

Diversification of the white-toothed shrews of the genus *Crocidura* (Insectivora: Soricidae) in East and Southeast Asia

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Abstract. The genus *Crocidura* is one of the largest genera among mammals and widely distributed in Eurasia, Africa, and Southeast Asia. We review the recent advances in taxonomic and phylogenetic studies of this genus in East and Southeast Asia. Sympatric distributions of two or more species are known in several localities. Karyotypes of East and Southeast Asian species are divided into several groups. From karyological comparison and molecular phylogeny, those groups are suggested to have formed by geographical isolation in islands and in the continent in East and Southeast Asia. To clarify evolutionary history of East and Southeast Asian species, comprehensive studies with the West Asian and European species from karyological and molecular approaches are desired.

Key words: Asia, biogeography, *Crocidura*, diversity, systematics.

White-toothed shrews of the genus *Crocidura* are the most diverse genus among mammals comprising of no less than 164 species, and widely distributed in the Ethiopian, Palearctic, and Oriental regions (Hutterer 1993; Wolsan and Hutterer 1998). Butler (1998) discussed from fossil evidence that the genus *Crocidura* had originated in Africa and radiated in the Miocene; and then had entered into Eurasia in the late Miocene. Karyological and biochemical studies suggested that the genus *Crocidura* could be divided into two distinct evolutionary clades: Afrotropical clade and Palearctic and Oriental clade, after separation of two primitive species of *C. luna* and *C. bottegi* in Africa (Maddalena 1990; Maddalena and Ruedi 1994). These clades are, however, controversial in monophyletic relationship of each clade. Because members of the Palearctic–Oriental clade were characterized by possessing the ancestral chromosomal condition of the genus *Crocidura* (Maddalena and Ruedi 1994), relationships within the Palearctic–Oriental members have been focused and studied from evolutionary point of view.

The genus *Crocidura* of crocidurine shrews also has been discussed concerning its monophyletic relationships. Non-monophyly of the genus *Crocidura* has been suspected in relation with *Suncus* and/or *Sylvisorex*; and

phylogenetic relationships among these genera have been discussed by many authors from morphological, biochemical, and molecular studies (Butler et al. 1989; Maddalena 1990; Corbet and Hill 1992; McLellan 1994; Butler 1998; Ruedi 1998; Jenkins et al. 1998; Motokawa et al. 2000; Quérouli et al. 2001; Bannikova et al. 2005; Stanley and Olson 2005). Those studies produced incongruent results due to the different species examined. In East and Southeast Asia, *Suncus* may be included within the genus *Crocidura* (e.g., Motokawa et al. 2000).

Many taxonomic and phylogenetic studies have been conducted recently for *Crocidura* shrews on East and Southeast Asia (Appendices 1 and 2), where the genus shows high species diversity within the Palearctic–Oriental regions. Based on these studies, several hypotheses about phylogenetic relationship and evolutionary history of the genus *Crocidura* have been proposed and tested (e.g., Maddalena and Ruedi 1994; Ruedi et al. 1998a; Motokawa et al. 2000; Biltueva et al. 2001; Ohdachi et al. 2004). The genus *Crocidura* became one of much studied animals, and accordingly used to be a model for zoogeography of terrestrial animals in East and Southeast Asia (Turner et al. 2001; van Welzen et al. 2003).

In this paper, we review recent advances in taxonomic

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and phylogenetic studies of the genus *Crocidura* in East and Southeast Asia; propose hypothesis on evolutionary history of the genus; and provide several unsolved questions to be studied in future.

Study regions and taxonomy

In this paper, we focus on *Crocidura* species distributed in East and Southeast Asia. In the continent and its offshore small islands, we review region of Korea, China and Indochina Peninsula to Malay Peninsula (Vietnam, Laos, Cambodia, Myanmar, Thailand, Malaysia, and Singapore). Because animal distribution may continuous over these regions, we used information from South Asia and North Asia for species concerned or related species when necessary. In insular region, we focus on East Asian island chain of Japan (the Japanese Archipelago and the Ryukyu Archipelago), Taiwan (including two islands off eastern coast, Lanyu and Lutaotao), and Korea (Cheju Island); Hainan island in China; Southeast Asian Islands of Malaysia, Indonesia, and Philippines (including Sumatra, Java, Borneo, Sulawesi, and Philippines).

Systematics of the *Crocidura* species has been much confused and is still controversial. In this paper, we started from a checklist of Hutterer (1993) and then incorporated many recent systematic studies to complete species list of East and Southeast Asian *Crocidura* (Table 1, Appendices 1 and 2). Because of recent drastic changes of taxonomic status at species level, some of past and recent reports of *Crocidura* species were difficult to fit with current taxonomy without reference to the voucher specimens. Thus, distribution ranges may be narrower than actual distribution in several species, especially in the continental species.

Species status

In East and Southeast Asia, 43 species of the genus *Crocidura* are recognized (Table 1). Many of species have been taxonomically confused, and species numbers have been underestimated; many undescribed species or cryptic species may still inhabit in East and Southeast Asia. To clarify phylogeny and evolution of the genus *Crocidura* in East and Southeast Asia, the alpha level taxonomy played the most important role. Hutterer (1993) recognized only 27 species from the same area, while we count 43 species (and 50 species/subspecies) (Table 1). Number of species increased approximately 160% in 12 years between 1993 and 2005. This increase

in species number is a result of taxonomic studies conducted after 1990 and reevaluation of specific status of many species. These studies were conducted from morphological study of external features and skull features, examination of karyotypes and intraspecific/interspecific chromosomal comparison by using differential staining techniques, examination of allozyme or biochemical variation, and recently increased DNA sequence and band analyses. New species and subspecies described since 1993 count four and one, respectively.

Ruedi (1995) made a revision of *Crocidura* species in the Sunda Shelf and Sulawesi and described two new species of *C. hutani* from Sumatra and *C. musseri* from Sulawesi. These findings of new species must have been possible with extensive revision of the genus in wide areas in Southeast Asia.

