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Author(s)	Dokuchaev, Nikolai E.; Kohno, Naoki; Ohdachi, Satoshi D.
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Reexamination of fossil shrews (*Sorex* spp.) from the Middle Pleistocene of Honshu Island, Japan

Nikolai E. Dokuchaev¹, Naoki Kohno² and Satoshi D. Ohdachi^{3,*}

¹ Institute of Biological Problems of the North, FEB RAS, Magadan, Russia

² National Museum of Nature and Science, Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan

³ Institute of Low Temperature Science, Hokkaido University, Sapporo 060-0819, Japan

Abstract. Taxonomic status of fossil *Sorex* shrew specimens from the late Middle Pleistocene of Honshu Island was addressed. Multivariate analyses of upper and lower jaws were conducted for the fossil specimens as well as for 8 species of Recent *Sorex* shrews from Japan and adjacent regions. It was confirmed that *S. shinto* and *S. hosonoi* already inhabited Honshu Island in the late Middle Pleistocene. Most fossil specimens previously referred to *S. minutissimus* and *S. gracillimus* in Honshu should be regarded as *S. hosonoi*, although some specimens could not be completely distinguished from *S. gracillimus*. Thus, the appearance of *S. hosonoi* ascends, at least, to the late Middle Pleistocene during which time they were more broadly distributed, including northern Honshu, than at present (only in central Honshu). Most middle size fossils should be regarded as *S. shinto*, but at least one specimen was identified as *S. caecutiens*. It was also demonstrated that other species of *Sorex* shrews larger than *S. shinto* and *S. hosonoi* were present during the Middle Pleistocene of Japan. Most of the large fossils were considered to be *S. isodon*, which had not been recorded from and is now absent in the Japanese Islands. In addition, there was one specimen of another large species, *S. unguiculatus*, in Honshu during the Middle Pleistocene, which now is absent in Honshu.

Key words: fossil, Honshu, morphometry, Pleistocene, *Sorex*.

Two endemic red-toothed shrews, *Sorex shinto* Thomas, 1907 and *S. hosonoi* Imaizumi, 1954, currently inhabit Honshu Island, and *S. shinto* occurs also on Shikoku and Sado islands (Abe 1994; Ohdachi et al. 2001, 2009). *Sorex shinto* and *S. hosonoi* are sister taxa of *S. caecutiens* Laxmann, 1788 and *S. minutissimus* Zimmermann, 1780, respectively (Ohdachi et al. 2001, 2006). Both of the latter two species are distributed in the Eurasian Continent, the Korean Peninsula, Sakhalin (= Karafuto) and Hokkaido, but not in southern Japanese islands including Honshu (Ohdachi et al. 2001, 2003, 2009).

Fossil *Sorex shinto* (or *S. cf. shinto*) is recorded from the Pleistocene of Honshu, Shikoku, and Kyushu (Kawamura and Sotsuka 1984; Kamei et al. 1988; Kawamura et al. 1989). *Sorex minutissimus* (or *S. cf. minutissimus*) is reported from the Pleistocene of Honshu (Hasegawa 1966; Rzebik-Kowalska and Hasegawa 1976). In “Catalogue of small mammal fossil specimens

at the National Science Museum, Tokyo”, many specimens of *Sorex* are listed from the Pleistocene of Honshu Island, and most are identified as *S. shinto* and only one as *S. minutissimus* (Tomida and Sakura 1991). In addition, a specimen that was referred to *S. gracillimus* Thomas, 1907, which is not distributed in Honshu, was reported from northernmost Honshu by Ohdachi et al. (1997) and Ohdachi (1999), based on personal communication with Naoki Kohno. This specimen tentatively is stored at the Iida City Museum (ICM).

These fossil specimens, however, are mostly fragmented; therefore, careful comparisons between extant and fossil specimens are needed to identify fossil species more exactly. A preliminary observation of these fossil specimens indicated the presence of three size groups. Therefore, a reexamination of these fossil specimens is necessary to determine the past distribution of *Sorex* shrews in Japan.

*To whom correspondence should be addressed. E-mail: ohd@pop.lowtem.hokudai.ac.jp

Fossil records play an important role in determining biogeographic history; thus, precise identification of fossils is essential. Dobson (1994) and Dobson and Kawamura (1998) discussed the history of the Japanese mammalian fauna including *Sorex* shrews, mainly based on fossil records. Nesterenko et al. (2002) examined the faunal history of *Sorex* shrews in Primorski territory of Far East of Russia, near the Japanese Islands. In addition, Ohdachi et al. (1997) hypothesized a biogeographical history of the Japanese *Sorex* community, mainly based on molecular phylogeny. However, these hypotheses might have led to the wrong conclusions because identifications of some fossil specimens might be in error.

Herein, we reexamine fossil specimens of *Sorex* at the National Museum of Nature and Science (NMNS) in Tokyo (formerly, the National Science Museum, Tokyo) and other specimens by multivariate analyses, comparing them with 8 Recent species of *Sorex* from Japan and adjacent regions. Finally, we propose a new hypothesis of the *Sorex* fauna in Honshu in the Middle Pleistocene.

Materials and methods

Samples

Ninety-one fossil samples of *Sorex* shrews from the Pleistocene of Honshu Island were examined. Among them, 83 samples were mandibles and 8 were the anterior part of crania. Due to the incompleteness of some specimens, 87 specimens were used for statistical analyses (Appendices 1 and 2). All specimens except for YH-13564 were those of NMNS collections; YH-13564 tentatively is stored at Iida City Museum (Nagano Prefecture, Japan). See Tomida and Sakura (1991) for detailed information of individual specimens at the National Museum of Nature and Science (NMNS). Specimen YH-13564, from northernmost Honshu, is a fossil which was suspected to be *S. gracillimus* in Ohdachi et al. (1997) and Ohdachi (1999). The localities of the fossil shrews from the late Middle Pleistocene deposits on Honshu Island are shown in Fig. 1.

Twelve Recent soricine shrew species inhabit Honshu and Hokkaido islands and neighboring regions: *S. shinto*, *S. hosonoi*, *S. caecutiens*, *S. isodon* Turov 1924, *S. unguiculatus* Dobson, 1890, *S. gracillimus*, *S. minutissimus*, *S. mirabilis* Ognev, 1937, *S. daphaenodon* Thomas, 1907, *S. tundrensis* Merriam, 1900, *S. roboratus* Hollister, 1913, and *Neomys fodiens* (Pennant, 1771) (Nesterenko 1999; Ohdachi 1999). Recently, *S. shinto* occurs in Honshu, Shikoku, and Sado Island, and *S. hosonoi* inhab-

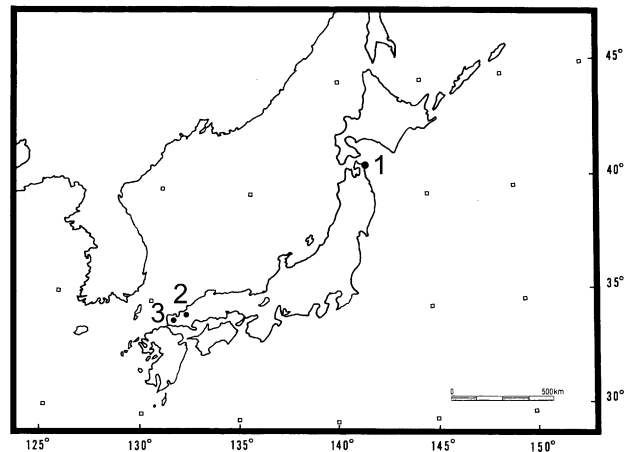


Fig. 1. Localities of fossil *Sorex* shrew deposits on Honshu Island, Japan. 1, Shiriyu Quarry, Aomori Prefecture; 2, Ikumo Quarry, Yamaguchi Prefecture; 3, Ando Quarry, Yamaguchi Prefecture. Refer to geologic descriptions in text for explanation of each locality.

