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Phylogenetic Relationships among East Asian Species of *Crocidura* (Mammalia, Insectivora) Inferred from Mitochondrial Cytochrome b Gene Sequences

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ABSTRACT—Phylogenetic relationships among the East Asian species of the genus *Crocidura* (Mammalia, Insectivora) were inferred from the partial sequences (402 base pairs) of the mitochondrial cytochrome b gene. Six species of *Crocidura* and one representative of another insectivoran genus *Suncus* were examined. In the neighbor joining tree, four distinct lineages were recognized: *C. lasiura* from northeastern China and Korea, and *C. dsinezumi* from the main-islands of Japan; *C. attenuata* from Taiwan; *C. watasei* from the Amami and Okinawa Groups, and *S. murinus* from the Miyako Group; and *C. suaveolens* from Tsushima and Taiwan, and *C. sibirica* from Central Asia in Russian territory. All these lineages excluding *C. lasiura* and *C. dsinezumi* were also recognized by the maximum parsimony analysis. Clustering of *C. watasei* with *S. murinus* suggested the non-monophyly of the genus *Crocidura* as of the present definition. Biogeographical implications of the present results were also discussed.

INTRODUCTION

*Crocidura* is the largest mammalian genus consisting of no less than 164 species of small terrestrial shrews widely distributed in the Palaearctic, Ethiopian and Oriental regions (Hutterer, 1993; Wolsan and Hutterer, 1998). The taxonomic arrangement of this genus is still problematic, because several authors studying morphological and genetic properties of its African components casted a doubt to the monophyly of the genus as in relation to other closely related genera, *Suncus* and *Sylvisorex* (Butler et al., 1989; Maddalena, 1990; McLellan, 1994). The non-monophyly as in relation to *Suncus* is also suspected for the Asian *Crocidura* species (Corbet and Hill, 1992), but without concrete evidence.

During the last decade, a number of systematic studies for the Asian *Crocidura* have been performed based on morphological, karyological, and genetic data (Ruedi et al., 1990, 1993, 1998; Heaney and Ruedi, 1994; Kitchener et al., 1994; Ruedi, 1995, 1996; Ruedi and Vogel, 1995; Jenkins and Smith, 1995; Motokawa et al., 1996, 1997; Fang et al., 1997; Motokawa, 1998; Motokawa and Harada, 1998), leading to drastic taxonomic changes from the previous arrangement (Ellerman and Morrison-Scott, 1951; Jenkins, 1976; Lekagul and McNeely, 1977; Jameson and Jones, 1977). In those recent studies, however, the phylogenetic relationships have been assessed only for the Southeast Asian species (Ruedi, 1996; Ruedi et al., 1998): no studies have been made for the comprehensive phylogeny of the East Asian species.

East Asia, consisting of a number of fairly old landbridge islands and the adjacent continent that range in both Palaearctic and Oriental faunal realms, is one of the most important regions to study mammal evolution. Such historical and biogeographical situations have let this region embrace a diverse, highly endemic mammal fauna (Abe et al., 1994;...
Motokawa, 1999; Lin and Lin, 1983). It is generally considered that the ancestors of the East Asian mammal lineages were originally dispersed from areas of both north and south of this region (Abe et al., 1994; Zhang et al., 1997), but the geographical origin of each lineage remains controversial.

In East Asia, seven species are currently recognized for the genus Crocidura: C. lasiura in the northeastern part of the Asian continent including Korean Peninsula; C. suaveolens in eastern continent including Korean Peninsula, Tsushima, and Taiwan; C. dsinezumi in the main-islands of Japan; C. orii in the Amami Group of the central Ryukyus; C. watasei in the Amami Group and the Okinawa Group of the central Ryukyus; C. attenuata in southeastern continent and Taiwan; and C. kurodai in Taiwan (Corbet, 1978; Corbet and Hill, 1992; Abe et al., 1994; Motokawa et al., 1996, 1997; Fang et al., 1997; Zhang et al., 1997; Motokawa, 1998). Of these, C. suaveolens is distributed almost throughout the Palearctic Eurasian continent, whereas C. attenuata occurs in the region from Taiwan to Malay Peninsula (Corbet, 1978; Corbet and Hill, 1992; Fang et al., 1997; Zhang et al., 1997). The remaining five species are endemic to East Asia.

