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Morphometric status of shrews of the *Sorex caecutiens/shinto* group in Japan

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Abstract. The morphometric relationships among five operational taxonomic units of the *Sorex caecutiens/shinto* group (Soricidae) (*S. caecutiens* of Hokkaido, *S. shinto shinto* of Honshu including the *S. chouei* holotype, *S. s. shikokensis* of Shikoku, and *S. s. sadonis* of Sado) in the Japanese Islands, were examined using uni- and multivariate analyses of 15 cranial, dental, and external characters. The morphological analyses showed that the shrew from Hokkaido (*S. caecutiens*) and those from Honshu, Shikoku, and Sado (*S. shinto*) were exclusively differentiated. In particular, the surface structure of the fourth upper premolar completely separated the two taxa. In contrast, *S. s. sadonis* from Sado could not be completely distinguished from related taxa from Honshu and Shikoku. Thus these morphometric analyses re-confirm that *S. caecutiens* of Hokkaido, and *S. shinto* from Honshu, Shikoku, and Sado, should be treated as two separate species, as has previously been proposed on the basis of a molecular phylogenetical study.

Key words: *Sorex caecutiens*, *S. shinto*, *sadonis*, *shikokensis*, taxonomy.

Thomas (1905, 1906) described *Sorex shinto* as a new shrew species from Honshu Island. Later, he described a new subspecies, *S. shinto saevus*, from Sakhalin Island and included the island of Hokkaido in its distributional range (Thomas 1907). Thomas (1907) did not find any morphological specific differences, however, among the shrews from Honshu, Hokkaido, and Sakhalin Islands.

In the years since Thomas's (1907) study, the taxonomic treatment of *S. shinto* and other taxa of the *Sorex caecutiens/shinto* group (in the sense of Ohdachi et al. 1997a) has varied. Bobrinskii et al. (1944) treated some medium-sized shrews from Eurasia, including *S. shinto* described by Thomas (1907), as a single species, *S. macropygmaeus* Miller, 1901. Ellerman and Morrison-Scott (1951) accepted Bobrinskii et al's (1944) systematic concept, but they synonymized *S. macropygmaeus* with *S. caecutiens* Laxmann, 1788. Stroganov (1957), who investigated the shrews from Sakhalin, Hokkaido, and the southern Kurile Islands in great details, concluded that the shrews in Hokkaido and Sakhalin, described as *S. shinto saevus* by Thomas (1907), should be included in *S. caecutiens*, as Ellerman and Morrison-Scott (1951) did. However, without inspecting *Sorex* samples from Honshu, Stroganov (1957)

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considered that the shrews of Honshu were a subspecies of *S. caecutiens*, *S. c. shinto*.

Since Stroganov's (1957) investigation, there have been two main opinions concerning the taxonomic status of *shinto* in the *caecutiens/shinto* group. On the one hand, some authors have objected to the specific rank of *shinto*, and have followed Stroganov (1957) in including it in *S. caecutiens* (e.g. Bobrinskii et al. 1965; Abe 1967, 1994; Gureev 1971, 1979; Yudin 1971, 1989; Corbet 1978; Gromov and Baranova 1981; Krivosheev 1984; Dolgov 1985; Okhotina 1993; Dobson 1994). Furthermore, with regard to the subspecific status of the *caecutiens/shinto* shrews of the Japanese Islands and vicinity, Abe (1967, 1994) treated the population of Honshu as *S. caecutiens shinto*, that of Shikoku as *S. c. shikokensis*, and that of Hokkaido and Sakhalin as *S. c. saevus*. On the other hand, some authors have been of the taxonomic opinion that *S. shinto* should be considered as an independent species that occurs in Honshu, Shikoku, and Hokkaido (and Sakhalin, according to some authors) while *S. caecutiens* across the Eurasian Continent (and in Sakhalin according to some authors), essentially following Thomas's (1907) position (e.g. Imaizumi 1949, 1960; Sokolov 1973; Yoshiyuki and Imaizumi 1986; Pavlinov and Rossolimo 1987; Hutterer 1993; Pavlinov et al. 1995; Wolsan and Hutterer 1998). In addition, Imaizumi (1954) described *S. chouei* from Honshu as a new species, although this was later synonymized with *S. caecutiens* (Abe 1967, 1994, 1996) or *S. shinto* (Imaizumi 1970; Hutterer 1993).