its only central Honshu. *Sorex unguiculatus*, *S. gracillimus*, and *S. minutissimus* occur in Hokkaido, Sakhalin, and the continent. *Sorex isodon*, *S. daphaenodon* and *Neomys fodiens* occur in Sakhalin and the continent. *Sorex mirabilis*, *S. tundrensis*, and *S. roboratus* are found only in the continent. However, because of unambiguous differences in cranial and dental morphology, *S. daphaenodon*, *S. tundrensis*, *S. roboratus*, and *N. fodiens* were examined only in the preliminary investigation and omitted in the present analyses. Specimens of Recent species of *Sorex* shrews, included in analyses are housed in the Natural History Museum at Botanic Garden of Hokkaido University (Sapporo, Japan), Institute of Biological Problems of the North (Magadan, Russia), and Siberian Zoological Museum (Novosibirsk, Russia). Samples of the Recent species were from Honshu, Shikoku, Hokkaido (Japan), Korea, and Siberia (Russia).

For the multivariate analyses, fossil specimens were divided into five groups depending on damage condition. The first group of samples included mandibles (lower jaws) with at least one tooth and the coronoid process. The second group had complete mandibles without teeth but with the coronoid process. The third group was composed of those with fragmented mandibles without a coronoid process but at least with one tooth. For the fourth group of mandibles, only character #1 (Fig. 2: thickness of a branch of the mandibles just after M_3) could be measured. The last group consisted of samples of the anterior part of skull.

Geologic settings

Locality 1: Shiriya Quarry. The Shiriya Quarry of Nittetsu Mining Corporation, which has been operating since 1957, is located near the promontory of Shiriya-zaki, Higashidori-mura, Aomori Prefecture, northernmost Honshu. Vertebrate fossils were found in the sediment composed of limestone breccia and yellowish coarse-grained marine sand that cover a tidal notch cut on the Mesozoic limestone at a northeastern slope on a previous quarry face at about 80 m high above sea level. It is equal to the level of the Third Coastal Terrace (Ohya and Ichinose 1957) around Shimokita Peninsula. The well-established correlation between the sea level of coastal terraces and geologic ages in this area suggests that the fossil bearing sediment was deposited in the late Middle Pleistocene (Miyachi 1985) and Oxygen Isotope Stage 7 (MIS 7; warm period). Hasegawa et al. (1988) provided brief accounts of the fossil bearing sediments and an annotated list of fossil vertebrates from this locality.

Locality 2: Ikumo Quarry (formerly Okamura Limestone Quarry). The Ikumo quarry, operated from 1926 to 1965, is located at the eastern slope of Mt. Kiwata-yama in Ikumo-naka, Ato-cho, Yamaguchi Prefecture, southwestern Honshu. Vertebrate fossils were found from fissure-fill sediments exposed on a restricted surface of the quarry (Hasegawa, 1966). These sediments were described briefly by Kawano and Takahasi (1966), and its geologic age was estimated to be late Middle Pleistocene based on U-series dating (ca. $184,000 \pm 13,000$ yr BP) and fluorine content (1.06%) of the fossil bones from the quarry (Kawamura, 1988). Hasegawa (1966) and Kawamura (1988) provided lists of fossil mammals from the quarry and discussed the characteristics of the mammalian assemblage.

Locality 3: Ando Quarry. The Ando Quarry, operated since 1947, is located at the western corner on the Nishi-Akiyoshidai Karst Plateau in Midorigaoka, Ofuku-shi, Yamaguchi Prefecture, southwestern Honshu. According to Hasegawa (1966), the vertebrate fossils were found from the sediments covering *Karren Feld* in the quarry. Hasegawa (1966) interpreted the sediments as collapsed cave fill, but the detailed stratigraphy including the fossil bearing sediment is unknown. Hasegawa (1966) also provided a list of fossil mammals from the quarry and considered its geologic age to be Middle Pleistocene based on characteristics of the mammalian assemblage. Kawamura (1988) also reported the fluorine content (ca. 1.04%) of the bones from the Quarry as well as the mammalian assemblage, which were very

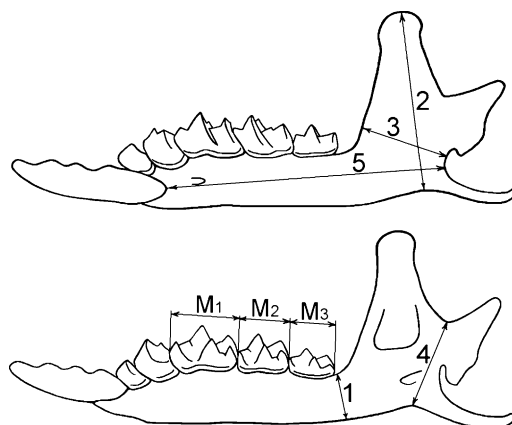


Fig. 2. Definitions of measurements for a mandible of *Sorex*.

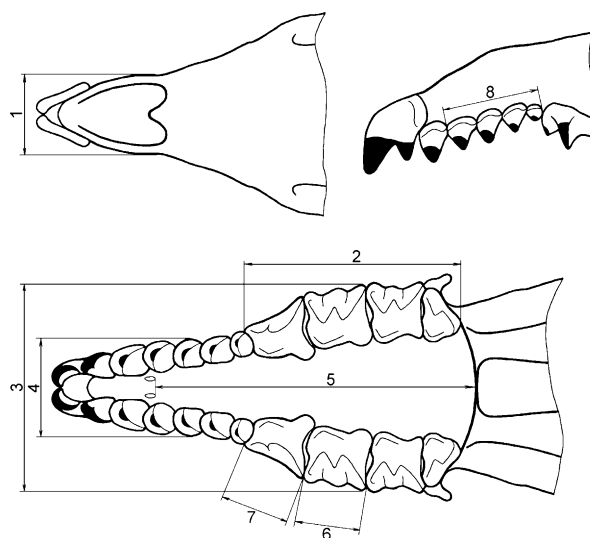


Fig. 3. Definitions of measurements for the anterior part of a skull of *Sorex*.

similar to those from Ikumo Quarry. Therefore, the fossil bearing sediments in the Ando Quarry could have been roughly contemporaneous with that of the Ikumo Quarry; i.e., the late Middle Pleistocene (Hasegawa 1966; Kawamura 1988).

Measurements

Skulls, mandibles and tooth characters from Recent and fossil *Sorex* shrews were measured to the nearest 0.01 mm with an ocular micrometer mounted in a binocular microscope (Figs. 2 and 3). For one fossil mandible (YH-13564), measurements were recorded from photographs.

When some characters could not be measured due to destruction of specimens, missing measurements were estimated using a well-established statistical method

(Sokal and Rohlf 1973). To estimate the missing measurements of fossil specimens, a simple regression analysis was conducted using the maximum correlation coefficients from samples of Recent species. The adequacy of this estimation of missing values was evaluated for some measurements of Recent specimens, by use of the same regression equation as follows. Three mandibular measurements, #2, #5 and M_1 (Fig. 2) of Recent *S. shinto* ($n = 25$) and *S. caecutiens* ($n = 30$) were estimated by the regression analysis. Then, the estimations were compared to the observed values. For measurement #2, deviations of the estimation from the observed value averaged 0.09 mm. This deviation satisfied 2.4% and 2.2% of the mean observed values for *S. shinto* and *S. caecutiens*, respectively. For measurement #5, the deviations averaged 0.08 mm (1.3% both for *S. shinto* and *S. caecutiens*). For M_1 , the mean deviation was 0.03 mm (2.2% for *S. shinto* and 2.1% for *S. caecutiens* respectively). Hence, deviations from the observed values were rather small (1.3–2.4% in this case). Thus, we believe that the present method of estimating missing values is reasonable.

