₂ (MPM-Fo 2911); a right M₂ (MPM-Fo 2912); two left M₃ (MPM-Fo 2932-2933); a right M₃ (MPM-Fo 2934).

Locality: Sabichi Fissure, Ishigaki Island; Layers 5-6 and indeterminate layer of Umabana-zaki Fissure, Yonaguni Island.

Measurements: See Tables 4 and 5.

Description: The crown of M¹ is higher than the radical part, in MPM-Fo 2915 and 2916. MPM-Fo 2917 preserves only a crown part due to being young or broken, but is as high as the other specimens of M¹. The occlusal surface has a slender, oval-shaped outline, and comprises three transverse laminae. The anterior lamina forms an asymmetric chevron, because the labial anterocone is more reduced than the anterostyle. The anterostyle shows a circle without a posterior spur. The labial anterocone also lacks a posterior

Table 4. Upper molar measurements (in mm) of the rodent remains from Ishigaki and Yonaguni Islands

	M ¹ L	M ¹ W	M ² L	M ² W	M ³ L	M ³ W
<i>Niviventer</i> sp.						
MPM-Fo 2902	2.92	1.76	-	-	-	-
MPM-Fo 2915	3.40	1.88	-	-	-	-
MPM-Fo 2916	3.47	2.15	-	-	-	-
MPM-Fo 2917	3.32	2.14	-	-	-	-
MPM-Fo 2919	-	-	3.34	1.93	-	-
MPM-Fo 2920	-	-	2.62	2.18	-	-
MPM-Fo 2921	-	-	-	-	1.59	1.67
<i>Mus musculus</i>						
MPM-Fo 2935	1.59	1.11	0.93	0.90	-	-

Table 5. Lower molar measurements (in mm) of the rodent remains from Ishigaki and Yonaguni Islands

	M ₁ L	M ₁ W	M ₂ L	M ₂ W	M ₃ L	M ₃ W
<i>Niviventer</i> sp.						
MPM-Fo 2922	3.44	1.77	2.36	1.89	-	-
MPM-Fo 2923	3.18	1.93	-	-	-	-
MPM-Fo 2924	3.29	1.88	-	-	-	-
MPM-Fo 2926	3.10	1.94	-	-	-	-
MPM-Fo 2928	3.34	1.93	-	-	-	-
MPM-Fo 2929	2.91	1.84	-	-	-	-
MPM-Fo 2930	2.99	1.86	-	-	-	-
MPM-Fo 2931	3.05	1.88	-	-	-	-
MPM-Fo 2927	3.27	1.93	-	-	-	-
MPM-Fo 2925	-	1.86	-	-	-	-
MPM-Fo 2911	-	-	2.44	2.18	-	-
MPM-Fo 2912	-	-	2.33	2.10	-	-
MPM-Fo 2932	-	-	-	-	1.94	1.68
MPM-Fo 2933	-	-	-	-	1.71	1.59
MPM-Fo 2934	-	-	-	-	1.61	1.63

spur. The middle lamina is similar to the anterior lamina, but is symmetrical. The occlusal outline is slender (bucco-lingually narrow) because the middle lamina bends at a right or acute

angle. There is no spur on the enterostyle and paracone of the middle lamina. The posterior lamina is simple, comprising large hypocone and small metacone. Either posterostyle or posterior