There has been the additional controversy in Japan concerning the taxonomic status of the Sado shrew as part of the *caecutiens/shinto* group. This taxon was first described by Yoshiyuki and Imaizumi (1986) from Sado Island. While some authors treat it as an independent species, *S. sadonis* Yoshiyuki *et* Imaizumi, 1986 (e.g. Abe 1994, 1996; Wolsan and Hutterer 1998), others suggest that it should be considered a subspecies of *S. shinto*, *S. s. sadonis* (Ohdachi et al. 1997a; Koyasu 1998).

Ohdachi et al. (1997a) recently used the DNA sequences of the mitochondrial cytochrome *b* gene to reveal the phylogenetical relationships among northeastern Asiatic soricine shrews. Their work indicated that all of the shrews from Honshu, Shikoku, and Sado should be considered as belonging to a single species, *S. shinto*, whereas those from Hokkaido and Sakhalin, belonged to the widespread Eurasian continental species, *S. caecutiens*. This taxonomic scheme has subsequently been followed by Koyasu (1998). No investigations have been made, however, of the morphological relationships among the local populations (or subspecies) of *S. caecutiens* and *S. shinto*.

Our goal was to reveal the morphological status of the *Sorex caecutiens/shinto* group in the Japanese Islands (Hokkaido, Honshu, Shikoku, and Sado). As a result of this research, we are able to offer a morphological diagnosis making it possible to distinguish *S. shinto* from *S. caecutiens* (in the sense of Ohdachi et al. 1997a and Koyasu 1998).

Materials and methods

We have followed the taxonomic approach of Ohdachi et al. (1997a) and Koyasu (1998) for the *caecutiens/shinto* group, and call the shrews of Hokkaido *S. caecutiens*, those of Honshu (including *S. chouei* Imaizumi, 1954) *S. shinto shinto*, those from Sado *S. s. sadonis*, and those from Shikoku *S. s. shikokensis*. These five operational taxonomic units (OTUs) were used for the present investigation. As to geographical terms, we refer the total area of Honshu, Shikoku, and Sado Islands to the "Honshu complex".

Specimens of the *Sorex caecutiens/shinto* group at the National Science Museum (Tokyo), the Natural History Museum, Faculty of Agriculture (K. Maekawa and H. Abe collections), and the Institute of Low Temperature Science (S. Ohdachi collection), Hokkaido University (Sapporo), were examined to provide the basic data for this study. Undamaged skulls of 40 *S. caecutiens* from Hokkaido, 45 *S. shinto* from Honshu (including the holotype of *S. chouei* Imaizumi, 1954, specimen code NSMT-M12513), one *S. s. shikokensis* from Shikoku (the holotype of *S. caecutiens shikokensis* Abe, 1967, NHMHU-13311), and six *S. s. sadonis* from Sado (including the holotype of *S. sadonis* Yoshiyuki *et* Imaizumi, 1986, NSMT-M16180) were used for the cranial and dental analyses, and 240 specimens of *S. caecutiens* from Hokkaido and 25 *S. shinto* from Honshu were used for the analysis of external characters. Specimen codes and locations are listed in the Appendix. Only young-of-the-year (=sexually immature) specimens were used for the cranial and external measurements, with the exception of the three holotype specimens, all of which had over-wintered (=sexually matured). The reason for choosing primarily immature shrews was that the skulls of the over-wintered shrews tend to be slightly smaller (Ognev 1933; Stroganov 1957; Abe 1967), their teeth may be worn, whereas their external characters, such as body length and body weight, tend to be much greater. The three holotypes were used only for the cranial analyses. Samples from both sexes were pooled for analysis, since there is no significant difference in skull size between males and females of the *caecutiens/shinto* group (Abe 1967).

Nine cranial and dental characters were measured. Definitions for these characters are as follows. 1) Condylobasal length: the length from the anterior medial point of the premaxillary bone to the posteriormost point on the occipital condyle. 2) Facial length: the length from the anterior medial point of the premaxillary bone to the posteriormost point of the foramen on the frontal bone. 3) Breadth of the braincase: the maximum width of the braincase. 4) Glenoid width: the maximum width between the right and left mandibular fossae. Definitions for (3) and (4) are illustrated in Dannelid (1994). 5) Width across the second upper unicuspids: the width between the outer margins of the right and left second upper unicuspids (U^2) viewed from the crown side. 6) Width across the second upper molars: the width between the outer margins of the right and left second upper molars (M^2) viewed from the crown. 7) Length of the upper molariform tooth row: the length from the anterior point of the fourth upper premolar (i.e. the superficial "third" premolar) to the posterior point of the third molar, viewed from the crown. 8) Length of upper unicuspid row: the length from the anterior point of the first unicuspid to the posterior point of the fifth unicuspid, viewed laterally. 9) Relative basal width of the mesostyle of the fourth upper premolar: length from the anterior point of the fourth upper premolar (Pm^4) to the posterior point of the mesostyle ("a–b" distance in Fig. 1) relative to Pm^4 length ("a–c" distance), expressed in percentage ("a–b"/"a–c" × 100). Here, we have followed Stroganov's (1957) and Dolgov's (1985) terminology for tooth anatomy.