In the present study, a part of the mitochondrial cytochrome b gene was sequenced for five of the East Asian Crocidura species, C. sibirica from Central Asia and Suncus murinus from East Asia, and resultant data were analysed phylogenetically. Our purposes are to hypothesize the phylogenetic relationships among them and to test the monophyly of the genus Crocidura.

### MATERIALS AND METHODS

We used 20 specimens of six Crocidura species and Suncus murinus (Table 1, Fig. 1, Appendix). Akademgorodok City in Russia, from which two specimens of C. sibirica were obtained (not plotted in Fig. 1), is located around 54°40’ N in latitude and 83°05’ E in longitude (Narita et al., 1995). A specimen of S. murinus was from a closed colony, which had been originated from wild caught animals on Taramajima of the Miyako Group, the southern Ryukyus (Oda, 1985).

In Table 1, Specimens of Crocidura and Suncus examined in the present study. Locality numbers given in brackets correspond to those in Fig. 1. Details of localities and voucher specimens are given in Appendix.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Number of specimens examined</th>
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</thead>
<tbody>
<tr>
<td>C. dsinezumi</td>
<td>Toyama [1]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Gifu [2]</td>
<td>1</td>
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<td></td>
<td>Chibujirma [3]</td>
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<td></td>
<td>Yakushima [5]</td>
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<tr>
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<td>China [12]</td>
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</tr>
<tr>
<td></td>
<td>Korea [11]</td>
<td>1</td>
</tr>
<tr>
<td>C. attenuata</td>
<td>Taichung [9]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Pingtung [10]</td>
<td>2</td>
</tr>
<tr>
<td>C. watasei</td>
<td>Amamiushima [6]</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Okinawajima [7]</td>
<td>2</td>
</tr>
<tr>
<td>C. suaveolens</td>
<td>Tsushima [4]</td>
<td>1</td>
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<tr>
<td></td>
<td>Okinawajima [7]</td>
<td>2</td>
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<tr>
<td>C. sibirica</td>
<td>Russia</td>
<td>2</td>
</tr>
<tr>
<td>S. murinus</td>
<td>Taramajima [8]</td>
<td>1</td>
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</table>

Specific names follow Wolsan and Hutterer (1998). The voucher specimens are deposited in the Zoological Department of Kyoto University (KUZ), Osaka City University Medical School (OCUMS), and School of Dentistry of Aichi-Gakuin University (AGUD). The sequence data of Soriculus caudatus, a member of a subfamily (Soricinae) different from that for the genera Crocidura and Suncus (Crocidurinae: Hutterer, 1993), was taken from Ohdachi et al. (1997) and was incorporated into the phylogenetic analyses as outgroup.

Liver samples were removed and stored at –80°C or in 95% ethanol until experiments. The DNA was extracted using the phenol-chloroform method described by Sambrook et al. (1989). A 402 base-pair fragment of the mitochondrial cytochrome b gene was analysed by using the semi-nested polymerase chain reactions (PCR) and direct sequencing method by Suzuki et al. (1997). The primers used for the first PCR (L14724 and H15915) and the second PCR (R-L14724 and U-H15155) are the same as those in Suzuki et al. (1997). Numbers refer to the positions of 3’ base of the primers in the complete sequence of human mitochondrial DNA (Anderson et al., 1981).

Phylogenetic relationships were inferred by two methods: the neighbor joining method (Salitou and Nei, 1987) using PHYLIP program version 3.5c (Felsenstein, 1993) on the basis of pairwise distances calculated following the two-parameter model of Kimura (1980); and the maximum parsimony method using the branch-and-bound search in PAUP (Phylogenetic Analysis Using Parsimony Version 3.1.1, Swoford, 1993) with all character state changes weighted equally. In both analyses, 1000 bootstrap replications (Felsenstein, 1985) were made to assess the degree of supports for internal branches.