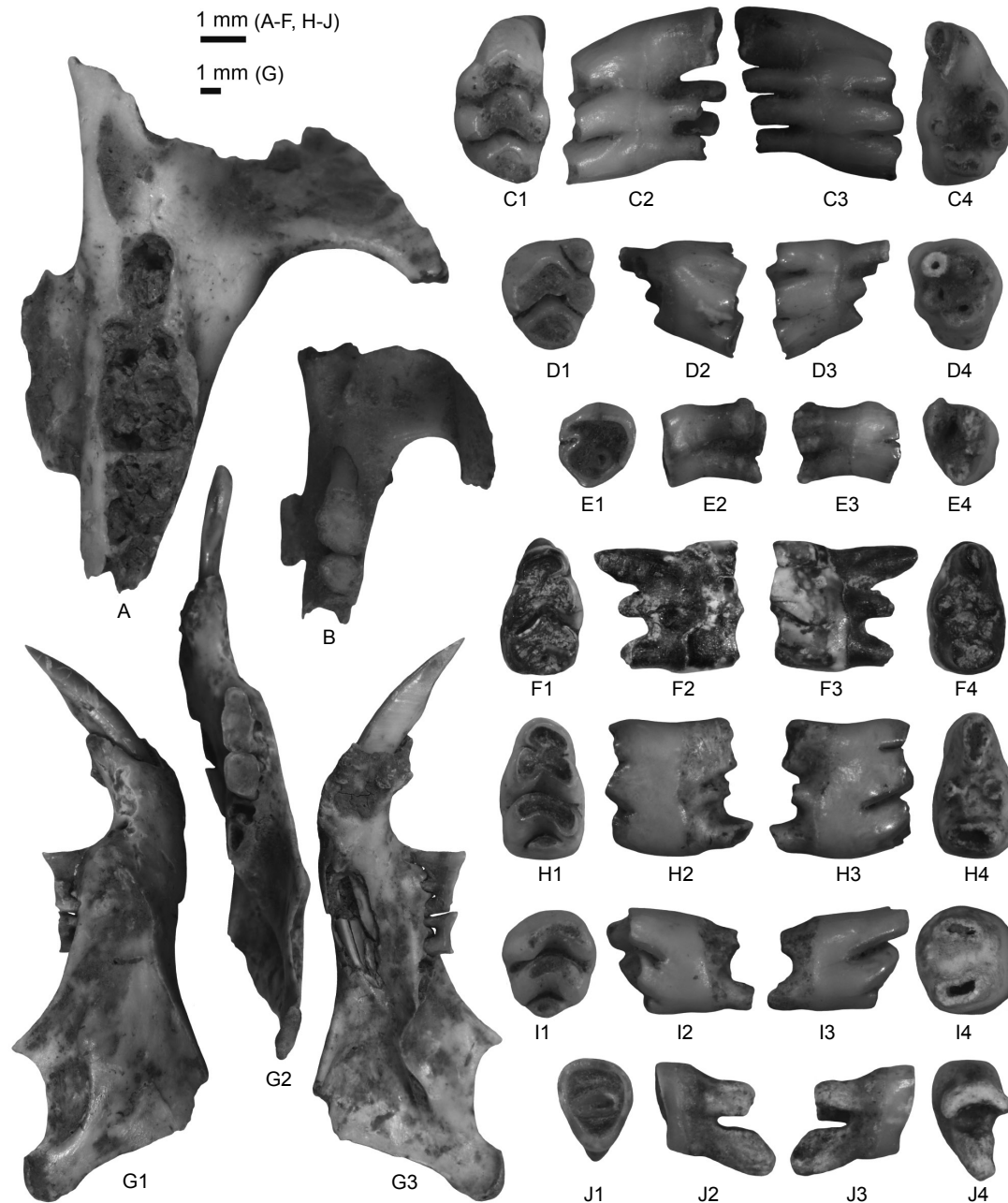


Fig. 11. *Niviventer* sp. (A, C-J) and *Mus musculus* (B) from Umabana-zaki Fissure and Sabichi Fissure. (A) MPM-Fo 2913, left maxilla, occlusal view. (B) MPM-Fo 2935, left maxilla with M¹ and M², occlusal view. (C) MPM-Fo 2916, left M¹ (C1, occlusal view; C2, buccal view; C3, lingual view; C4, radical view). (D) MPM-Fo 2920, right M² (D1, occlusal view; D2, buccal view; D3, lingual view; D4, radical view). (E) MPM-Fo 2921, left M³ (E1, occlusal view; E2, buccal view; E3, lingual view; E4, radical view). (F) MPM-Fo 2902, left M¹ (F1, occlusal view; F2, buccal view; F3, lingual view; F4, radical view). (G) MPM-Fo 2916, right mandible with M₁ and M₂ (G1, buccal view; G2, occlusal view; G3, lingual view). (H) MPM-Fo 2929, right M₁ (H1, occlusal view; H2, buccal view; H3, lingual view; H4, radical view). (I) MPM-Fo 2912, right M₂ (I1, occlusal view; I2, buccal view; I3, lingual view; I4, radical view). (J) MPM-Fo 2932, left M₃ (J1, occlusal view; J2, buccal view; J3, lingual view; J4, radical view).

cingulum is absent. The hypocone expands antero-posteriorly, as a rounded diamond shape. The metacone is very small, and separated from the paracone by a gap. The number of roots is five: large anterior root, large posterior root, small buccal root, and two small lingual roots.