Skull and tooth characters were measured using an ocular micrometer under a binocular microscope, with the exception of the condylobasal length, which was measured using callipers. Most characters were measured to the nearest 0.01 mm, however condylobasal length was measured to the nearest 0.1 mm. The relative width of Pm^4 mesostyle was measured, using digitally-saved images from a photo-capturing system: OLYMPUS microscope (SZH10), OLYMPUS-Ikegami CCD camera (ICD-740), and a Macintosh computer

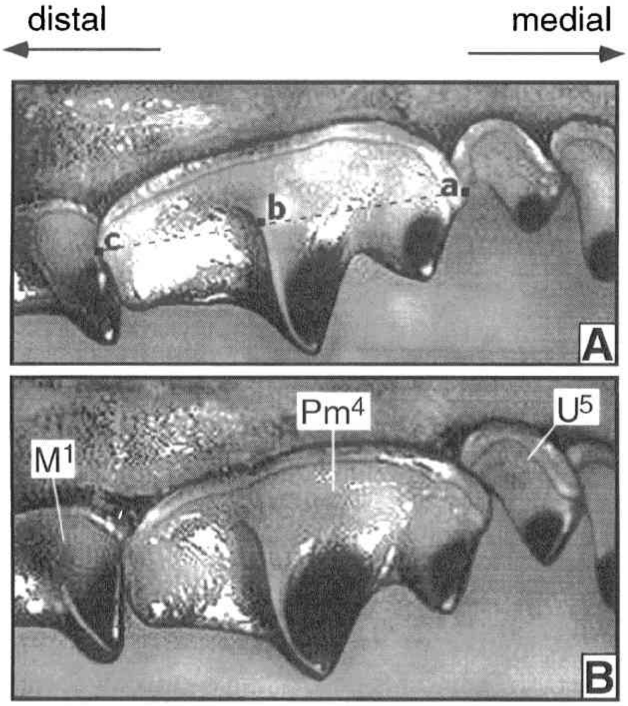

Fig. 1. Buccal view of the fourth right upper premolar of (A) *Sorex shinto* from Honshu (specimen code, SO-96misc15) and (B) *S. caecutiens* from Hokkaido (SO-88n105). Pm^4, fourth upper premolar; M^1, first upper molar; U^5, fifth unicuspid.

(Performa 5430).

Six external characters, body weight, total body length, tail length, hind-foot length, tail ratio, and hind-foot ratio, were used in the analyses. Measurements of the external characters were obtained from the original specimen labels, once doubtful data has been carefully eliminated. Data from both sexes were combined, since there are no sexual differences in the external characters of young shrews in the *caecutiens/shinto* group (Abe 1967). For our purposes, the tail ratio was calculated as the percentage tail length to head and body length, and the hind-foot ratio was the percentage to tail length.

Multivariate factor, cluster, and discriminant analyses were carried out, using the nine cranial characters. For cluster analysis, the nearest neighbor method using Euclidean distance was applied. Differences in means of cranial and external characters between *S. caecutiens* in Hokkaido and *S. shinto* in Honshu were tested using Student's *t*-test for most characters and Mann-Whitney's *U*-test for ratios (relative width of Pm^4 mesostyle, relative tail length, and relative hind foot length).

Results

The cranial characters of the shrews from Hokkaido (*S. caecutiens*) were found to be significantly larger than in those of the shrews from Honshu (*S. s. shinto*) (Table 1). Remarkable differences between these two taxa were found in the relative basal width of

Table 1. Means ± 1*SE*, ranges (in parentheses), and the results of *t*- and *U*-tests of cranial characters in *Sorex caecutiens* from Hokkaido Island and *S. s. shinto* from Honshu Island. All the specimens were the young animals. *U*-test was conducted for relative basal width of Pm^4 mesostyle, and *t*-tests for the other characters.