### RESULTS

Nucleotide sequence data of 402 base-pairs of the cytochrome b gene are given in Fig. 2. Fourteen haplotypes were observed from the 20 specimens. Of the 402 base-pairs sequenced, 123 sites (30.6%) were variable among 15 haplotypes including the outgroup. Percentage similarities are shown in Table 2. Two haplotypes, differing from each other in one nucleotide site (99.8% similarity), were found in three specimens of C. suaveolens from Taichung. Four haplotypes showing a geographic pattern, were observed in C. dsinezumi (96.0–99.5%): two from the main-islands of Japan (Toyama and Gifu) and the remaining two from small adjoining islands (Chibujirma and Yakushima). Intraspecific geographical divergences were also observed between specimens of C. lasiura from China and Korea (99.0%); C. attenuata from Taichung and Pingtung (99.5%); and C. suaveolens from Tsushima and Taichung (98.8–99.0%). On the other hand, specimens of C. watasei from Amamioshima and Okinawajima showed no sequence differences. The pairwise sequence similarities between conspecifics were consistently larger (96.0–99.8%) than the pairwise values for different species of the genus Crocidura (85.3–94.3%). The similarities of Suncus murinus with Crocidura species examined were mostly smaller (83.8–86.8%) than those within Crocidura, but with a slight overlap.

The neighbor joining tree is shown in Fig. 3A. Monophyly was supported for each of the species having more than one haplotype (74.9–98.4% bootstrap values) and four major clusters were formed with more than 50% bootstrap values: C. dsinezumi and C. lasiura; C. attenuata; C. watasei and S.
Phylogenetic Relationships of Crocidura

Fig. 1. The map showing sampling localities of the species of Crocidura and Suncus examined in the present study. Locality numbers refer to those in Table 1.

DISCUSSION

The genus Suncus, broadly occurring in Africa, and South and Southeast Asia, is considered to be closely related to the genus Crocidura (Corbet and Hill, 1992). Since the former is morphologically distinguished from the latter only by the retention of four upper unicuspid teeth, validity of the current taxonomic arrangement of the two genera has required verifications (Corbet and Hill, 1992). Our results showed that C. watasei is more closely related to S. murinus than to other East Asian Crocidura, and this supports the non-monophyly of the genus in its current arrangement as was suspected by a few previous authors (Butler et al., 1989; Maddalena, 1990; McLellan, 1994). Geographically, both the genus Suncus as a whole and S. murinus are considered to have been originated in South Asia (Butler, 1998; Yosida, 1982). It is thus likely that S. murinus and C. watasei had derived from a common ancestor in South Asia.

In the neighbor joining analysis, C. dsinezumi from the main-islands of Japan was exclusively clustered with C. lasiura from northeastern China and Korea. These two species have similar karyotypes (2n=40), both consisting of three meta- or submetacentric, four subtelocentric, and twelve acrocentric pairs in autosomes (FN=56) (Harada et al., 1985; Zima et al., 1998: see Maddalena and Ruedi [1994] for chromosome terminology). Such a chromosomal arrangement is also shared by two Oriental species: C. attenuata from Taiwan (Motokawa