Jenkins and Smith (1995) described *C. hilliana* as a new species from Thailand based on remains recovered from owl pellets. In describing *C. hilliana*, Jenkins and Smith (1995) also established an identification key among *C. hilliana*, *C. attenuata* and *C. fuliginosa*, the latter two of which are medium to large sized *Crocidura* and had been much confused taxonomically in East and Southeast Asia (e.g., Jenkins 1976, 1982; Heaney and Timm 1983; Corbet and Hill 1992; Ruedi 1995).

Lunde et al. (2004) described a new species of *C. kegoensis* from Vietnam, that is a small species in Southeast Asia. The same specimen was firstly reported as *Crocidura* sp. by Feiler and Ziegler (1999). In describing the new species, Lunde et al. (2004) revised *C. horsfieldii* group, which is small *Crocidura* and another example that had been much confused taxonomically in East and Southeast Asia. Corbet and Hill (1992) and Hutterer (1993) included *watasei*, *tadae*, *kurodai*, *wuchihensis*, *indochinensis* as junior synonym or subspecies of *C. horsfieldii* from East and Southeast Asia. Currently, *C. horsfieldii* is confined to India and Sri Lanka, and all of the above-mentioned synonyms are separated as *C. watasei*, *C. tadae tadae*, *C. tadae kurodai*, *C. wuchihensis*, and *C. indochinensis* (Motokawa et al. 1996, 2004; Motokawa 1999; Fang and Lee 2002; Lunde et al. 2003, 2004). Fang and Lee (2002) described a new subspecies of *C. tadae lutaotaoensis* from Lutaotao, a small offshore island of eastern Taiwan.

In addition to describing new species, important works were division of species and changing in combination of synonyms. Many studies have been focused on taxonomic statuses on many synonyms and geographic variation of species group previously treated as one species.

Table 1. Species of the genus *Crocidura* occurred in East and Southeast Asia. Species name, distribution, karyotype (2n, diploid chromosome number; FN, fundamental number including two X chromosomes; X, X chromosome; Y, Y chromosome; M, metacentric; SM, submetacentric; ST, subtelocentric; A, acrocentric; chromosome terminology following Maddalena and Ruedi 1994), and availability of the mitochondrial cytochrome b gene sequence data (○, available) are indicated. References for each species are given in Appendices 2.

Species	Distribution	Karyotype				Cyt b
		2n	FN	X	Y	
<i>C. dsinezumi</i>	Japan (main islands)	40	56	SM	ST	○
<i>C. orii</i>	Central Ryukyus	–	–	–	–	–
<i>C. watasei</i>	Central Ryukyus	26	52	SM	A	○
<i>C. lasiura</i>	Korea, China, Russia	40	54	M	A	○
<i>C. sibirica</i>	Russia, Mongolia, China	40	50	M	ST	○
<i>C. tanakae</i>	Taiwan	40	56	SM	A	○
<i>C. gmelini</i>	China	–	–	–	–	–
<i>C. shantungensis</i>	China, Korea, Cheju Is., Tsushima Is., Taiwan	39, 40	50	M, SM	A	○
<i>C. tadae tadae</i>	Lanyu, offshore island of Taiwan	40	–	–	–	–
<i>C. tadae kurodai</i>	Taiwan	40	56	SM	A	○
<i>C. tadae lutaoensis</i>	Lutao, offshore island of Taiwan	40	–	–	–	–
<i>C. vorax</i>	China, Lao PDR	–	–	–	–	–
<i>C. rapax</i>	China	–	–	–	–	–
<i>C. attenuata</i>	China, Vietnam, Thailand, Burma, Bhutan, Nepal, India, Philippines	35, 36, 38	54	SM	A	○
<i>C. fuliginosa</i>	Burma, China, Thailand, Vietnam, Lao PDR, P. Malaysia	40	54–58	SM	SM, A	○
<i>C. malayana</i>	P. Malaysia and offshore islands	38, 39, 40	62–68	SM, ST	M, SM	–
<i>C. hilliana</i>	Thailand, Lao PDR	50	66	SM	ST	–
<i>C. indochinensis</i>	Myanmar, China, Vietnam	–	–	–	–	–
<i>C. wuchihensis</i>	China (Hainan Island), Vietnam	–	–	–	–	–
<i>C. kegoensis</i>	Vietnam	–	–	–	–	–
<i>C. negligens</i>	P. Malaysia and offshore islands	38	62	ST	SM	–
<i>C. monticola</i>	P. Malaysia, Thailand, Sumatra, Java, Borneo, Lesser Sunda	–	–	–	–	–
<i>C. lepidura</i>	Sumatra	37, 38	54	A	SM	○
<i>C. hutanis</i>	Sumatra	36	54	ST	–	–
<i>C. beccarii</i>	Sumatra	38	56	ST	SM	○
<i>C. vosmaeri</i>	Sumatra (Banka island)	–	–	–	–	–
<i>C. paradoxura</i>	Sumatra	–	–	–	–	○
<i>C. brunnea brunnea</i>	Java	38	56	SM	A	○
<i>C. brunnea pudjonica</i>	Java, Bali	–	–	–	–	–
<i>C. orientalis orientalis</i>	Java	38	56	ST	M	–
<i>C. orientalis lawuana</i>	Java	38	56	ST	SM	–
<i>C. baluensis</i>	Borneo	–	–	–	–	–
<i>C. foetida foetida</i>	Borneo	38	56	ST	–	○
<i>C. foetida doriae</i>	Borneo	38	56	ST	SM	–
<i>C. foetida kelabit</i>	Borneo	38	56	ST	SM	–
<i>C. elongata</i>	Sulawesi	30, 34	56, 62	SM	A	○
<i>C. musseri</i>	Sulawesi	32	54	–	–	○
<i>C. rhoditis</i>	Sulawesi	30	50	SM	ST	○
<i>C. nigripes nigripes</i>	Sulawesi	38	56	SM	–	○
<i>C. nigripes lipara</i>	Sulawesi	38	56	SM	ST	○
<i>C. lea</i>	Sulawesi	–	–	–	–	○
<i>C. levicula</i>	Sulawesi	34	52	SM	SM	○
<i>C. palawanensis</i>	Philippines (Palawan)	–	–	–	–	–
<i>C. grayi</i>	Philippines (Luzon and Mindoro)	38	58	ST	SM	–
<i>C. beatus</i>	Philippines (Mindanao)	38(?)	–	–	–	○
<i>C. mindorus</i>	Philippines (Mindoro and Sibuyan)	–	–	–	–	○
<i>C. negrina</i>	Philippines (Negros)	–	–	–	–	–
<i>C. grandis</i>	Philippines (Mindanao)	–	–	–	–	–
<i>C. tenuis</i>	Timor	–	–	–	–	–
<i>C. trichura</i>	Christmas Is.	–	–	–	–	–