Cranial and dental characters	*S. caecutiens* in Hokkaido ($n=40$)	*S. s. shinto* in Honshu ($n=44$)	*t* or *U*-test	
			t or *U*	*P*
Condylobasal length (mm)	18.0±0.05 (17.0–18.5)	17.4±0.06 (16.5–18.1)	7.75	<0.001
Facial length (mm)	9.02±0.033 (8.55–9.55)	8.70±0.051 (8.12–9.35)	5.10	<0.001
Breadth of braincase (mm)	9.17±0.031 (8.80–9.60)	8.73±0.034 (8.32–9.30)	9.30	<0.001
Glenoid width (mm)	5.04±0.021 (4.70–5.30)	4.78±0.022 (4.55–5.15)	8.38	<0.001
Width across U^2 (mm)	1.81±0.009 (1.70–1.95)	1.73±0.012 (1.50–1.90)	5.56	<0.001
Width across M^2 (mm)	4.23±0.016 (4.05–4.50)	4.11±0.020 (3.85–4.40)	4.73	<0.001
Length of upper molariform tooth row (mm)	4.35±0.014 (4.20–4.60)	4.20±0.017 (3.95–4.42)	6.68	<0.001
Length of upper unicuspid row (mm)	2.73±0.011 (2.55–2.85)	2.49±0.012 (2.34–2.65)	15.30	<0.001
Relative basal width of Pm^4 mesostyle (%)	61.2±0.20 (59.3–65.2)	54.9±0.20 (52.1–57.2)	272.0	<0.001

Pm^4 mesostyle and the length of the unicuspid row (Table 1). While almost all craniometric characters overlapped between the two taxa, no overlap was found in observed values of the relative width of the Pm^4 mesostyle (Table 1). The shrews from Hokkaido were heavier, and had longer hind feet than the shrews from Honshu, but they did not differ in their total body length (Table 2).

The shrews of Hokkaido could not be distinguished from the shrews of the Honshu complex (*S. shinto* sspp.) on the basis of the first rotated factor of the factor analysis of the craniometrical characters (Fig. 2), and the average first factor value of Hokkaido shrews was intermediate between those of the shrews from Honshu, and the shrews from Sado and Shikoku (*S. s. sadonis* and *S. s. shikokensis*) (Fig. 2). The second rotated factor, however, clearly distinguished between the shrews of Hokkaido and of the Honshu complex (Fig 2). The second rotated factor was greatly contributed to by the relative width of the Pm^4 mesostyle, as well as the length of upper unicuspid row (Table 3).

Cluster analysis showed that the Hokkaido shrews are distant from the shrews of the Honshu complex, which occur in a closely related single cluster (Fig. 3). Within the cluster for the Honshu complex, the shrews from Sado and Shikoku formed a secondary cluster.

According to discriminant analysis, five out of the nine characters were significant enough to be able to distinguish between the shrews of Hokkaido and of the Honshu complex. The discriminant function between the two shrew groups was as follows:

Table 2. Means±1*SE*, ranges (in parentheses), and the results of *t*- and *U*-tests of external characters in *Sorex caecutiens* from Hokkaido Island and *S. s. shinto* from Honshu Island. These specimens were all of young animals. *U*-tests were conducted for the two characters of ratio, and *t*-tests for the other characters.

External characters	*S. caecutiens* in Hokkaido (n=240)	*S. s. shinto* in Honshu (n=25)	*t* or *U*–test	
			t or *U*	*P*
Weight (gram)	5.0±0.03	4.4±0.11	5.55	<0.001
	(4.0–6.7)	(3.5–5.9)		
Total body length (mm)	113.8±0.25	112.6±0.91	1.36	*ns**
	(98–126)	(108–125)		
Length of tail (mm)	48.2±0.22	50.7±0.55	3.52	<0.01
	(40.0–58.0)	(46.0–56.5)		
Length of hind foot (mm)	12.4±0.03	12.0±0.08	4.84	<0.001
	(11.1–13.5)	(11.2–12.9)		
Tail ratio to head & body length (%)	73.8±0.44	82.4±1.84	1392.0	<0.001
	(60.0–103.6)	(66.2–98.2)		
Hind-foot ratio to tail length (%)	25.8±0.11	23.7±0.30	1065.5	<0.001
	(21.5–30.5)	(21.7–26.4)		

* $P>0.05$.