A preliminary analysis showed that fossil specimens of lower jaws could be divided into three size groups: i.e., small, medium, and large. For the small-sized fossils (NMNS PV-8248, 8330, 8333, 8348-1, 8352, and YH-13564), missing values were estimated by equations of simple regression based on Recent specimens of *S. hosonoi* and *S. minutissimus*. For the large-sized fossils (PV-8338, 8339, and 8359), missing values were estimated by simple regression equations based on Recent specimens of *S. isodon* and *S. unguiculatus*. The remainder of mandible fossils were regarded as the medium-sized group, and missing values were estimated by equations calculated from Recent specimens of *S. caecutiens* and *S. shinto*. Estimated values for missing measurements are marked with bold type with an asterisk (Appendix 1).

For the most well-preserved fossil fragments of the anterior part of crania, it was possible to record some measurements (Fig. 3). For the remainder, missing measurements also were estimated as for the mandibles. Missing values were estimated, by comparison with 20 individuals from each of four Recent species of shrews, *S. caecutiens*, *S. shinto*, *S. isodon*, and *S. unguiculatus*. Estimated measurements are marked in bold type with an asterisk (Appendix 2).

Statistical tests

Canonical discriminant analysis was used and conducted separately for lower and upper jaws. Confidence probability limits was always 0.95. All calculations were performed with the program Systat 8.0 (SPSS, Chicago).

Comparison of dental morphology

It is very difficult to identify morphological differences between *S. shinto* and *S. caecutiens*, because they have similar cranial morphology. Dokuchaev et al. (1999), however, demonstrated that *S. shinto* had an obviously narrower mesostyle of Pm^4 than *S. caecutiens* in Hokkaido. As a complementary analysis, we used this character to determine whether a fossil should be classified as *S. shinto* or *S. caecutiens* for the available specimens.

Likewise, *S. unguiculatus* and *S. isodon* have similar cranial morphology. However, there are several morphological differences in dental characters (Dolgov 1985). For instance, unicuspid (U) of *S. isodon* gradually become smaller from the first to the fifth, whereas height of U^2 is shorter than that of U^3 in *S. unguiculatus* or is nearly the same size as U^3 . We examined such dental characters to determine whether a fossil should be regarded as *S. isodon* or *S. unguiculatus*.

Results

The first group of fossil specimens

In the analysis of the first specimen group, Recent species of shrews were divided into four size groups (Appendix 1; also see the first discriminant score 1 in Fig. 4): small (*S. minutissimus*, *S. gracillimus* and *S.*

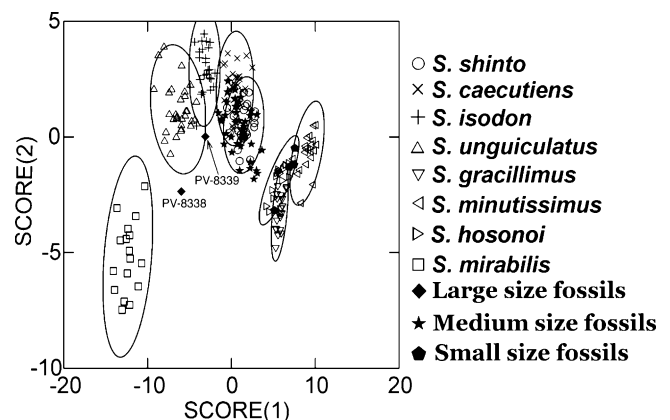


Fig. 4. A plot of the first 2 discriminant analysis axes for 8 mandible characters in 8 Recent *Sorex* shrew species and the first fossil group, which includes mandibles (lower jaws) with at least one tooth and the coronoid process. Ellipses represent 95% confidence limits.

hosonoi), medium (*S. caecutiens* and *S. shinto*), large (*S. isodon* and *S. unguiculatus*), and very large (*S. mirabilis*).

For small Recent species, plots of *S. hosonoi* and *S. gracillimus* on the first and second discriminant score axes largely overlapped, although the latter tended to have smaller values on discriminant function axis 2 (Fig. 4). *Sorex minutissimus* was distinguishable from *S. gracillimus* on discriminant function axis by score 1 value (Fig. 4). The two medium sized species, greatly overlapped, but *S. shinto* tended to have smaller values on discriminant function axis 2. In large and very large Recent species, all samples of *S. mirabilis* showed negative second discriminant score values and all specimens of *S. isodon* and some of *S. unguiculatus* positive values (Fig. 4). However, there was no overlapping of the 95% confidence ellipses on the scattergram between the former and the latter two species.

Fossil specimens were divided into three size groups: small, medium, and large (Appendix 1, Fig. 4). Most of the fossils were classified as into the medium-sized group. Four specimens (PV-8330, 8348-1, 8352, and YH-13564) fell into the small and two (PV-8338 and 8339) into the large-sized groups (Fig. 4).

The four small-sized fossils are within the 95% confidence ellipse of Recent *S. hosonoi* (Fig. 4). However, one fossil was plotted within the overlapped area between *S. hosonoi* and *S. gracillimus*, and three were within the overlapped area between *S. hosonoi* and *S. minutissimus* (Fig. 4).

The medium-sized fossils were distributed closely to the Recent medium-sized group (*S. caecutiens* and *S. shinto*) (Fig. 4). Further, the fossils group was closer to, or explicitly fell within, the 95% confidence ellipse of Recent *S. shinto*, although the 95% confidence ellipses of Recent *S. shinto* and *S. caecutiens* largely overlapped. Some fossil specimens fell outside the 95% confidence limit of *S. shinto* (Fig. 4).

One large-sized fossil specimen (PV-8339) fell on the border of the *S. unguiculatus* 95% confidence limit, and another one (PV-8338) differed from both Recent *S. isodon* and *S. unguiculatus* although it is closer to the latter species (Fig. 4). However, the two fossils were rather different from *S. mirabilis*.

Then, we reanalysed small-sized fossils and Recent species (*S. minutissimus*, *S. gracillimus*, and *S. hosonoi*) (Fig. 5) and medium- and large-sized fossils and Recent species (*S. shinto*, *S. caecutiens*, *S. isodon*, *S. unguiculatus*, and *S. mirabilis*) (Fig. 6), separately. Four specimens of

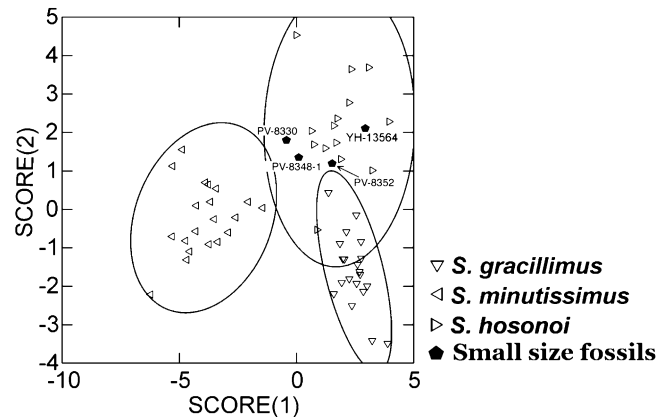


Fig. 5. A plot of the first 2 discriminant axes for 8 mandible characters in 3 small Recent species of *Sorex* and 4 small-size specimens from the first fossil group. Ellipses represent 95% confidence limits.