The crown of M^2 (MPM-Fo 2920) is as high as the longest root of the tooth. It has a rounded triangular outline in the occlusal view. The occlusal pattern is simple, without any additional spurs or cusps. The labial anterocone is always absent. The anterostyle is well-developed, with a circular or semi-circular outline. The anterostyle is isolated from the first lamina, even at a strong wear stage. The first lamina of M^2 is similar to the middle lamina of M^1 . The joint between the enterostyle and the protocone is clearly constricted. Each enterostyle and paracone of MPM-Fo 2919 connects with the posterior lamina, or the hypocone, due to wear. The hypocone forms a circular shape, without either posterostyle or posterior cingulum. The number of roots is basically four.

The occlusal surface of M^3 (MPM-Fo 2921) is strongly worn, showing an inverted triangular outline. There is a weak sinus between the anterostyle and the enterostyle. The enterostyle, paracone, and hypocone are fused to one another, and form an isolated fold on the postero-buccal part. There are three roots.

The crown of M_1 is comparatively high even at a strong wear point. The occlusal surface, with a rounded rectangular outline, comprises three laminae and a posterior cingulum. The anterior

lamina is composed of two cusps, i.e. the labial anteroconid and the lingual anteroconid. The anterior lamina shows a semicircular shape in the occlusal view, owing to strong wear. The lingual anteroconid is slightly larger than the labial anteroconid. The middle lamina forms a chevron shape by the protoconid and the metaconid, and connects to the anterior lamina at the center. The protoconid is as large as the metaconid. The posterior lamina is also chevron-shaped, comprising the hypoconid and the entoconid. This lamina has a mesial mure between the cusps. MPM-Fo 2902 has a cingulum at the buccal corner of the hypoconid, instead of the accessory cusps. MPM-Fo 2928 has neither accessory cusp nor cingulum on the occlusal surface. The posterior cingulum is large, isolated, and elongated bucco-lingually. There are four roots: the anterior and posterior roots are large, and the buccal and lingual roots are small.

The crown of M_2 is considerably higher, relative to its radical part. The occlusal surface shows a rounded quadrilateral outline, and comprises two chevron-shaped laminae and a posterior cingulum. The labial anteroconid is vestigial or absent at an early wear stage. The anterior chevron comprises the protoconid and the metaconid: the former is larger than the latter. The protoconid almost connects to the labial anteroconid. The posterior chevron is isolated from the first chevron and the posterior cingulum by deep gaps. The hypoconid is slightly larger than the entoconid. There is a weak cingulum on the