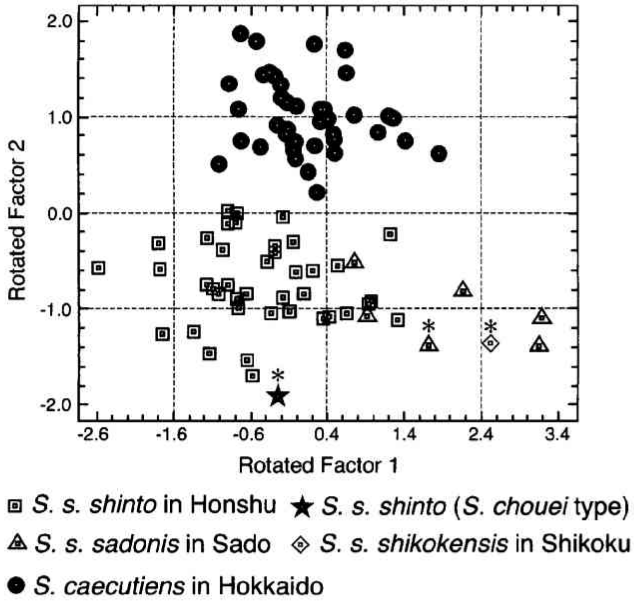

Fig. 2. Plot of the first two factor scores for nine cranial and dental characters of shrews of the *Sorex caecutiens/shinto* group on the Japanese Islands. Three symbols with asterisks (*) are the holotypes for *S. chouei*, *S. c. shikokensis*, and *S. sadonis*, which are treated as *S. s. shinto*, *S. s. shikokensis*, and *S. s. sadonis* in the present study, respectively.

Table 3. Varimax rotated factor matrix for nine cranial and dental characters of the *Sorex caecutiens/shinto* group in Japan. See the caption of Fig. 1 for abbreviation.

Character	Rotated loadings	
	I	II
Width across M^2	0.931	0.089
Width across U^2	0.861	0.154
Length of upper molariform tooth row	0.833	0.356
Condylobasal length	0.686	0.573
Facial length	0.667	0.507
Glenoid width	0.665	0.473
Cranial breadth	0.587	0.678
Relative width of Pm^4 mesostyle	0.063	0.922
Length of upper unicuspid row	0.333	0.899
Percent of total variance explained	45.8%	34.3%

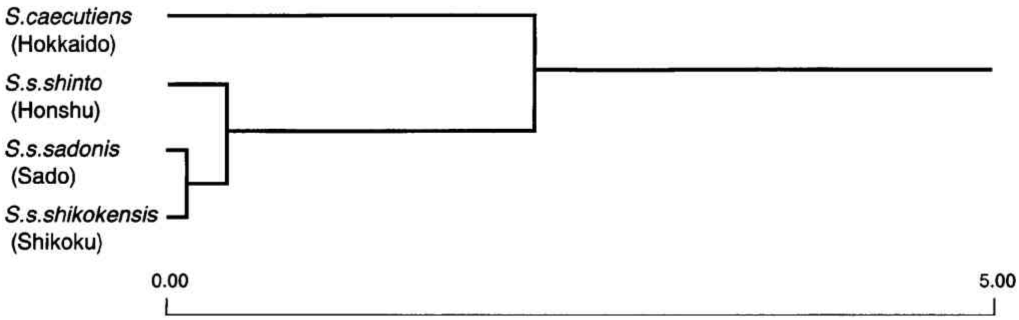

Fig. 3. A dendrogram generated by cluster analysis of nine cranial and dental characters of shrews of the *Sorex caecutiens/shinto* group on the Japanese Islands, based on single linkage method. The distance is multivariate Euclidean distance of the nine characters.

$$Z=-47.6-1.1(FL)+8.9(LUU)+4.9(U^2U^2)-2.4(M^2M^2)+0.6(RMW),$$

where FL=facial length, LUU=length of upper unicuspid row, U^2U^2=width across the second upper unicuspids, M^2M^2=width across the second upper molars, RMW=relative mesostyle width of Pm^4. The group centroids are +3.36 for the shrews of Hokkaido, and −2.58 for those of the Honshu complex. All the specimens were correctly classified into the two groups (probability of misclassification=0.0%).

Discussion

The morphometric analyses clearly showed that the shrews of Hokkaido (*S. caecutiens*) is morphologically different from the shrews of Honshu complex (*S. shinto* sspp.) (Figs. 2 and 3). The most important difference is in the shape of the upper premolar (Fig. 1 and Table 3). Dokuchaev (1978) found that *S. caecutiens* retains a well developed mesostyle of

Pm^4, which is a notable difference between it and several other shrew species. This feature is consistent in *S. caecutiens* throughout its trans-continental Eurasian range. In the present study, we found the same morphotype of the Pm^4 mesostyle in all of the Hokkaido shrews we examined (Fig. 1-B), while the mesostyle of Pm^4 of the shrews from the Honshu complex was less developed (Fig. 1-A). For instance, the relative width of Pm^4 in Honshu shrews never reaches values found in Hokkaido shrews (Table 1).