Currently recognized 43 species have roughly 40 more junior synonyms in total, including names over the range discussed in this paper (Appendix 1). Revised systematics are summarized in Ruedi (1995) for species in the Sunda Shelf and Sulawesi, Heaney and Ruedi (1994) for the Philippine species, Motokawa (1999) for the Japanese species, Fang et al. (1997) and Fang and Lee (2002) for the Taiwan species, Jiang and Hoffmann (2001) for the Chinese species, and Jenkins and Smith (1995) and Lunde et al. (2003, 2004) for the continental species. Many other taxonomic studies at species level were conducted for species in Japan (Motokawa et al. 1996, 2003; Motokawa 1998, 2003; Takada et al. 2004), Taiwan (Motokawa et al. 1997, 2003, 2004), Korea (Iwasa et al. 2001; Han et al. 2002; Motokawa et al. 2003), China (Hoffmann 1996; Lazell 1998; Motokawa et al. 2001), other continental areas (Davison et al. 1982; Jenkins 1982; Heaney and Timm 1983; Davison 1984; Ruedi et al. 1990; Motokawa and Harada 1998; Smith et al. 1998; Robinson 1999; Feiler and Ziegler 1999), and Southeast Asian Islands (Kitchener et al. 1994; Heaney et al. 1998; Meek 2000).

As mentioned above, medium–large sized *C. fuliginosa*–*C. attenuata* (and –*C. malayana*) species complex and small sized *C. horsfieldii* species complex were important works to revise. In addition, *C. suaveolens* species complex has also been confused and a taxon to be revised. As seen in Corbet and Hill (1992) and Hutterer (1993), this small species was thought to be widely distributed from Europe to East Asia. Hoffmann (1996) designated neotype and revised taxonomic position of *Sorex gmelini* as a valid species of *C. suaveolens* species complex and he recognized three species of *C. shantungensis*, *C. suaveolens*, and *C. gmelini* within *C. suaveolens* sensu lato. Jiang and Hoffmann (2001) gave a detail of systematics and distribution of this group; they recognized *C. gmelini* and *C. shantungensis* in East Asia, and considered *C. suaveolens* to be distributed from Europe to West Asia.

While most of recent studies increased number of *Crociodura* species distributed in East and Southeast Asia, only one example that reduced species number is the case in small sized *C. monticola*. Ruedi (1995) considered *C. monticola* to be widely distributed in Southeast Asia from Malay Peninsula and Thailand in south of the Isthmus of Kra, Sumatra, Java, Borneo, and Lesser Sunda Islands; and to include *C. maxi* and *C. neglecta* as junior synonyms. *Crociodura maxi* and *C. neglecta* had been separated as one or two valid species distinct

from *C. monticola* (Davison et al. 1982; Davison 1984; Jenkins 1982; Corbet and Hill 1992; Kitchener et al. 1994).

Sympatric distribution

In several localities in East and Southeast Asia, sympatric (including syntopic) distributions of more than two *Crociodura* species are known (Table 2). Pattern and pair of sympatric distribution of *Crociodura* species is assumed to be formed by the past dispersal history as well as the past and present ecological competition between two or more species.

In the northern temperate region, only one or two species are distributed in given locality, and coexisting two shrew species tend to have different body sizes, probably

Table 2. Sympatric or syntopic species pairs of the genus *Crociodura* reported from East and Southeast Asia. Sympatric or syntopic pair, number of co-existing species (*n*), and locality are given. Jiang and Hoffmann (2001)'s *C. horsfieldii* may represents *C. indochinensis*.

Sympatric or syntopic pairs	<i>n</i>	Locality
<i>C. orii/C. watasei</i>	2	C. Ryukyus ^c
<i>C. tadar kurodai/C. tanakae</i>	2	Taiwan ^d
<i>C. shantungensis/C. tanakae</i>	2	Taiwan ^b
<i>C. shantungensis/C. lasiura</i>	2	northern China ^c
<i>C. fuliginosa/C. attenuata/C. vorax/ C. horsfieldii</i>	4	Yunnan, China ^c
<i>C. fuliginosa/C. vorax/C. rapax</i>	3	Yunnan, China ^c
<i>C. fuliginosa/C. attenuata</i>	2	southern China ^c
<i>C. attenuata/C. shantungensis</i>	2	southern China ^c
<i>C. vorax/C. rapax</i>	2	southern China ^c
<i>C. fuliginosa/C. horsfieldii</i>	2	southern China ^c
<i>C. rapax/C. horsfieldii</i>	2	southern China ^c
<i>C. attenuata/C. vorax</i>	2	southern China ^c
<i>C. fuliginosa/C. vorax</i>	2	southern China ^c
<i>C. attenuata/C. horsfieldii</i>	2	southern China ^c
<i>C. fuliginosa/C. attenuata/C. wuchihensis</i>	3	Vietnam ^f
<i>C. malayana/C. monticola</i>	2	P. Malaysia ^a
<i>C. malayana/C. negligens</i>	2	P. Malaysia ^a
<i>C. lepidura/C. beccarii/C. paradoxura</i>	3	Sumatra ^a
<i>C. brunnea brunnea/C. orientalis orientalis</i>	2	Java ^a
<i>C. brunnea brunnea/C. monticola</i>	2	Java ^a
<i>C. brunnea pudjonia/C. orientalis lawuana</i>	2	Java ^a
<i>C. brunnea pudjonia/C. monticola</i>	2	Java ^a
<i>C. nigripes lipara/C. musseri/C. lea/ C. elongata/C. rhoditis</i>	5	Sulawesi ^a
<i>C. nigripes nigripes/C. lea/C. elongata/ C. rhoditis</i>	4	Sulawesi ^a