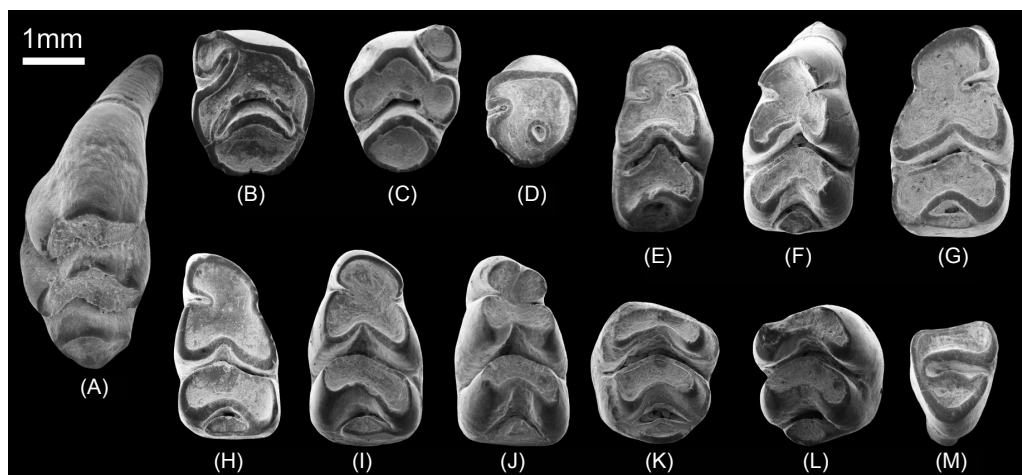


Fig. 12. SEM images of the molar occlusal surfaces of *Niviventer* sp. from Umabana-zaki Fissure and Sabichi Fissure. (A) MPM-Fo 2916, left M^1 ; (B) MPM-Fo 2919, left M^2 ; (C) MPM-Fo 2920, right M^2 ; (D) MPM-Fo 2921, left M^3 ; (E) MPM-Fo 2902, left M_1 ; (F) MPM-Fo 2923, left M_1 ; (G) MPM-Fo 2924, left M_1 ; (H) MPM-Fo 2928, right M_1 ; (I) MPM-Fo 2929, right M_1 ; (J) MPM-Fo 2930, right M_1 ; (K) MPM-Fo 2911, left M_2 ; (L) MPM-Fo 2912, right M_2 ; (M) MPM-Fo 2934, right M_3 .

buccal side of the hypoconid of MPM-Fo 2911, but any accessory cusps are absent in all specimens. The posterior cingulum shows a diamond shape in the occlusal view. There are two large roots.

The occlusal surface of M_3 shows an inverted triangular shape, elongated antero-posteriorly. The enamel pattern is composed of two transverse laminae. The labial anteroconid and any accessory cusps are absent. There are two roots: the anterior root is elongated transversely, drawing an arc, and the posterior root is well-developed antero-posteriorly.

Remarks: Rodents on Ishigaki and Yonaguni Islands are currently composed only of cosmopolitan (domestic) species, such as *Rattus rattus*, *R. norvegicus*, and *Mus musculus* (Motokawa 2000). The referred specimens belong to a medium-sized rat, and are characterized by slender outline, chevron-shaped laminae without spurs, small labial anterocone on M^2 , five roots on M^1 , and four roots on M_1 . These characteristics are usually represented by common rats, such as *R. rattus* and *R. norvegicus* (Musser 1981). However, most of the molars are higher than those of *Rattus*, therefore, the form from Sabichido Cave and Umabana-zaki Fissure is different from both *R. rattus* and *R. norvegicus* occurring on Ishigaki and Yonaguni Islands. The Late Pleistocene sediments on Miyako Island recovered extinct murids, *Rattus miyakoensis* (Kawaguchi et al. 2009) or *Diplothrix* sp. (Nakagawa et al. 2012). This species resembles *Diplothrix legata* currently occurring on Amami, Tokunoshima, and Okinawa Islands (Hasegawa 1985; Iwasa 2009b), but they are clearly larger than the specimens examined in this study.

More than 30 species of rats and mice live in the Indomalayan Region (Corbet and Hill 1992), and some of them share tooth characters with *Rattus*. Chaimanee (1998) indicated that *Rattus* was phylogenetically close to *Maxomys*, *Berylmys*, *Bandicota*, *Niviventer*, and *Leopoldamys*, based on molar morphology. Furthermore, Zheng (1993) reported some extinct genera of rats from the Pleistocene of Central China, such as *Qianomys* and *Wushanomys*. Among these murids, the pattern of M_2 is the best similar to white-bellied rats, *Niviventer*, rather than the other genera in having no labial anteroconid, no buccal accessory cusp, and a single anterior root (Musser 1981; Zheng 1993).

Musser (1981) listed tooth diagnosis of *Niviventer* as follow: (1) four roots beneath M_1 in all species; (2) lamina shaped like a chevron on

M^2 ; (3) lower molars simple; (4) anterolabial cusp (labial anteroconid in this paper) on M_2 usually absent; (5) anterior lamina on M_1 composed of two small cusps, usually connecting to each other and forming an oblong or triangular lamina that is much narrower than the middle lamina. All of these features are observed in the specimens described in this study. Moreover, his comparisons indicated that the combination of slender outline and asymmetrical first lamina of M_1 always distinguish between *Niviventer* and *Rattus*.