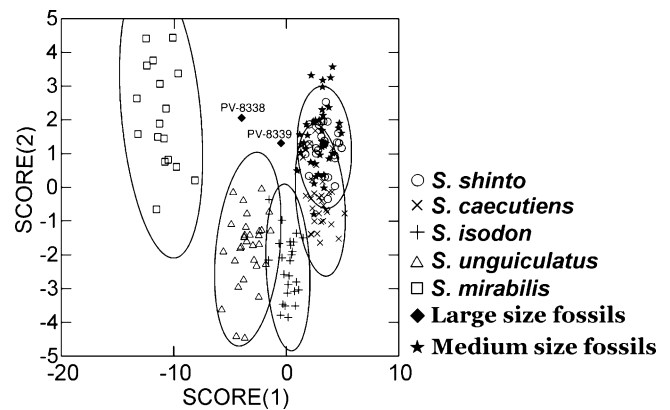


Fig. 6. A plot of the first 2 discriminant analysis axes for eight mandible characters in five medium and large recent *Sorex* species and medium- and large-size specimens from the first fossil group. Ellipses represent 95% confidence limits.

small-sized fossils, including specimen YH-13564 that was suspected to be *S. gracillimus* (Ohdachi et al 1997; Ohdachi 1999), were plotted within the 95% confidence ellipse of *S. hosonoi* (Fig. 5). The medium-sized fossil group was plotted more closely to the range of *S. shinto* than in the initial analysis on the first discriminant axis (Figs. 4 and 6). As happened in the initial analysis, the two large-sized fossils plotted closer to *S. unguiculatus* and *S. isodon* than to *S. mirabilis* (Figs. 4 and 6).

The second group of fossil specimens

In the analysis of the second group of lower jaw specimens without teeth, fossil specimens were divided into medium- and large-sized specimens (Fig. 7 and Appendix 1). Most fossils were classified within the medium-sized group, and only one specimen (PV-8359) was classified with the large-sized species of shrews. The

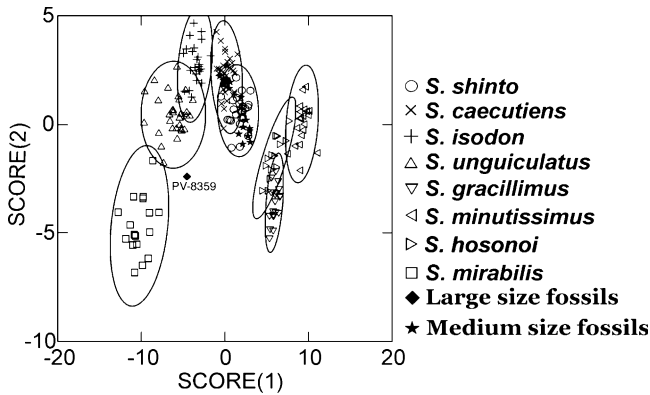


Fig. 7. A plot of the first 2 discriminant analysis axes for eight mandibular characters in eight Recent *Sorex* species and the second fossil group, which has complete mandibles without teeth but with the coronoid process. Ellipses represent 95% confidence limits.

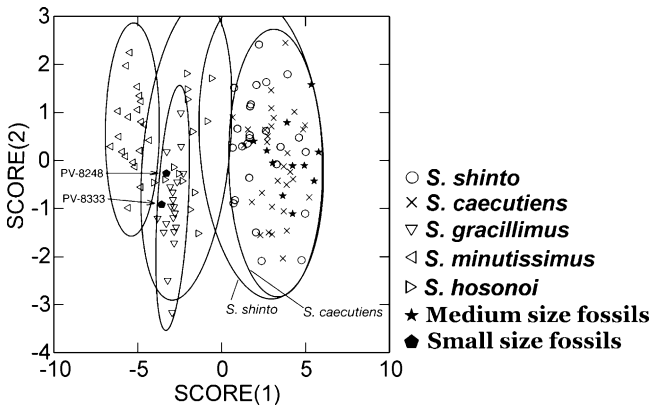


Fig. 8. Plot of the first two discriminant analysis axes for eight lower jaw characters in five Recent *Sorex* species and the third fossil group, which has fragmented mandibles without a coronoid process but at least with one tooth.

plotting pattern for the first two discriminant axes for Recent species (Fig. 7) was almost the same as that for the first specimen group (Fig. 4). Eight medium-sized fossils fell within the 95% confidence limit of *S. shinto* and outside the 95% confidence ellipse of *S. caecutiens* (Fig. 7). The remaining 8 medium-sized fossils were plotted in the area of overlap of the 95% confidence ellipses of *S. caecutiens* and *S. shinto*. The large fossil specimen was situated closer to *S. unguiculatus* than to *S. isodon* and *S. mirabilis* (Fig. 7).

The third group of fossil specimens

Because these fossils were divided into small- and medium-sized groups (Fig. 8 and Appendix 1), this analysis included five Recent species of small- and medium-sized *Sorex* shrews. When plotted, Recent small- and medium-sized species *S. caecutiens*, *S.*

shinto, *S. hosonoi*, and *S. minutissimus* had largely overlapping 95% confidence ellipses (Fig. 8). This was particularly true for *S. gracillimus* with *S. hosonoi* and *S. caecutiens* with *S. shinto*. Thus, in this analysis, it is very difficult to distinguish *S. gracillimus* from *S. hosonoi* and *S. caecutiens* from *S. shinto*.

All medium-sized fossils fell within the 95% confidence ellipses of *S. shinto* and *S. caecutiens* (Fig. 8). The small fossil (PV-8248), which was regarded as *S. minutissimus* in the original description (Tomida and Sakura 1991), fell within the 95% confidence limits of *S. hosonoi* and *S. gracillimus* (Fig. 8). The other small fossil (PV-8333) also was situated within the 95% confidence ellipses of *S. hosonoi* and *S. gracillimus*.

The fourth group of fossil specimens

Measurements of “character #1” of all mandible fragments of the fourth specimen group were included in the ranges of Recent *S. shinto* and *S. caecutiens* and excluded from the other Recent species (Appendix 1). However, the values of *S. shinto* and *S. caecutiens* were largely overlapped. Therefore, these fossils were referred to *S. shinto* or *S. caecutiens*.

The anterior part of fossil shrew skulls

For medium-sized fossils, PV-8297 fell within the overlapping area of the 95% confidence ellipses of *S. shinto* and *S. caecutiens* whereas PV-19056 was closest to *S. caecutiens* and rather distant from *S. shinto* (Fig. 9). All large-sized fossils were within the 95% confidence ellipse of Recent *S. isodon*, and obviously different from *S. unguiculatus* (Fig. 9).

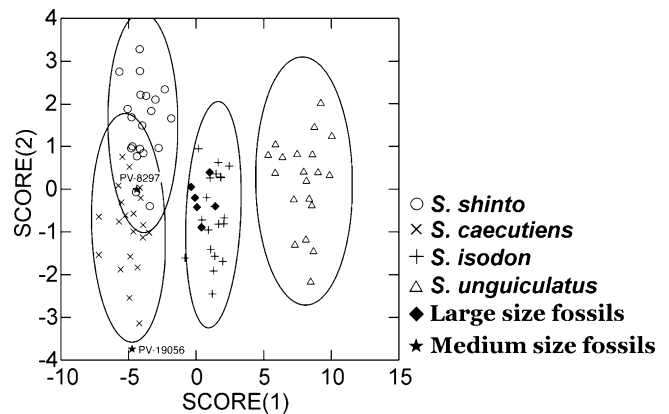


Fig. 9. Plot of the first 2 discriminant analysis scores for eight characters of the anterior part of skull in four Recent *Sorex* species and fossil specimens. Ellipses represent 95% confidence limits.