murinus; and C. sibirica and C. suaveolens. Such relationships other than the monophyly of C. dsinezumi and C. lasiura were also recognized in the maximum parsimony tree (Fig. 3B).
et al., 1997; Fang et al., 1997), and *C. fuliginosa* from Malay Peninsula (2n=40, FN=54–58 with intraspecific variation; Ruedi et al., 1990; Ruedi and Vogel, 1995). Dobson (1994) assumed on the basis of fossil evidence that the ancestral form of *C. dsinezumi* had migrated to Japan from eastern China or Korean Peninsula by the middle Pleistocene. In these possible “original regions” of *C. dsinezumi*, two congeneric species, *C. suaveolens* and *C. lasiura*, are currently distributed (Corbet, 1978), of which *C. suaveolens* was considered to be closer to *C. dsinezumi* by several authors (Kuroda, 1934; Jenkins, 1976) mainly because of their similar body sizes. Our molecular data, as well as previous karyological data (2n=40, FN=50 in *C. suaveolens*: Tsuchiya, 1987), however, suggest that *C. dsinezumi* actually shared the latest common ancestor not with *C. suaveolens*, but with *C. lasiura*.

The geographic origin of the common ancestor of *C. dsinezumi* and *C. lasiura* also remains uncertain. Some authors (Corbet, 1978; Corbet and Hill, 1992; Hutterer, 1993) considered that the Shanghai form (*C. campuslincolnensis*) in the south of Yangtze River, a border of the Palaearctic and Fig. 2. Aligned sequences for 402 base-pairs of the cytochrome *b* gene in *Crocidura* and *Suncus*. Dots indicate identity with the sequence of *Soriculus caudatus*, which data are taken from Ohdachi et al. (1997).
Table 2.  Percentage similarities of cytochrome b sequences of Crocidura, Suncus, and Soriculus caudatus (outgroup taxon).

<table>
<thead>
<tr>
<th>Sample</th>
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<td>3. C. dsinezumi Toyama</td>
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<td>7. C. lasiura China</td>
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</table>

Fig. 3.  The neighbor joining (A) and maximum parsimony (B) trees for Crocidura and Suncus inferred from the cytochrome b gene sequences. Soriculus caudatus was used as outgroup. Nodal values indicate percent supports (>50%) for branches in 1000 bootstrap replications.
Oriental mammal faunas in eastern China (Huang, 1985; Zhang et al., 1997), is conspecific with C. lasiura. Although the present results do not give any information regarding the relationship of this lineage (C. lasiura and C. dsinezumi), the high karyological similarity with the Oriental C. attenuata and C. fuliginosa (see Zima et al., 1998) and the distribution of the species of C. lasiura crossing Yangtze River suggest the southern origin of C. lasiura and C. dsinezumi.

Crocidura watasei is an endemic species to the central Ryukyus, which ancestor may have colonized there during the late Miocene (Motokawa, 1999) when the most recent landbridge connected the central Ryukyus to the continent (Ota, 1998). This species is characterized by its unique karyotype with the reduced chromosome number (2n=26, FN=52) within the genus Crocidura (Maddalena and Ruedi, 1994). Nevertheless, the G-banding pattern of C. watasei is highly homologous to the typical 2n=40, FN=56 format (e.g., C. dsinezumi), and their differences are thus explained by assuming the occurrences of several Robertsonian fusions and translocations in the process of emergence of the former (Harada et al., 1985). Two geographic groups (i.e., northern and southern groups) are recognized in C. watasei on the basis of the morphometric variation (Motokawa et al., 1996), but in the present study no sequence differences were detected between one specimen from Amamioshima in the northern group and two from Okinawajima in the southern group.

The close relationship between C. sibirica from Central Asia and C. suaveolens from East Asia is well demonstrated in the present study. The standard karyotypes of these two species are same (2n=40, FN=50), comprising of two metacentric, two submetacentric and 15 acrocentric pairs in autosomes (Grafodatsky et al., 1988; Tsuchiya, 1987; Fang et al., 1997). This karyotypic format is also shared by the Central Asian and European C. suaveolens and C. gueldenstaedtii (Catzellis et al., 1985; Zima et al., 1998). Geographic ranges of the Crocidura species having the 2n=40, FN=50 format, almost exclusively spread over the Palaearctic region. But in East Asia, the range of C. suaveolens slightly extends to the southern side of Yangtze River in the continent (Zhang et al., 1997) and to Taiwan in the insular region (Fang et al., 1997). Fang et al. (1997) discussed that the Taiwanese C. suaveolens might have migrated from continent China in no earlier than the Pleistocene. Our results also suggest the recent colonization of C. suaveolens to Taiwan from the north, because the genetic divergence among populations of the species from Taiwan and Tsushima is smaller than that observed between C. dsinezumi populations.