Niviventer is one well-diversified genus in Asia, and includes 18 extant species and one extinct species: *N. andersoni*, *N. brahma*, *N. cameroni*, *N. confucianus*, *N. coning*, *N. cremoriventer*, *N. culturatus*, *N. eha*, *N. excelsior*, *N. fratemus*, *N. fulvescens*, *N. hinpoon*, *N. langbinis*, *N. lepturus*, *N. lotipes*, *N. niviventer*, *N. preconfucianus*, *N. rapit*, and *N. tenaster* (Musser 1981; Zheng 1993; Musser and Carleton 2005). According to these studies, all *Niviventer* species have small differences on upper molars, comparing with the fossil form from Umabana-zaki Fissure: *N. andersoni* and *N. brahma* have a distinct labial anterocone; *N. eha* has a posterior spur with the hypocone; *N. excelsior* and *N. fulvescens* have a prominent lingual anterocone; *N. confucianus* and *N. hinpoon* have the enterostyle extending posteriorly; *N. coninga* and *N. culturatus* have the protocone extending anteriorly and the enterostyle and paracone extending posteriorly; *N. preconfucianus*, which was found from the Pleistocene of China (Zheng 1993), is similar in shape but smaller.

Niviventer is not currently distributed in Japan, including the Ryukyu Islands, but the referred specimens share many molar characteristics with *Niviventer* rather than with *Rattus*. In recent years, the Late Pleistocene and Holocene deposits on Ishigaki Island (Shiraho-Saonetabaru cave site) yielded a great deal of rodent remains, and most of these were also classified into a species of *Niviventer* (Kawamura and Kawamura 2013). This form is conspecific basically with the specimens described in this study.

***Mus musculus* Linnaeus, 1758**

(Fig. 11B)

Genus *Mus* Linnaeus, 1758

Material examined: A left maxilla with M^1 and M^2 (MPM-Fo 2935).

Locality: Indeterminate layer, Umabana-zaki

Fissure, Yonaguni Island.

Measurement: See Tables 4 and 5.

Description: The maxilla (MPM-Fo 2935) preserves M¹ and M². The teeth are strongly worn. The size is very small, like of a mouse. The posterior end of the incisive foramen reaches as far as the center of M¹ in the occlusal view. There is a small masseteric knob under the zygomatic plate. Enamel structures of the teeth almost disappear due to wearing. The anterostyle on the anterior lamina of M¹ shifts posteriorly, and approaches the enterostyle on the middle lamina. The posterostyle or posterior cingulum is absent on M¹. M¹ has three roots, and M² has at least two roots.

Remarks: *Mus musculus* is a small-sized murid, with three roots on M¹, and this character distinguishes the species from other extant Ryukyu murids all representing distinctly larger-bodied genera, such as *Rattus*, *Tokudaia*, and *Diplothrix*. *Apodemus* and *Micromys* are common in mainland Japan (Honshu, Shikoku, and Kyushu), but they are different from MPM-Fo 2935 in having well-developed posterostyle on M¹. Another species of *Mus*, *M. caroli*, is known in the Ryukyu area (Motokawa 2000), but this species usually lacks the masseteric knob that is occurred in living *M. musculus* and MPM-Fo 2935.

Distribution: Cosmopolitan (Iwasa 2009a).

DISCUSSION

Two specimens analyzed for ¹⁴C dating in this study indicated the late Holocene age, strictly after historic times. The past mammalian fauna in Honshu or Kyushu is always represented by extant species since the Holocene (Kawamura 1998, 2014). However, extinct *Niviventer* had been dominant on Ishigaki Island until later Holocene (¹⁴C dates: ca. 2–4 ka), based on the fossil record from Shiraho-Saonetabaru cave site (Kawamura and Kawamura 2013).