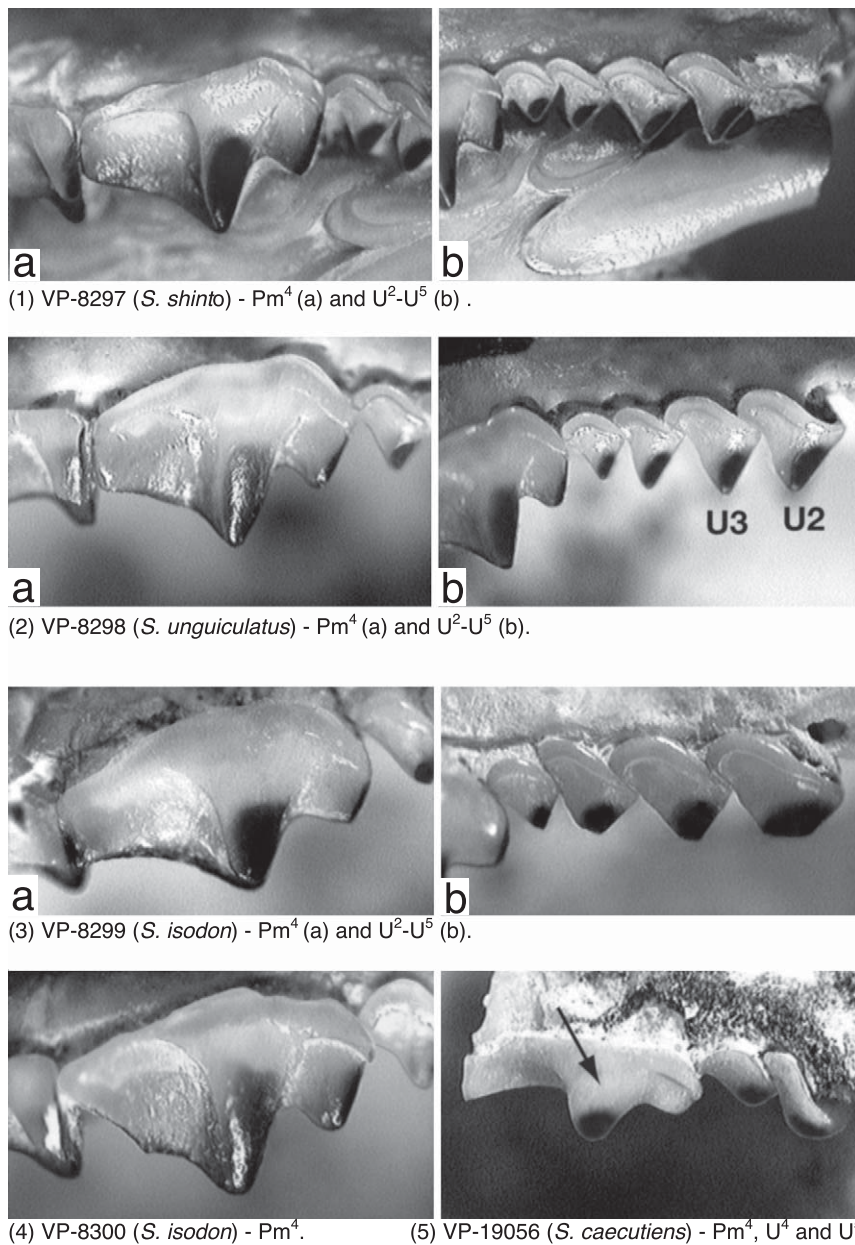


Fig. 10. The pictures of the teeth of upper jaws of fossil *Sorex* shrews.

Qualitative dental morphology

According to Dokuchaev et al. (1999), *S. caecutiens* in Hokkaido has the most massive mesostyle of Pm⁴ among the 8 Recent species examined. For specimens that this diagnostic character could be analyzed, only specimen VP-19056 could be classified as *S. caecutiens* (Fig. 10-5). Relative basal width of Pm⁴ mesostyle of this specimen (an arrow in Fig. 10-5) was about 59%. It is more similar to *S. caecutiens* than *S. shinto* (Dokuchaev et al. 1999). This specimen was from the northernmost part of Honshu (#1 in Fig. 1). Based on mesostyle development of Pm⁴, the other medium fossil specimens of upper jaws

available for this analysis were identified as *S. shinto*.

There also is a difference in the degree of the mesostyle development on Pm⁴ in *S. isodon* and *S. unguiculatus*. In *S. isodon*, mesostyle of Pm⁴ is massive and is developed to the same degree as in *S. shinto*. Specimens PV-8299 and PV-8300 of large-sized fossils had the same morphology of mesostyles on Pm⁴ as in Recent *S. isodon* (Figs. 10-3a and 10-4). Only one exception of this dental diagnosis was found for PV-8298 (Fig. 10-2a). In this fossil specimen, the mesostyle on Pm⁴ was less massive (Fig. 10-2a) as in *S. unguiculatus*. In addition, unicuspid tooth row pattern of this specimen (Fig. 10-2b)

Table 1. Summary of morphological analyses of fossils

	small specimens	medium specimens	large specimens
1st fossil group (Figs. 4, 5 & 6)	<i>S. hosonoi</i> (all specimens)	some obviously <i>S. shinto</i> and the others <i>S. shinto/caecutiens</i> . As a group, referred to <i>S. shinto</i> .	similar to <i>S. isodon</i> and <i>S. unguiculatus</i>
2nd fossil group (Fig. 7)	–	some obviously <i>S. shinto</i> and the others <i>S. shinto/caecutiens</i> . As a group, referred to <i>S. shinto</i> .	closer to <i>S. unguiculatus</i>
3rd fossil group (Fig. 8)	<i>S. hosonoi/S. gracillimus</i> , not <i>S. minutissimus</i>	<i>S. shinto/caecutiens</i>	–
4th fossil group (Append. 1)	–	<i>S. shinto/caecutiens</i>	–
anterior part of skull (Fig. 9)	–	<i>S. shinto</i> and <i>S. caecutiens</i>	<i>S. isodon</i> (all specimens)
dental morphotype (Fig. 10)	–	<i>S. shinto</i> and <i>S. caecutiens</i>	2 specimens are obviously <i>S. isodon</i> , but 1 specimen <i>S. unguiculatus</i>

showed the size of U^3 is nearly equal to U^2 , which is the morphotype of *S. unguiculatus* (Dolgov 1985).

Discussion

Four fragments of mandible fossils (NMNS-PV-8330, 8348-1, 8352, and YH-13564) were classified as *S. hosonoi* (Fig. 5), although they could not be discriminated from *S. gracillimus* in the first analysis (Fig. 4). Among them, one specimen (YH-13564) was referred to *S. gracillimus* (Ohdachi et al. 1997; Ohdachi 1999) and the other three were recorded as *S. shinto* (Tomida and Sakura 1991). A specimen (PV-8248), which was reported as *S. minutissimus* (Tomida and Sakura 1991), is not *S. minutissimus* (Fig. 8). Finally, PV-8248 and PV-8333 could not be identified clearly as either *S. hosonoi* or *S. gracillimus* (Fig. 8) although we suppose they are *S. hosonoi*.