Butler (1998) supposed from fossil evidence that the common ancestor of the genus Crocidura had evolved in Africa during the late Miocene and subsequently migrated to the Eurasian region. Such a view is also supported by the protein and chromosomal data (Maddalena, 1990; Maddalena and Ruedi, 1994). According to the hypothetical scenario of Maddalena and Ruedi (1994), this ancestral stock had the karyotype of 2n=38 and FN=54 to 58, characterized by the occurrence of four metacentric pairs. The 2n=40, FN=56 karyomorph restricted to the southeastern continent and East Asia is much similar to the hypothetical ancestral format in general arrangement including the presence of four meta- or submetacentric pairs in autosomes. In addition, C. attenuata is distantly related to the other species with the 2n=40, FN=56 karyotypes (C. dsinezumi and C. lasiura) (Fig. 3), and this suggests the plesiomorphic state of the 2n=40, FN=56 format in the East Asian Crocidura. The common ancestor of the species with the 2n=40, FN=50 karyomorph (e.g., C. suaveolens, C. sibirica) might have emerged somewhere in the Palaearctic region from the 2n=40, FN=56 lineage.

The present molecular and the previous karyological data strongly suggest that the East Asian Crocidura is a mixture of southern and northern elements that are characterized by different fundamental numbers in karyotypes (FN=56 and 50, respectively). Future studies based on more species from the Palaearctic and Oriental parts of the continent should be performed to reconstruct the phylogenetic relationships of the genus Crocidura.

ACKNOWLEDGMENTS

We wish to express our sincere thanks to M. Asakawa for providing a specimen of C. dsinezumi from Chibujima; to S. Alba, S. Hattori, H. Ota, M. Izawa, S. Matsumura, S.-L. Chen, and J. Motokawa for helping with field work; and to K. Serizawa for laboratory assistance. We also thank to T. Hikida, M. Honda, and J. Motokawa for critical comments on early versions of the manuscripts. This study was supported in part by a grant from the Fujiwara Natural History Foundation (to MM), Grant-in-Aid for Encouragement of Young Scientists from the Japan Society for the Promotion of Sciences (No. 11740472, to MM), and Grant-in-Aid for Scientific Research (C) from the Japan Ministry of Education, Science, Sports and Culture (No. 09839037, to KK).

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Specimens examined in this study.
They are deposited with the numbers given in parentheses. See text for abbreviations of acronyms.

*Crocidura dsinezumi*: Tateyama-machi, Toyama, Japan (OCUMS 3703); Shirakawa-mura, Gifu, Japan (OCUMS 4346); Chiburijima Island, Oki Group, Japan (KUZ-M 951); Yakushima Island, Osumi Group, Japan (KUZ-M 938, 941). *C. lasiura*: Changchun, Jilin Province, China (AGUD 900722–55); Hapcheon Gun, Kyungsangnam Do, Korea (OCUMS 5272). *C. attenuata*: Taichung, Taiwan, R.O.C. (KUZ-M 1121); Pingtung Hsien, Taiwan, R.O.C. (OCUMS 6865, 6866). *C. watasei*: Amamioshima Island, Amami Group, Japan (OCUMS 2470); Okinawajima Island, Okinawa Group, Japan (KUZ-M 419, 440). *C. suaveolens*: Tsushima Island, Japan (KUZ-M 1432); Taichung, Taiwan, R.O.C. (KUZ-M 966, 1127 [Taichung-1], KUZ-M 1128 [Taichung-2]). *C. sibirica*: Academgorodok City, Russia (OCUMS 6410, 6412). *Suncus murinus*: Taramajima Island, Miyako Group, Japan (OCUMS 6882).