The ages for the fossil assemblages from Sabichi Fissure (230 ± 20 yBP) and Umabana-zaki Fissure (1,760 ± 20 yBP) were supported by a sufficient yield of collagen (12.5% and 3.17% for each sample). However, these dates may be only advisory because they are too young for the occurrence time of an extinct species of *Niviventer* which is discussed by Kawamura and Kawamura (2013). In any case, the present discovery indicates that the Yaeyama Islands (at least Ishigaki and Yonaguni Islands) had a peculiar fauna that was different from Miyako Island, owing

to the occurrence of *Niviventer* and to the absence of Miyako species (*Microtis fortis* or *Diplothrix* sp.).

The appearance of *Niviventer* may indicate the faunal correlation between the Yaeyama Islands and the Eurasian continent because the latter displays the original distribution of extant and extinct *Niviventer* species (Corbet and Hill 1992; Zheng 1993). However, the form from Ishigaki and Yonaguni Islands is probably different from all known species of *Niviventer*, as found in this study. Kawamura and Kawamura (2013) mentioned that Ishigaki Island has formed an island-type fauna, including a peculiar form of *Niviventer*, since Marine oxygen Isotope Stage (MIS) II of the Quaternary. Yonaguni Island is also regarded as having the same condition as Ishigaki Island, based on the fossil assemblage from Umabana-zaki Fissure. Therefore, there was no faunal correlation (migration) between the Yaeyama Islands and Miyako Island or the Eurasian continent since the Late Pleistocene.

Currently, non-volant mammals on Yonaguni Island are represented only by cosmopolitan or domestic animals. These species usually inhabit houses or farms; therefore, human activities (e.g., ship transportation) have likely influenced their dispersion after the historical age. However, the fossil assemblage from Umabana-zaki Fissure basically includes extinct species, *Niviventer* sp., and lacks domestic rats, such as *Rattus rattus* and *R. norvegicus*. In case of the fossil assemblage from Shiraho-Saonetabaru cave site, *Rattus* sp. appeared after ca. 2 ka (¹⁴C date) with the disappearance of *Niviventer* sp. (Kawamura and Kawamura 2013). If *Rattus* sp. was introduced into the Yaeyama Islands around this age, *Niviventer* sp. from Umabana-zaki Fissure was likely the last population that survived on Yonaguni Island. On the other hand, the much younger age of the fossil assemblage from Sabichi Fissure probably causes the rare frequency of *Niviventer* sp., although the estimated age is preliminary at present.

Umabana-zaki Fissure yielded two cosmopolitan species, *Mus musculus* and *Pipistrellus* cf. *abramus*, which are distributed widely in Asia at the present time (Iwasa 2009a; Kawai 2009). If these species originate from the same horizon as that of *Niviventer* sp., they have been native on Yonaguni Island since ca. AD 300, in the middle of the Okinawa Midden Culture. *Suncus murinus*, distributed originally in the Indomalaya region, is also considered to have spread alongside modern human beings. In Japan, populations on the Ryukyu Islands have naturally

dispersed from the Asian continent, while those in Kyushu were introduced by humans (Motokawa 2007). The remains of *Suncus murinus* were not found from Umabana-zaki Fissure but found from the modern age of Sabichi Fissure. A few specimens of *Suncus* cf. *murinus* or *Suncus* sp. have been found from the Late Pleistocene and Holocene deposits on Ishigaki and Miyako Island (Nakagawa et al. 2012; Kawamura and Kawamura 2013), but further examination based on additional specimens are needed for concrete fossil evidence on the dispersion time of this species.

CONCLUSIONS

The late Holocene small mammal faunas on Ishigaki and Yonaguni Islands are similar to each other, but they are completely different from the Late Pleistocene or Holocene fauna on Miyako Island and the Eurasian continent (including Taiwan). These island-type faunas probably occurred on the Yaeyama Islands before the Late Pleistocene due to the isolation of these islands from the other areas. The Late Pleistocene and Holocene rodents on Ishigaki and Yonaguni Islands are represented by *Niviventer* sp. with a different form from living species in Eurasia. This rodent likely survived until the late Holocene on both Ishigaki and Yonaguni Islands.

List of abbreviations

L, length of crown; W, width of crown; Wa, anterior width of crown; Wp, posterior width of crown.

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