Morphology of some medium-sized fossils was obviously within the size range of Recent *S. shinto* whereas others were within that of Recent *S. caecutiens* (Figs. 4, 6, 7 and 8). And, some were within the overlapping area of the 95% confidence ellipses of Recent *S. shinto* and *S. caecutiens* (Figs. 4, 6, and 7). However, as a group, most medium-sized fossils were more closely related to Recent *S. shinto* (Table 1), although their morphology as shown in the plots indicates a little deviation from that of Recent *S. shinto*. One medium-sized fossil from northernmost Honshu (VP-19056) was classified as *S. caecutiens* according to multivariate analysis (Fig. 9). It was also identified as *S. caecutiens* by the morphology of Pm^4 mesostyle (Fig. 10-5). The other middle-sized fossils examined should be referred to *S. shinto*.

Six upper jaws of large-sized fossils were classified as

S. isodon according to multivariate analysis (Fig. 9), although upper tooth morphology of one specimen (PV-8298) showed a morphotype of *S. unguiculatus* (Fig. 10). Two fossil mandibles (PV-8338 and -8339) fell within a large-sized group; however, it was not possible to positively identify them. Certainly, they are similar to *S. isodon* or *S. unguiculatus* (Figs. 4 and 6). In addition, one large-sized specimen (PV-8359) was more similar to *S. unguiculatus* (Fig. 7). Thus, we cannot conclude whether these specimens should be referred to *S. isodon* or *S. unguiculatus*. However, it was confirmed that during the Middle Pleistocene one or two species of *S. isodon/unguiculatus* group (Ohdachi et al. 1997, 2006) inhabited Honshu Island.

Conclusion

Most medium- and small-sized fossils of *Sorex* shrews excavated from Honshu Island are supposed to be of 2 species, *S. shinto* and *S. hosonoi* (Table 1), although there is some ambiguity regarding their taxonomic identification (some specimens could not completely distinguished from *S. caecutiens* and *S. gracillimus*, respectively). *Sorex shinto* and *S. hosonoi* on Honshu Island are sibling species of *S. caecutiens* and *S. minutissimus*, respectively (Ohdachi et al. 1997, 2006). Thus, it is proposed that in the Middle Pleistocene, *S. shinto* and *S. hosonoi* already were “speciated” from their common ancestors with *S. caecutiens* and *S. minutissimus*, respectively. The ancestors of these species probably colonized into Honshu from Korean Peninsula in the Early Pleistocene or the Late Pliocene. Furthermore, one medium fossil from northernmost Honshu was identified as *S. caecutiens*. Thus it is suggested that *Sorex caecutiens* might have

immigrated into northern Honshu from Hokkaido before Tsugaru Strait was opened, but *S. caecutiens* was completely replaced by *S. shinto* in Honshu after the Middle Pleistocene. More precise investigation of the process of the appearance/disappearance of *S. caecutiens* in northern Honshu is desired to investigate to understand evolutionary process of Japanese mammalian fauna.

In addition to *S. shinto* and *S. hosonoi*, there existed 2 large-sized species of *Sorex* in Honshu of the Middle Pleistocene (Table 1). The large-sized fossil species morphologically are obviously *S. isodon* but others could not be positively identified as either *S. isodon* or *S. unguiculatus* (Table 1). However, one fossil was identified as *S. unguiculatus*. *Sorex unguiculatus* and *S. isodon* are sister species (Ohdachi et al. 1997, 2006) and are morphologically (Dolgov 1985) and ecologically (Churchfield et al. 1999) similar, and co-exist in Sakhalin and the northeastern Asian Continent (Ohdachi 1999). Ancestral populations of these species appeared on Honshu Island in the Middle Pleistocene, when there was a land bridge between Honshu Island and the Korean Peninsula (Dobson 1994; Dobson and Kawamura 1998). It is estimated that the Korean Strait finally remained open after 430,000 (MIS 12) or 630,000 (MIS 16) years ago based on the recent estimation of the immigration times of extinct proboscideans into the Japanese Islands and sea-level changes (Rohling et al. 1998; Konishi and Yoshikawa 1999). More exhaustive research of the large-sized *Sorex* shrew fossils is needed. The reason why Pleistocene *Sorex isodon* and *S. unguiculatus* disappeared from Honshu Island is still open to question.

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Appendix 1.

Measurements (in mm) of mandibles of the recent and fossil *Sorex* shrews. Estimated values for the fossils are marked with bold type with asterisks. See Fig. 2 for definitions of characters. For fossil specimens, scientific names in parentheses are those identified in the present study. In the specimen list of the National Museum of Nature and Science (Tomida and Sakura 1991), all specimens except for PV-8248 were described as “*Sorex shinto*” whereas PV-8248 was identified as “*Sorex minutissimus*”. All samples except YH-13564 are those of National Museum of Nature and Science, Tokyo, and the specimen YH-13564 tentatively is stored at Iida City Museum (Nagano Prefecture, Japan).