^a Ruedi 1995, ^b Fang et al. 1997, ^c Motokawa 1999, ^d Yu et al. 2001, ^e Jiang and Hoffmann 2001, ^f Lunde et al. 2003.

resulting from “competition in the past” in sympatric shrews (Kirkland 1991; Hanski 1994; Yu et al. 2001): e.g., *C. lasiura* is much larger than *C. shantungensis* in northeastern Asia (e.g., Jones and Johnson 1960).

Similar trend in size difference is also observed in subtropical sympatric *Crocidura* species pairs: large *C. orii* and small *C. watasei* in Amamiyoshima in the central Ryukyus, although available information of these two species are scarce and they may have parapatric distribution with overlap (Motokawa 1999); large *C. tanakae* and small *C. tadae kurodai* in mountains of Taiwan (Yu et al. 2001); large *C. tanakae* and small *C. shantungensis* in lowland Taiwan (Fang et al. 1997). In Taiwan, additional species of shrews *Chodsigoa sodalis* and *Suncus murinus* are also distributed in mountains and lowlands, respectively; and they are sympatric with two *Crocidura* species above mentioned (Fang et al. 1997; Yu et al. 2001). Yu et al. (2001) discussed that co-existence of *C. tanakae* and *C. tadae kurodai* can be maintained by abundant food supplies around year and annually continuous breeding activity. Those two species may utilize different size or kind of food, and they may have different life cycle (Yu et al. 2001).

In the continent and Southeast Asian islands, number of sympatric species is variable among localities (Table 2). In islands, historical factors such as time and number of migration may have affected the number of species distributed and coexisted. It is interesting that five and four species coexist in Sulawesi and Yunnan Province of China. Five species in central Sulawesi (*C. nigripes lipara*, *C. musseri*, *C. lea*, *C. elongata*, and *C. rhoditis*) were reported as syntopic distribution (Ruedi 1995). This suggests that tropical environment have potential to inhabit as many as five species of *Crocidura* shrews. Ecological and behavioral interactions and life history comparison among syntopic species are interesting to resolve mechanism of coexistence, and comparative studies between different areas (e.g., tropical, subtropical, and temperate regions) are desired to be conducted.

Phylogenetic reconstructions

In the genus *Crocidura*, many species show similar morphological features, so that overall size has considered one of good identification key, as well as bristle hairs abundance and its distribution on the tail (e.g., restricted to base of tail, half of tail, almost of tail). These identification keys are often useful between sympatric or parapatric species in given place: e.g., identifi-

cation of three species in Taiwan, *C. tanakae*, *C. tadae kurodai*, and *C. shantungensis* (see Fang et al. 1997). On the other hand, different local populations of same species sometimes much differ in its overall size. One example is body and skull size difference among populations of *C. shantungensis* in Cheju Island, Tsushima Island, Korean Peninsula and Taiwan; Tsushima Island population is similar to the Korean Peninsula population, while the Cheju Island population and the Taiwan population are much larger than the Tsushima/Korean Peninsula populations; and these three (Tsushima Island plus Korean Peninsular populations, the Cheju population, and the Taiwan population) may be recognized as separate subspecies (Motokawa et al. 2003). In contrast, they showed a little sequence difference in mitochondrial cytochrome b gene (Motokawa et al. 2000; Ohdachi et al. 2004). Extent of morphological sexual dimorphism was also differed among populations (Motokawa et al. 2003): the Taiwan population showed extensive sexual dimorphism, while the Tsushima Island and Korean Peninsula populations showed little difference between sexes (the Cheju Island population have not been examined due to limited specimens). This example suggests that skull features could be change within a short period and sometimes provide insufficient information to reconstruct phylogenetic relationships among species. Combination of characters not only from skull but also from external features, and for both metric and non-metric characters, may give useful information for phylogenetic relationships among species (e.g., Heaney and Ruedi 1994 for phylogenetic relationships among Philippine *Crocidura* species), but useful characters are limited as Heaney and Ruedi (1994) could examine only eight non-metric characters for phylogenetic purposes.

Therefore, genetic markers became more useful tool to reconstruct phylogenetic relationships in the genus *Crocidura*; and many studies have been conducted for East and Southeast Asian *Crocidura* species by genetic markers using karyological analyses (Ruedi et al. 1990; Maddalena and Ruedi 1994; Ruedi and Vogel 1995; Motokawa et al. 1997, 2001, 2004; Fang et al. 1997; Motokawa and Harada 1998; Zima et al. 1998; Biltueva et al. 1999, 2001; Fang and Lee 2002), allozyme or biochemical analyses (Ruedi et al. 1990, 1993; Heaney and Ruedi 1994; Ruedi 1996), mitochondrial cytochrome b gene sequence analyses (Ohdachi et al. 1997, 2004; Ruedi et al. 1998a, b; Motokawa et al. 2000, 2001, in press; Iwasa et al. 2001; Han et al. 2002), mitochondrial control region sequence analyses (Hausser et al. 1998),

and DNA restriction site analyses (Bannikova et al. 1996; Iwasa et al. 2001).