George (1988) treated *S. shinto* from Honshu as a separate species from *S. caecutiens*, based on allozyme analysis. Ohdachi et al. (1997a) showed that the shrews of Honshu and Shikoku were clearly distinct from those of Hokkaido, Sakhalin, and the Eurasian Continent, based on mitochondrial DNA sequences (see also Fumagalli et al. 1999). According to their phylogenetical relationships (George 1988; Ohdachi et al. 1997a; Fumagalli et al. 1999) and their morphological differences (Figs. 2 and 3), *S. caecutiens* and *S. shinto* should be treated as two separate species.

In contrast, among the four OTUs from the Honshu complex (*S. s. shinto* including *S. chouei* holotype, *S. s. shikokensis*, and *S. s. sadonis*), no clear morphological demarcations were found, although only a small number of specimens were examined for the last three units (Fig. 2). *Sorex chouei* was described on the basis of one specimen of an old individual with very worn teeth (Imaizumi 1954), and its holotype lay in an extreme point within the variation of *S. shinto* (Fig. 2), which might be attributed to by the very worn condition of its teeth. *Sorex s. shikokensis* is a larger relative of *S. s. shinto* in Honshu (Abe 1967), however the genetic distance between them is very small (Ohdachi et al. 1997a). The specimen of *S. s. shikokensis* dropped within the range of *S. s. sadonis* (Fig. 2) and was morphologically similar to the latter (Fig. 3). In addition, we examined more than ten *S. s. shikokensis* that had over-wintered and confirmed that they were morphologically similar to *S. s. sadonis* (this data was not used in the present analyses in order to minimize the potential influence of age).

The molecular phylogenetical study suggested that the Sado Shrew, *S. s. sadonis*, should be considered as a subspecies or local population of *S. shinto* (Ohdachi et al. 1997a). Cranial and dental morphology confirmed that the Sado shrew was similar to the other taxa in the *S. shinto* complex (Fig. 3), and that there was morphological overlap between them (Fig. 2), although the Sado Shrews do have larger skulls than those of Honshu (as does *S. s. shikokensis*), longer claws on the forelegs, and darker pelage (Yoshiyuki and Imaizumi 1986).

According to Ohshima (1990, 1991, 1992), Sado Island was separated from proto-Honshu in the middle Pleistocene, long before the formation of the Tsugaru Strait, that separates Honshu and Hokkaido, which is estimated to have been formed 100–150 10^3-years ago. In contrast, Ohdachi et al. (1997b) have doubted the earlier formation of the Sado Strait than the Tsugaru Strait, because of the molecular phylogeny of the *caecutiens/shinto* group. Likewise, a more recent date for the isolation of Sado Island has been suggested by Tokuda (1941, 1969) on the basis of an examination of the distribution and morphological variation among rodents. The Sado shrew might, therefore, have separated from the Honshu population of *S. shinto* recently (after 150 10^3-years ago at the most). Furthermore, other small mammals, such as *Apodemus argenteus* (Temminck, 1844), *A. speciosus* (Temminck, 1844), and *Mogera tokudae* Kuroda, 1940 (the Sado mole) are found on both Sado and Honshu Islands (Abe 1994, 1995, 1997). Fossil *A. argenteus* have been found from earlier periods in the Pleistocene than the genus *Sorex* from Honshu Island, and the earliest fossils of *A. speciosus* and *Mogera* sp. were from the same period as *Sorex* sp. (Kawamura et al. 1989). In the case of *M. tokudae*, morphological and molecular phylogenetical characteristics of the populations of Sado and Honshu reveal that they are closely related to one other (Abe 1995; Okamoto 1998), as is the case in the shrews of the *caecutiens/shinto* group. At least, the extant *Apodemus* spp. and *M. tokudae* of Sado, whose origins seem to be older than or contemporaneous with *Sorex*, are considered conspecific with their Honshu counterpart populations. Therefore, the subspecific rank of *S. shinto sadonis* is considered to be the more appropriate taxonomic status for the Sado shrew, than *S. sadonis*, as suggested by Ohdachi et al. (1997a) and Koyasu (1998). In order to determine morphological status of *S. s. sadonis* within *S. shinto* more clearly, however, morphological comparisons, such as those of fur colour and claw length, should be conducted using larger sample sizes.