Species and/or specimen code, locality (n)	Characters							
	#1	#2	#3	#4	#5	M ₁	M ₂	M ₃
► Group: Recent species								
<i>S. shinto</i> , Honshu (25)	1.06 ± 0.017 ^{a)} 0.94–1.22	3.77 ± 0.029 3.53–4.10	1.71 ± 0.017 1.53–1.85	1.84 ± 0.015 1.72–2.02	6.03 ± 0.038 5.68–6.38	1.39 ± 0.011 1.29–1.50	1.19 ± 0.009 1.10–1.30	1.03 ± 0.013 0.95–1.17
<i>S. caecutiens</i> , Hokkaido (20) and Primorye (10)	1.09 ± 0.010 1.00–1.20	4.05 ± 0.023 3.75–4.32	1.80 ± 0.011 1.66–1.90	1.92 ± 0.014 1.75–2.10	6.13 ± 0.023 5.77–6.32	1.42 ± 0.009 1.30–1.50	1.19 ± 0.007 1.11–1.28	1.05 ± 0.011 0.95–1.18
<i>S. isodon</i> , Primorye (20) and Magadan region (5)	1.32 ± 0.017 1.22–1.55	4.58 ± 0.021 4.36–4.80	2.07 ± 0.015 1.90–2.22	2.29 ± 0.022 2.10–2.50	6.67 ± 0.041 6.35–7.22	1.53 ± 0.008 1.47–1.60	1.30 ± 0.010 1.23–1.43	1.08 ± 0.011 0.95–1.20
<i>S. unguiculatus</i> , Hokkaido (20) and Primorye (10)	1.39 ± 0.021 1.20–1.70	4.78 ± 0.043 4.48–5.42	2.29 ± 0.020 2.07–2.49	2.43 ± 0.025 2.20–2.75	7.32 ± 0.058 6.90–8.10	1.67 ± 0.008 1.58–1.75	1.37 ± 0.009 1.30–1.50	1.15 ± 0.007 1.10–1.30
<i>S. gracillimus</i> , Hokkaido (20)	0.80 ± 0.008 0.73–0.88	2.86 ± 0.013 2.73–2.96	1.51 ± 0.013 1.40–1.60	1.43 ± 0.008 1.37–1.50	5.52 ± 0.026 5.34–5.73	1.20 ± 0.003 1.15–1.22	1.05 ± 0.010 0.98–1.12	0.94 ± 0.011 0.87–1.05
<i>S. minutissimus</i> , Hokkaido (14), Primorye (1) and Korea (5)	0.73 ± 0.011 0.61–0.80	2.65 ± 0.024 2.31–2.79	1.29 ± 0.014 1.20–1.41	1.21 ± 0.013 1.01–1.30	4.68 ± 0.041 4.45–5.07	1.08 ± 0.007 1.02–1.14	0.99 ± 0.008 0.93–1.05	0.83 ± 0.009 0.75–0.90
<i>S. hosonoi</i> , Honshu (14)	0.85 ± 0.022 0.74–0.99	3.01 ± 0.019 2.91–3.12	1.55 ± 0.026 1.42–1.70	1.40 ± 0.020 1.20–1.49	5.43 ± 0.051 5.11–5.81	1.22 ± 0.011 1.13–1.27	1.09 ± 0.008 1.04–1.14	0.93 ± 0.011 0.87–1.02
<i>S. mirabilis</i> , Primorye (17)	1.50 ± 0.017 1.38–1.60	4.98 ± 0.041 4.65–5.30	2.64 ± 0.027 2.48–2.82	2.68 ± 0.029 2.50–2.95	8.39 ± 0.078 7.85–8.95	1.98 ± 0.013 1.90–2.08	1.73 ± 0.019 1.60–1.80	1.38 ± 0.015 1.27–1.50
► Group: First group fossils (n = 41)								
PV-8304 (<i>S. shinto</i>)	1.28	4.25	2.00	2.10	6.41	1.43	1.23	1.22
PV-8305 (<i>S. shinto</i>)	1.28	4.11	1.92	2.10	6.59	1.50	1.32	1.17
PV-8306 (<i>S. shinto</i>)	1.21	4.27*	1.77	2.08	6.43	1.48	1.29	1.15*
PV-8307 (<i>S. shinto</i>)	1.21	4.14	1.84	1.99	6.02	1.57	1.35	1.17
PV-8308 (<i>S. shinto</i>)	1.31	3.96	1.83	1.95	6.25	1.46	1.26	1.10
PV-8309 (<i>S. shinto</i>)	1.28	4.23	1.91	2.10	6.28	1.59	1.39	1.25*
PV-8310 (<i>S. shinto</i>)	1.17	3.93	1.89	1.88	6.28*	1.36	1.24	1.10*
PV-8311 (<i>S. shinto</i>)	1.03	3.49	1.67	1.73	5.91	1.39	1.21	1.03
PV-8312 (<i>S. shinto</i>)	1.31	4.08	2.18	1.86	6.44	1.43*	1.22*	1.11
PV-8314 (<i>S. shinto</i>)	1.10	3.83	1.95	1.94	6.37*	1.39	1.20	1.03
PV-8315 (<i>S. shinto</i>)	1.27	4.23	1.93	2.09	6.34*	1.58*	1.38	1.24*
PV-8317 (<i>S. shinto</i>)	1.37	4.02	1.88	2.05	6.26*	1.60	1.32	1.18*
PV-8318 (<i>S. shinto</i>)	1.06	3.65	1.77	1.75	6.10*	1.47	1.14	1.06

Species and/or specimen code, locality (n)	Characters							
	#1	#2	#3	#4	#5	M ₁	M ₂	M ₃
PV-8319 (<i>S. shinto</i>)	1.11	3.94	1.63	1.93	5.89*	1.46	1.24	1.11
PV-8320 (<i>S. shinto</i>)	1.07	3.73	1.75	1.75	6.07*	1.45	1.21*	1.07*
PV-8329 (<i>S. shinto</i>)	1.01	3.55	1.61	1.71	5.86*	1.40*	1.17	1.03*
PV-8330 (<i>S. hosonoi</i>)	0.77	2.86	1.35	1.32	4.93*	1.20*	1.08	0.97
PV-8335 (<i>S. shinto</i>)	1.11	3.52	1.76	1.79	6.11	1.21	1.11	0.97
PV-8336 (<i>S. shinto</i>)	1.27	3.95	1.81	1.89	5.99	1.54	1.26*	1.12*
PV-8337 (<i>S. shinto</i>)	1.12	3.78	1.85	1.90	6.22*	1.34	1.16	1.02
PV-8338 (<i>S. isodon</i> or <i>S. unguiculatus</i>)	1.47	4.37	2.22	2.34	7.23	1.80	1.44*	1.25*
PV-8339 (<i>S. isodon</i> or <i>S. unguiculatus</i>)	1.24	4.21	1.94	2.12	6.36*	1.71	1.39*	1.22*
PV-8340 (<i>S. shinto</i>)	1.18	4.06	1.95	1.94*	6.37*	1.47	1.33	1.17
PV-8341 (<i>S. shinto</i>)	1.20	4.06	1.77	1.95	6.10*	1.58	1.34	1.12
PV-8343 (<i>S. shinto</i>)	1.02	3.64*	1.75	1.73	5.85	1.51	1.33	1.13
PV-8344 (<i>S. shinto</i>)	1.19	4.05	1.86	1.84	6.23*	1.48	1.23	1.08
PV-8345 (<i>S. shinto</i>)	1.21	4.03	1.92	1.87	6.32*	1.45	1.21*	1.07*
PV-8346 (<i>S. shinto</i>)	1.28	4.20	1.97	2.05	6.40*	1.59	1.30*	1.16*
PV-8347 (<i>S. shinto</i>)	1.11	3.52	1.86	1.78	6.23*	1.34	1.07	1.02
PV-8348-1 (<i>S. hosonoi</i>)	0.82	2.97	1.44	1.40	5.12	1.14	1.02	0.97
PV-8349 (<i>S. shinto</i>)	1.18	3.79	1.78	1.83	6.11*	1.45	1.21*	1.07*
PV-8350 (<i>S. shinto</i>)	0.98	3.34	1.58	1.67	5.82*	1.34	1.20	0.94
PV-8351 (<i>S. shinto</i>)	1.08	3.91	1.84	1.90	6.20*	1.42*	1.20*	1.07
PV-8352 (<i>S. hosonoi</i>)	0.83	2.89	1.44	1.38	5.19*	1.22	1.00	0.98
PV-8357 (<i>S. shinto</i>)	1.22	3.76*	1.61	1.80	5.86*	1.44*	1.23	1.05
PV-8362 (<i>S. shinto</i>)	1.20	4.25*	1.91	2.07	6.31*	1.45*	1.24	1.11
PV-8363 (<i>S. shinto</i>)	1.03	3.95	1.72	1.97	6.01*	1.41*	1.19	1.11
PV-8365 (<i>S. shinto</i>)	1.08	3.72*	1.64	1.82*	5.91*	1.41*	1.19	1.01
YH-13564 (<i>S. hosonoi</i>)	0.81	2.91	1.48	1.40	5.31*	1.32	1.16*	1.01*
PV-19043 (<i>S. shinto</i>)	0.98	3.41	1.56	1.69	5.89	1.35	1.19	1.05*
PV-19044 (<i>S. shinto</i>)	1.05	3.66*	1.61	1.79*	5.86*	1.36*	1.14	0.97
PV-19046 (<i>S. shinto</i>)	1.02	3.40	1.65	1.65	5.92*	1.36	1.16*	1.02*
PV-19049 (<i>S. shinto</i>)	1.13	3.84	1.77	1.89	6.10*	1.45	1.30	1.09
PV-19050 (<i>S. shinto</i>)	1.00	3.72	1.78	1.54	5.98	1.48	1.23*	1.09*
PV-19051 (<i>S. shinto</i>)	0.99	3.45	1.64	1.72	5.00	1.43*	1.21	1.03
► Group: Second group fossils (n = 17)								
PV-8297 (<i>S. shinto</i>)	1.12	3.65	1.65	1.80	6.00			
PV-8313 (<i>S. shinto</i>)	1.17	4.07	1.83	2.02	6.19*			
PV-8316 (<i>S. shinto</i>)	1.20	4.16*	1.84	2.02	6.20*			
PV-8322 (<i>S. shinto</i>)	1.23	3.98	1.77	2.05	6.10*			
PV-8323 (<i>S. shinto</i>)	1.26	4.17	1.90	2.05	6.29*			
PV-8325 (<i>S. shinto</i>)	1.19	4.08	1.76	2.02	6.08*			
PV-8327 (<i>S. shinto</i>)	1.04	3.64	1.70	1.77	6.00*			
PV-8342 (<i>S. shinto</i>)	1.09	3.96	1.71	1.98	6.01*			
PV-8348-2 (<i>S. shinto</i>)	1.09	3.54	1.63*	1.78	5.89*			
PV-8353 (<i>S. shinto</i>)	0.96	3.75*	1.63	1.79	5.89*			
PV-8354 (<i>S. shinto</i>)	0.99	3.47	1.62	1.73	5.88*			
PV-8356 (<i>S. shinto</i>)	1.16	4.10	1.89	1.88	6.28*			
PV-8359 (<i>S. isodon</i> or <i>S. unguiculatus</i>)	1.26	4.32	2.23	2.29	7.13*			
PV-8361 (<i>S. shinto</i>)	1.02	3.67	1.75	1.79	6.07*			
PV-8364 (<i>S. shinto</i>)	1.06	3.50	1.91	1.73	5.86*			
PV-8366-1 (<i>S. shinto</i>)	0.97	3.52	1.64	1.71	5.91*			
PV-19045 (<i>S. shinto</i>)	1.04	3.52	1.67	1.73	5.87			