Maddalena and Ruedi (1994) discussed the chromosome evolution in the genus *Crocidura*; they hypothesized that the ancestral karyotype of this genus is $2n = 36-40$ ($2n$: diploid chromosome number) and $FN = 54-58$ (FN : fundamental number including two X chromosomes); and the genus *Crocidura* is divided into two evolutionary lineages after splitting of *C. luna* and *C. bottegi* in Africa, the African clade and the Palearctic and Oriental clade. Palearctic and Oriental clade have karyotypes with stability or decreasing chromosome number ($2n = 22-40$, $FN = 34-68$) from the hypothesized ancestral karyotype, while the African clade is characterized by possessing karyotypes with increased chromosome and fundamental numbers ($2n = 42-60$, $FN = 66-86$) from the ancestral karyotype.

Since Maddalena and Ruedi (1994), karyological information for East and Southeast Asian *Crocidura* has been much increased. As well, differential staining karyotype techniques such as G-band and C-band revealed relationships between different karyotypes (Biltueva et al. 1999, 2001). These increased information on East and Southeast Asian *Crocidura* almost support the view of Maddalena and Ruedi (1994), and suggests that the Palearctic and Oriental species can be subdivided into several groups based on karyotypes. It may be possible to reconstruct evolutionary history from chromosome rearrangement patterns in combination with geographic distribution and the recently increased molecular phylogenetic data. We propose a hypothetical view from available information until now.

Karyotype groups and evolution

Currently available data for karyotypes of East and Southeast Asian *Crocidura* are summarized in Table 1. We compared conventional karyotypes from figures given in the original reference when possible. As a result, we can recognize several karyotype groups. First group is found in species in Southeast Asian islands of Sumatra, Java, Borneo, Philippines, and Sulawesi including ten species (14 species/subspecies): *C. negligens*, *C. lepidura*, *C. hutanis*, *C. beccarii*, *C. brunnea brunnea*, *C. orientalis orientalis*, *C. orientalis lawuana*, *C. foetida foetida*, *C. foetida doriae*, *C. foetida kelabit*, *C. grayi*, *C. beatus*, *C. nigripes nigripes*, and *C. nigripes lipara*. These species have karyotypes with $2n = 36-38$ and $FN = 54-62$ (Ruedi and Vogel 1995; Rickart 2003) and those

karyotypes can be regarded closely related to the hypothesized ancestral karyotype of the genus *Crocidura* (karyotypes of several species were not figured in report by Ruedi and Vogel 1995, but they are assumed to be similar to the other species) proposed by Maddalena and Ruedi (1994) with $2n = 36-40$ and $FN = 54-58$. These karyotypes have the smallest acrocentric autosome pair similar in size to the second smallest acrocentric pair.

Second group is found in four species in Sulawesi: *C. elongata*, *C. musseri*, *C. rhoditis*, and *C. levicula*. These species have decreased $2n$ from the ancestral karyotype: $2n = 30-34$ and $FN = 50-62$ (Ruedi and Vogel 1995). The smallest two acrocentric pairs are similar in size in these species. Five species karyotyped from Sulawesi are classified into the first and second groups. Molecular study suggested that the first group (one species including two subspecies: *C. n. nigripes* and *C. n. lipara*) is closely related to the other Southeast Asian islands species, while the second group (four species: *C. elongata*, *C. musseri*, *C. rhoditis*, and *C. levicula*; and one more species not karyotyped, *C. lea*) formed a distinct lineage that is sister group of the other Southeast Asian islands and the continental species (*C. fuliginosa*, Ruedi et al. 1998a, b). Species in Sulawesi are considered to have colonized in two different times, and the second group here is thought to be the early immigrants (Ruedi 1996, Ruedi et al. 1998a).

Third group is found in five species in East Asia and the continent with $2n = 40$ and $FN = 56$ karyotype: *C. fuliginosa*, *C. dsinezumi*, *C. lasiura*, *C. tanakae*, and *C. tadar kurodai* (Orlov and Bulatova 1983; Wang et al. 1983; Harada et al. 1985; Tada and Obara 1986; Ruedi et al. 1990; Ruedi and Vogel 1995; Motokawa et al. 1997, 2001, 2004; Fang et al. 1997; Zima et al. 1998; Biltueva et al. 1999; Fang and Lee 2002). Because short arm of the smallest subtelocentric pair is short and sometimes regarded as acrocentric, this karyotype was also reported as $FN = 54$; but we considered $FN = 56$. In *C. fuliginosa*, intraspecific chromosome variation was reported and FN varied from 54 to 58 (Wang et al. 1983; Ruedi et al. 1990; Ruedi and Vogel 1995). In this group, the smallest acrocentric autosome pair is much smaller than the second smallest pair that distinguishes this karyotype group from the first and second karyotype groups in Southeast Asian islands. The Chinese *C. attenuata* has karyotypes of $2n = 35, 36, 38$ and $FN = 54$, with individual Robertsonian variation (Motokawa et al. 2001). These karyotypes are obviously derived from $2n = 40$ and $FN = 56$ karyotype recently through rearrangements

by at least one tandem translocation as revealed from G-band chromosome comparison and cytochrome b gene analysis with the Taiwan *C. tanakae* (see Motokawa et al. 2001). *Crocidura tanakae* was previously classified conspecific with the continental *C. attenuata*, but Motokawa et al. (2001) proposed to separate *C. tanakae* as a different species by those karyological differences.

Fourth group includes only a species *C. watasei* in the central Ryukyus, which is considered to have been isolated in the central Ryukyus since the Pliocene (Motokawa 2000). This species has karyotype with $2n = 26$ and $FN = 52$ (Harada et al. 1985), characterized by reduced chromosome number compared with the other East and Southeast Asian species. G-band karyotype comparison suggested that *C. watasei* had derived from $2n = 40$ and $FN = 56$ karyotype with five Robertsonian fusion and two centromere-telomere translocations (Harada et al. 1985).

Fifth group is found in two species in East Asia: *C. shantungensis* and *C. sibirica* with $2n = 40$ and $FN = 50$ karyotype (Tsuchiya 1987; Graphodatsky et al. 1988; Fang et al. 1997). The smallest acrocentric pair is similar in size to the second smallest acrocentric pair. This karyotype is also observed in West Asian and European species of *C. gueldenstaedtii* and *C. suaveolens* (Catzefflis et al. 1985; Graphodatsky et al. 1988; Zima et al. 1998; Biltueva et al. 1999). In Tsushima Island of Japan, individual chromosome variation was reported as $2n = 39-40$ and $FN = 50$ (Tsuchiya 1987). This variation is considered the Robertsonian polymorphism (Tsuchiya 1987).