To summarize, morphological analysis has clearly demonstrated that *S. caecutiens* and *S. shinto* should be treated as separate species, as has previously been proposed by Ohdachi et al. (1997a) on the basis of their molecular phylogenetical study. Furthermore, morphological research also suggests that the shrew of Sado Island should be included within *S. shinto*.

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Appendix.

Codes of specimens used for analyses. Deposit places are National Science Museum (NSMT), Natural History Museum, Hokkaido University (NHMHU, HA, KM), and Institute of Low Temperature Science, Hokkaido University (SO).

Cranial Measures

S. caecutiens in Hokkaido

HA-1037, HA-1044, HA-1064, HA-1084, HA-1108, HA-1151, HA-1178, HA-1181, HA-1187, HA-1199, SO-88n105, SO-88n141, SO-88n169, SO-88n197, SO-88n203, SO-88n207, SO-88n248, SO-88n263, SO-88n264, SO-88n265, SO-88n285, SO-88n329, SO-88n336, SO-88n370, SO-88n377, SO-88n378, SO-89nn38, SO-96misc-5, SO-96misc-25, SO-96misc-26, SO-96misc-27, SO-96misc-28, SO-96misc-29, SO-96misc-30, SO-96misc-31, SO-96misc-32, SO-96misc-33, SO-96misc-34, SO-97/8/16-10, SO-97/9/1-1

S. s. shinto in Honshu

HA-1215, HA-6137, NSMT-M12479, NSMT-M12513 (holotype of *S. chouei* Imaizumi, 1954), NSMT-M13366, NSMT-M13397, NSMT-M13398, NSMT-M15593, NSMT-M15594, NSMT-M15595, NSMT-M15598, NSMT-M15599, NSMT-M15611, NSMT-M15613, NSMT-M16082, SO-95misc-2, SO-96misc-9, SO-96misc-10, SO-96misc-11, SO-96misc-13, SO-96misc-14, SO-96misc-15, SO-96misc-16, SO-96misc-17, SO-96misc-18, SO-96misc-19, SO-96misc-20, SO-96misc-21, SO-96misc-22, SO-96misc-57, SO-97/8/2-1, SO-97/8/5-1, SO-97/8/6-2, SO-97/8/6-3, SO-97/8/6-4, SO-97/8/6-5, SO-97misc-17, SO-97misc-18, SO-97misc-19, SO-97misc-37, SO-97misc-39, SO-97misc-40, SO-97misc-42, SO-97misc-134, SO-98misc-1

S. s. sadonis in Sado

NSMT-M16180 (holotype of *S. sadonis* Yoshiyuki et Imaizumi, 1986), NSMT-M26593, NSMT-M26600, NSMT-M26601, NSMT-M26602, NSMT-M27286

S. s. shikokensis in Shikoku

NHMHU-13311 (holotype of *S. caecutiens shikokensis* Abe, 1967)