Species and/or specimen code, locality (n)	Characters							
	#1	#2	#3	#4	#5	M ₁	M ₂	M ₃
► Group: Third group fossils (n = 13)								
PV-8248 (<i>S. hosonoi</i> or <i>S. gracillimus</i>)	0.71					1.18	0.90	0.77*
PV-8321 (<i>S. shinto/caecutiens</i>)	1.19					1.49	1.37	1.23*
PV-8324 (<i>S. shinto/caecutiens</i>)	1.15					1.39	1.19	1.09
PV-8326 (<i>S. shinto/caecutiens</i>)	1.28					1.47	1.33	1.16
PV-8328 (<i>S. shinto/caecutiens</i>)	1.08					1.48	1.20	1.08
PV-8331 (<i>S. shinto/caecutiens</i>)	1.16*					1.52	1.25*	1.11*
PV-8332 (<i>S. shinto/caecutiens</i>)	1.07*					1.39	1.11	0.97*
PV-8333 (<i>S. hosonoi</i> or <i>S. gracillimus</i>)	0.79*					1.18	1.05*	0.91*
PV-8355 (<i>S. shinto/caecutiens</i>)	1.19					1.42	1.23	1.09*
PV-8360 (<i>S. shinto/caecutiens</i>)	1.18					1.53	1.31	1.14
PV-19047 (<i>S. shinto/caecutiens</i>)	1.07					1.46	1.28	1.14*
PV-19048 (<i>S. shinto/caecutiens</i>)	0.94					1.41	1.29	1.06
PV-19052 (<i>S. shinto/caecutiens</i>)	1.12*					1.46	1.18	1.04*
► Group: Fourth group fossils (n = 8)								
PV-8358 (<i>S. shinto/caecutiens</i>)	1.12							
PV-8366-2 (<i>S. shinto/caecutiens</i>)	1.17							
PV-8366-3 (<i>S. shinto/caecutiens</i>)	1.16							
PV-8366-4 (<i>S. shinto/caecutiens</i>)	1.18							
PV-8366-5 (<i>S. shinto/caecutiens</i>)	1.07							
PV-8366-6 (<i>S. shinto/caecutiens</i>)	1.14							
PV-8366-8 (<i>S. shinto/caecutiens</i>)	1.19							
PV-8366-9 (<i>S. shinto/caecutiens</i>)	1.21							

^{a)} $X \pm SE$, Range

Appendix 2.

Measurements (in mm) of upper part of skulls of Recent and fossil *Sorex* shrews. Estimated values for the fossils are marked with bold type and asterisks. Refer to Fig. 3 for definitions of characters. Latin names in parentheses are those identified in the present study. In the specimen list of the National Museum of Nature and Science (Tomida and Sakura 1991), all specimens were described as “*Sorex shinto*”.

Species and specimen code	Characters							
	#1	#2	#3	#4	#5	#6	#7	#8
► Group: Recent species								
<i>S. shinto</i> (n = 20)	1.55 ± 0.055 ^{a)} 1.40–1.60	4.26 ± 0.076 4.10–4.35	4.07 ± 0.103 3.88–4.20	1.85 ± 0.055 1.76–1.94	6.11 ± 0.141 5.80–6.35	1.33 ± 0.031 1.30–1.38	1.36 ± 0.040 1.30–1.43	2.11 ± 0.066 1.98–2.20
<i>S. caecutiens</i> (n = 20)	1.54 ± 0.012 1.45–1.60	4.37 ± 0.021 4.20–4.65	4.19 ± 0.023 4.00–4.42	1.18 ± 0.011 1.10–1.25	6.29 ± 0.032 6.00–6.57	1.38 ± 0.008 1.30–1.44	1.39 ± 0.011 1.30–1.50	2.24 ± 0.015 2.10–2.37
<i>S. isodon</i> (n = 20)	1.65 ± 0.037 1.60–1.70	4.63 ± 0.084 4.40–4.80	4.60 ± 0.098 4.35–4.76	2.13 ± 0.049 2.05–2.20	6.61 ± 0.134 6.40–6.85	1.45 ± 0.040 1.38–1.50	1.51 ± 0.043 1.40–1.60	2.19 ± 0.068 2.05–2.30
<i>S. unguiculatus</i> (n = 20)	1.87 ± 0.065 1.75–2.05	5.13 ± 0.090 4.95–5.28	5.18 ± 0.165 4.93–5.45	2.35 ± 0.059 2.25–2.45	7.19 ± 0.209 6.80–7.60	1.61 ± 0.035 1.55–1.70	1.72 ± 0.053 1.60–1.85	2.36 ± 0.084 2.22–2.55
► Group: Fossils								
PV-8297 (<i>S. shinto</i>)	1.40	4.40	3.95	1.70	5.84*	1.35	1.40	1.92
PV-8298 (<i>S. unguiculatus</i>)	1.60	4.65	4.40	2.00	6.45	1.50	1.45	2.12
PV-8299 (<i>S. isodon</i>)	1.60	4.60	4.50	2.12*	6.40	1.40	1.44	2.22
PV-8300 (<i>S. isodon</i>)	1.60*	4.60	4.45	2.12*	6.45	1.40	1.45	2.14*
PV-8301 (<i>S. isodon</i>)	1.61*	4.66*	4.47*	2.15*	6.64*	1.45	1.52*	2.20*
PV-8302 (<i>S. isodon</i>)	1.61*	4.53*	4.47*	2.09*	6.48*	1.45	1.45	2.15*
PV-8303 (<i>S. isodon</i>)	1.66*	4.64*	4.60*	2.14*	6.61*	1.46*	1.50	2.19*
PV-19056 (<i>S. caecutiens</i>)	1.52*	4.29*	4.14*	1.92*	6.17*	1.36*	1.36	2.16*

^{a)} $X \pm SE$, Range