There are two more species, which were karyotyped in East and Southeast Asia: *C. malayana* ($2n = 38-40$, $FN = 62-68$) in Malay Peninsula (Ruedi et al. 1990; Ruedi and Vogel 1995) and *C. hilliana* ($2n = 50$, $FN = 66$) in Thailand (Motokawa and Harada 1998). Among the Palearctic and Oriental species, these two species are characterized by having karyotypes with increased fundamental number. As discussed by Motokawa and Harada (1998), *C. attenuata* described by Tsuchiya et al. (1979) ($2n = 50$, $FN = 66$) is thought to actually represent *C. hilliana*. There is no evidence to support close phylogenetic relationships of *C. malayana* and *C. hilliana* with increased fundamental number.

Our hypothesized karyological relationships among karyotype groups are given in Fig. 1. Southeast Asian karyotypes (the first group) with $2n = 36-38$ and $FN = 54-62$ can be considered to be closely related to the ancestral karyotype of the genus *Crocidura* proposed by

Maddalena and Ruedi (1994). Old Sulawesi species karyotypes (the second group) with $2n = 30-34$ and $FN = 50-62$ are likely to have derived from the ancestral karyotype in reducing chromosome number. As mentioned above, East Asian karyotype (the third group) with $2n = 40$ and $FN = 56$, as well as *C. attenuata* karyotypes with intraspecific chromosome variation ($2n = 35, 36, 38$ and $FN = 54$) and *C. watasei* karyotype with $2n = 26$ and $FN = 52$ are karyologically closely related from each other. Eurasian karyotype (the fourth group) with $2n = 40$ and $FN = 50$ is suggested to be closely related to $2n = 40$ and $FN = 56$ karyotype from G-band comparison of several *Crocidura* species (Biltueva et al. 1999, 2001). Relationship of karyotypes with increased fundamental number in *C. malayana* and *C. hilliana* could not be identified, because banding karyotypes have not been obtained.

Recent evidences from molecular phylogeny give some more suggestion in chromosome evolution and species phylogeny of East and Southeast Asian *Crocidura*. Available molecular data almost support the karyotype groupings as well as providing some useful information. East Asian karyotype ($2n = 40$ and $FN = 56$) species are suggested not to constitute a monophyletic group in relation to $2n = 26$ and $FN = 52$ species and $2n = 40$ and $FN = 50$ species (Motokawa et al. 2000, 2001; Han et al. 2002). This may suggest that $2n = 40$ and $FN = 56$ karyotype was the ancestral karyotype for the continental and East Asian *Crocidura*, from which $2n = 40$ and $FN = 50$, and $2n = 26$ and $FN = 52$ karyotypes had derived.

From fossil evidence, the genus *Crocidura* is considered to have migrated to Eurasia in the late Miocene (Butler 1998). Because *C. watasei* with $2n = 26$ and $FN = 52$ karyotype is thought to have migrated to the central Ryukyu islands in the late Miocene (Motokawa 2000) from biogeographic view; it is suggested that karyotype divergence of East and Southeast Asian *Crocidura* resulting formation of at least five major karyotype groups may have taken place soon after the migration of the genus *Crocidura* into Asia. These karyotype groups might have been produced by geographical isolation in islands (e.g., Southeast Asian islands, Sulawesi, Ryukyus) and within the continent: $2n = 40$ and $FN = 56$ karyotype probably originated in south, while $2n = 40$ and $FN = 50$ karyotype originated in north by some dispersal barriers (e.g., Ruedi et al. 1993; Motokawa et al. 2000).

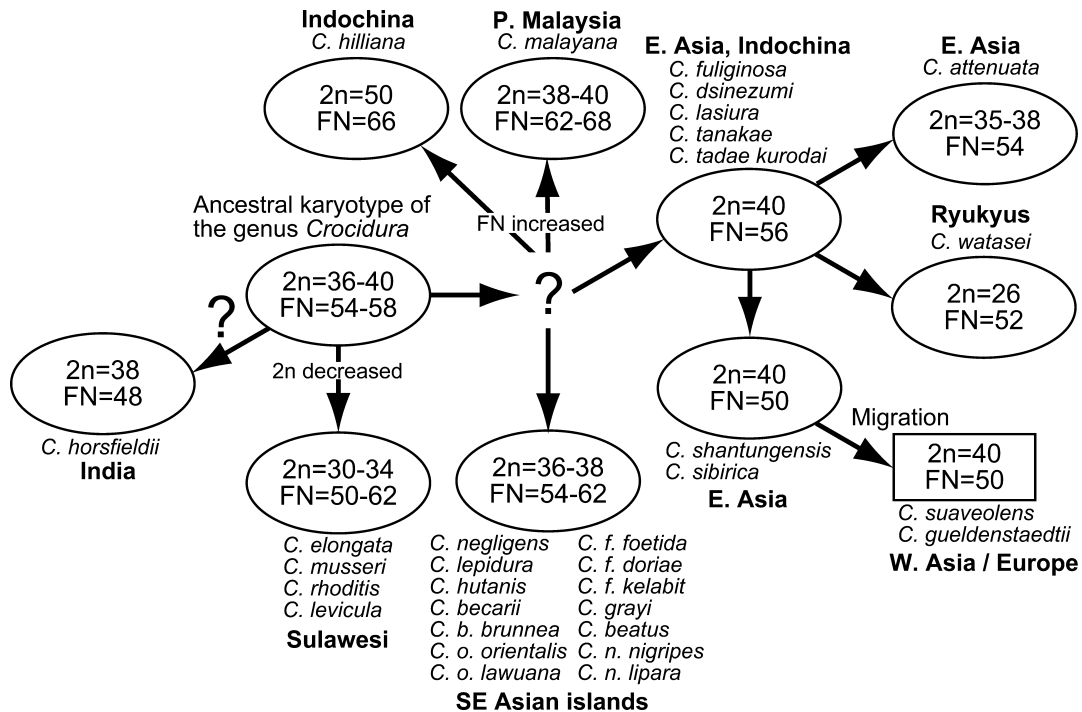


Fig. 1. Hypothesized karyological relationships of the genus *Crocidura* in East and Southeast Asia.