External Measures

S. caecutiens in Hokkaido

KM-ki112, KM-ko103, KM-ko104, KM-ko121, KM-ko122, KM-ko50, KM-ko51, KM-ko52, KM-ko70, KMko72, KM-ko74, KM-ko83, KM-ko92, KM-ko93, KM-ko94, KM-sh9, KM-tom1, KM-tom3, KM-tom4, KM-tom5, KM-tom7, KM-tom8, KM-tom9, KM-tom19, KM-tom20, KM-tom21, KM-tom22, KM-tom27, KM-tom28, KM-tom29, KM-tom30, KM-tom31, KM-tom32, KM-tom8-53, KM-tom8-54, KM-tom8-57, KM-tom8-58, KM-tom8-67, KM-tom8-68, KM-tom8-69, KM-tom8-70, KM-tom8-71, KM-tom8-72, KM-tom8-73, KM-tom8-74, KM-tom8-75, KM-tom8-76, KM-tom8-77, KM-tom8-78, KM-tom8-79, KM-tom8-82, KM-tom8-92, KM-tom8-93, KM-tom8-94, KM-tom8-95, KM-tom8-128, KM-tom8-130, KM-tom8-131, KM-tom8-132, KM-tom8-132/2, KM-tom8-133, KM-tom8-136, KM-tom8-139, KM-tom8-140, KM-tom8-143, KM-tom8-144, KM-tom8-145, KM-tom8-150, KM-tom8-151, KM-tom8-152, KM-tom8-153, KM-tom8-154, KM-tom8-156, KM-tom8-157, KM-tom8-163, KM-tom8-164, KM-tom8-165, KM-tom8-167, KM-tom8-168, KM-tom8-169, KM-tom8-171, KM-tom8-172, KM-tom8-176, KM-tom8-177, KM-tom8-178, KM-tom8-180, KM-tom8-181, KM-tom8-183, KM-tom9-31, KM-tom9-32, KM-tom9-34, KM-tom9-35, KM-tom9-36, KM-tom9-37, KM-tom9-38, KM-tom9-47, KM-tom9-48, KM-tom9-49, KM-tom9-51, KM-tom9-52, KM-tom9-58, KM-tom9-60, KM-tom9-71, KM-tom9-72, KM-tom9-73, KM-tom9-74, KM-tom9-75, KM-tom9-76, KM-tom9-77, KM-tom9-81, KM-tom9-82, KM-tom9-84, KM-tom9-86, KM-tom9-87, KM-tom9-93, KM-tom9-96, KM-tom9-97, KM-tom9-98, KM-tom9-130, KM-tom9-134, KM-tom9-137, KM-tom9-139, KM-tom9-140, KM-tom9-142, KM-tom9-144, KM-tom9-148, KM-tom9-149, KM-tom9-150, KM-tom9-151, KM-tom9-152, KM-tom9-153, KM-tom9-154, KM-tom9-157, KM-tom9-158, KM-tom9-159, KM-ton66a, SO-1-4, SO-30-1, SO-30-2, SO-31-1, SO-31-2, SO-88c025, SO-88c026, SO-88c060, SO-88c067, SO-88c068, SO-88f053, SO-88f065, SO-88f070, SO-88f096, SO-88f105, SO-88f110, SO-88f123, SO-88f126, SO-88f128, SO-88f132, SO-88f133, SO-88n105, SO-88n168, SO-88n169, SO-88n197, SO-88n203, SO-88n207, SO-88n248, SO-88n263, SO-88n264, SO-88n265, SO-88n274, SO-88n285, SO-88n336, SO-88t002, SO-88t006, SO-88t009, SO-88t012, SO-88t016, SO-89nn021, SO-89nn022, SO-89nn038, SO-89nn045, SO-94/9/13-8, SO-94/9/13-9, SO-94/9/13-10, SO-94/9/13-11, SO-94/9/14-7, SO-94/9/14-8, SO-94/9/14-9, SO-94/9/14-10, SO-94sc3, SO-95/7/12-3, SO-95/7/13-4, SO-95/7/13-10, SO-97/8/16-4, SO-97/8/16-5, SO-97/8/16-6, SO-97/8/16-7, SO-97/8/16-8, SO-97/8/16-9, SO-97/8/16-10, SO-97/8/16-11, SO-97/8/16-12, SO-97/8/16-13, SO-97/8/16-14, SO-97/8/16-15, SO-97/8/16-16, SO-97/8/16-17, SO-97/8/16-18, SO-97/8/17-5, SO-97/8/17-6, SO-97/8/17-7, SO-97/8/17-8, SO-97/8/17-9, SO-97/8/17-10, SO-97/8/17-11, SO-97/8/17-12, SO-97/8/17-13, SO-97/8/17-14, SO-97/8/17-15, SO-97/8/30-2, SO-97/8/31-1, SO-97/8/31-2, SO-97/8/31-9, SO-97/9/1-1, SO-97/9/19-8, SO-97/9/19-9, SO-97/9/19-10, SO-97/9/19-11, SO-98/6/19-6, SO-98/6/19-7, SO-98/6/20-10, SO-98/6/20-11, SO-98/6/20-12, SO-98/7/29-4, SO-98/7/29-5, SO-98/7/29-6, SO-98/7/30-6, SO-98/7/30-7, SO-98/7/30-8, SO-98/7/31-4, SO-98/7/31-5, SO-98/7/31-7

S. s. shinto in Honshu

SO-96misc-9, SO-96misc-10, SO-96misc-11, SO-96misc-13, SO-96misc-14, SO-96misc-15, SO-96misc-16, SO-96misc-17, SO-96misc-18, SO-96misc-19, SO-96misc-20, SO-96misc-21, SO-96misc-22, SO-97misc-37, SO-97misc-39, SO-97misc-40, SO-97misc-133, SO-97misc-134, SO-97/8/2-1, SO-97/8/5-1, SO-97/8/6-1, SO-97/8/6-2, SO-97/8/6-3, SO-97/8/6-4, SO-97/8/6-5