Unsolved questions

There are still many problems in Southeast and East Asian *Crocidura* species phylogeny and evolution to be solving in future. First question is whether Southeast Asian karyotypes with $2n = 36-38$ and $FN = 54-62$ represent or the most closely related to the ancestral karyotype of the genus *Crocidura*. Another candidate more closely related to the ancestral karyotype is East Asian $2n = 40$ and $FN = 56$ karyotype. Many species in the continent especially in the southern China and Indochina Peninsula have not been karyotyped. Karyological examination of these species including banding techniques such as G-band karyotypes is desired to be performed. More studies should also be focused on $2n = 38$ and $FN = 48$ karyotype found in Indian *C. horsfieldii* (Krishna Rao and Aswathanarayana 1978; Aswathanarayana 2003).

Second question is concerning to evolution of $2n = 40$ and $FN = 56$ species and their monophyletic relationships. Previous molecular studies of the genus *Crocidura* provided phylogenetic relationships in separated area such as in East Asia (Motokawa et al. 2000, 2001; Han et al. 2002; Ohdachi et al. 2004), Southeast Asia (Ruedi et al. 1998a, b) and Europe (Vogel et al. 2003). Comprehensive molecular phylogenetic study covering

the Palearctic and Oriental regions are desired to solve phylogenetic relationships among species with $2n = 40$ and $FN = 56$ and related karyotypes.

If $2n = 40$ and $FN = 50$ karyotype had derived in East Asia from $2n = 40$ and $FN = 56$ karyotype, members possessing similar karyotype in Europe and West Asia (*C. suaveolens* and *C. gueldenstaedtii*) must have migrated from East Asia (Fig. 1). In Europe and West Asia, the other distinct karyotypes are also known: $2n = 42$ and $FN = 60$ in *C. russula*, $2n = 42$ and $FN = 70-72$ in *C. cossyrensis*, $2n = 28$ and $FN = 56$ in *C. leucodon*, $2n = 36$ and $FN = 56$ in *C. sicula* and *C. canariensis*, $2n = 34$ and $FN = 44$ in *C. zimmermanni*, $2n = 28$ and $FN = 46$ in *C. ramona*, and $2n = 22$ and $FN = 34$ in *C. serezykensis* (Ivanitskaya et al. 1996; Zima et al. 1998; Biltueva et al. 2001; Vogel et al. 2004). Some of these species may also have close relationships with East and Southeast Asian species, but comparative study has been limited (Biltueva et al. 2001). There are many systematic problems also among European species (e.g., Sarà and Vogel 1996; Vogel and Sofianidou 1996; Molina et al. 2003; Vogel et al. 2004; Brutto et al. 2004; Cosson et al. 2005; Brändli et al. 2005; Poulakakis et al. 2005) and some of those problems may be clarified by reconstructing Eurasian (Asia and Europe) wide karyological relationships and molecular phylogeny. Biltueva et al.

(2001) suggested close karyological relationships between East Asian $2n = 40$ and $FN = 56$ karyotype and *C. leucodon* $2n = 28$ and $FN = 56$ karyotype, but this relationship may discordant with molecular phylogeny (Vogel et al. 2003; Bannikova et al. 2005). This may be a result of parallel chromosome rearrangements in different clades.

Because of high chromosome variability and species richness, *Crociodura* shrews are good example to study animal biogeography and phylogeny. In addition, within species, chromosome and high level of molecular divergences have recently been reported: e.g., individual chromosome polymorphism in *C. attenuata* in the continental China (Motokawa et al. 2001), geographic Y chromosome variation in *C. tadae kurodai* in Taiwan (Motokawa et al. 2004), extensive cytochrome b gene variation between two geographical races in *C. dsinezumi* in Japan (Han et al. 2002; Ohdachi et al. 2004; Motokawa et al. in press). In future, *Crociodura* shrews will also provide good examples for study of speciation events.

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Appendix 1.

Crocicidura species in East and Southeast Asia, and the species names used in Hutterer (1993) in parenthesis and junior synonyms. See Appendix 2 for reference.

C. dsinezumi (*C. dsinezumi*): *chisai*, *intermedia*, *okinoshimae*, *umbrina*. *C. orii* (*C. orii*). *C. watasei* (*C. horsfieldii*). *C. lasiura* (*C. lasiura*): *campuslincolnensis*, *lizenkani*, *sodyi*, *thomasi*, *yamashinai*. *C. sibirica* (*C. sibirica*): *ognevi*. *C. tanakae* (*C. attenuata*). *C. gmelini* (–): *hyrcania*, *mordeni*, *ilensis*, *lignicolor*, *lar*. *C. shantungensis* (*C. suaveolens*, *C. dsinezumi*): *hosletti*, *quelpartis*, *phaeopus*, *coreae*, *utsuryoensis*. *C. tadae tadae* (*C. horsfieldii*). *C. tadae kurodai* (*C. horsfieldii*). *C. tadae lutoaensis* (–). *C. vorax* (*C. pullata*). *C. rapax* (*C. pullata*). *C. attenuata* (*C. attenuata*): *grisea*, *kingiana*, *rubricosa*. *C. fuliginosa* (*C. fuliginosa*, *C. malayana*): *dracula*, *gravida*, *praedax*. *C. malayana* (*C. malayana*): *klossii*, *aoris*, *aagardi*. *C. hilliana* (–). *C. indochinensis* (*C. horsfieldii*). *C. wuchihensis* (*C. horsfieldii*). *C. kegoensis* (–). *C. negligens* (*C. malayana*): *maporensis*, *tionis*. *C. monticola* (*C. monticola*, *C. maxi*, *C. neglecta*): *maxi*, *neglecta*. *C. lepidura* (*C. fuliginosa*): *villosa*. *C. hutanis* (–). *C. beccarii* (*C. beccarii*, *C. malayana*): *weberi*. *C. vosmaeri* (*C. fuliginosa*). *C. paradoxura* (*C. paradoxura*, *C. attenuata*): *aequicauda*. *C. brunnea brunnea* (*C. fuliginosa*): *brevicauda*, *melanorhyncha*. *C. brunnea pudjonica* (*C. fuliginosa*). *C. orientalis orientalis* (*C. fuliginosa*). *C. orientalis lawuana* (*C. fuliginosa*). *C. baluensis* (*C. fuliginosa*). *C. foetida foetida* (*C. fuliginosa*). *C. foetida doriae* (*C. fuliginosa*). *C. foetida kelabit* (*C. fuliginosa*). *C. elongata* (*C. elongata*). *C. musseri* (–). *C. rhoditis* (*C. rhoditis*). *C. nigripes nigripes* (*C. nigripes*). *C. nigripes lipara* (*C. nigripes*). *C. lea* (*C. lea*). *C. levicula* (*C. levicula*). *C. palawanensis* (*C. palawanensis*). *C. grayi* (*C. grayi*): *halconus*. *C. beatus* (*C. beatus*): *parvacauda*. *C. mindorus* (*C. mindorus*). *C. negrina* (*C. negrina*). *C. grandis* (*C. grandis*). *C. tenuis* (*C. tenuis*, *C. fuliginosa*). *C. trichura* (*C. attenuata*).

Appendix 2.

Reference for Table 1 and Appendix 1.

C. dsinezumi: Harada et al. 1985; Tada and Obara 1986; Ruedi 1993; Biltueva et al. 1999, 2001; Motokawa 1999, 2003; Motokawa et al. 2000; Han et al. 2002; Ohdachi et al. 2004. *C. orii*: Motokawa 1998, 1999. *C. watasei*: Harada et al. 1985; Motokawa et al. 1996, 2000; Motokawa 1999; Biltueva et al. 2001; Ohdachi et al. 2004. *C. lasiura*: Orlov and Bulatova 1983; Zima et al. 1998; Motokawa et al. 2000; Ohdachi et al. 2004. *C. sibirica*: Graphodatsky et al. 1988; Motokawa et al. 2000; Jiang and Hoffmann 2001; Biltueva et al. 2001; Ohdachi et al. 2004. *C. tanakae*: Motokawa et al. 1997, 2000, 2001; Fang et al. 1997. *C. gmelini*: Hoffmann 1996; Jiang and Hoffmann 2001. *C. shantungensis*: Tsuchiya 1987; Hoffmann 1996; Fang et al. 1997; Motokawa 1999; Motokawa et al. 2000, 2003; Iwasa et al. 2001; Jiang and Hoffmann 2001; Ohdachi et al. 2004. *C. tadae tadae*: Fang and Lee 2002. *C. tadae kurodai*: Fang et al. 1997; Fang and Lee 2002; Motokawa et al. 2004; Ohdachi et al. 2004. *C. tadae lutoaensis*: Fang and Lee 2002. *C. vorax*: Jiang and Hoffmann 2001. *C. rapax*: Jiang and Hoffmann 2001. *C. attenuata*: Heaney and Ruedi 1994; Lazell 1998; Heaney et al. 1998; Feiler and Ziegler 1999; Motokawa et al. 2001; Jiang and Hoffmann 2001; Lunde et al. 2003. *C. fuliginosa*: Wang et al. 1983; Ruedi et al. 1990, 1998; Ruedi 1995, 1996; Ruedi and Vogel 1995; Robinson 1999; Jiang and Hoffmann 2001; Lunde et al. 2003. *C. malayana*: Ruedi et al. 1990; Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. hilliana*: Jenkins and Smith 1995; Motokawa and Harada 1998; Smith et al. 1998; Robinson 1999. *C. indochinensis*: Lunde et al. 2003, 2004. *C. wuchihensis*: Lunde et al. 2003, 2004. *C. kegoensis*: Feiler and Ziegler 1999; Lunde et al. 2004. *C. negligens*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. monticola*: Kitchener et al. 1994; Ruedi 1995, 1996. *C. lepidura*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. hutanis*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. beccarii*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. vosmaeri*: Ruedi 1995. *C. paradoxura*: Ruedi 1995, 1996; Ruedi et al. 1998. *C. brunnea brunnea*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. brunnea pudjonica*: Kitchener et al. 1994; Ruedi 1995. *C. orientalis orientalis*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. orientalis lawuana*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. baluensis*: Ruedi 1995. *C. foetida foetida*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. foetida doriae*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. foetida kelabit*: Ruedi 1995, 1996; Ruedi and Vogel 1995. *C. elongata*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. musseri*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. rhoditis*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. nigripes nigripes*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. nigripes lipara*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. lea*: Ruedi 1995, 1996; Ruedi et al. 1998. *C. levicula*: Ruedi 1995, 1996; Ruedi and Vogel 1995; Ruedi et al. 1998. *C. palawanensis*: Heaney and Ruedi 1994; Heaney et al. 1998. *C. grayi*: Heaney and Ruedi 1994; Ruedi 1996; Heaney et al. 1998; Rickart 2003. *C. beatus*: Heaney and Ruedi 1994; Ruedi 1996; Ruedi et al. 1998; Heaney et al. 1998; Rickart 2003. *C. mindorus*: Heaney and Ruedi 1994; Ruedi 1996; Heaney et al. 1998; Ruedi et al. 1998. *C. negrina*: Heaney and Ruedi 1994; Heaney et al. 1998. *C. grandis*: Heaney and Ruedi 1994; Heaney et al. 1998. *C. tenuis*: Ruedi 1995. *C. trichura*: Ruedi 1995; Meek 2000.