Chapter 10

Descriptions of New Species of *Crocidura* (Soricomorpha: Soricidae) from Mainland Southeast Asia, with Synopses of Previously Described Species and Remarks on Biogeography

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ABSTRACT

The species of *Crocidura* occurring in southern China, northern Myanmar and Vietnam, are reviewed and defined based on morphology and multivariate analyses. Three new species are described: *C. cranbrooki* from northern Myanmar, *C. annamitensis* from the Annamite Mountains of Vietnam, and *C. guy* from the Viet Bac limestone region in northeastern Vietnam. Enhanced comparative descriptions, distribution, and remarks on taxonomy are provided for each of the other nine species previously reported from the region: *C. fuliginosa*, *C. attenuata*, *C. sokolovi*, *C. vorax*, *C. rapax*, *C. indochinensis*, *C. wuchihensis*, *C. kegoensis*, and *C. zaitsevi*.

INTRODUCTION

White-toothed shrews of the genus *Crocidura* range throughout Africa and across Europe and the Palaearctic to Southeast Asia as far as islands to the east of Sulawesi. The genus comprises more than 172 species (Hutterer, 2005)—the largest number for any genus of mammal, yet throughout its range it is typically among the least known member of the mammal fauna. This is particularly true for mainland Southeast Asia, a topographically and ecologically complex region where the faunas of the southern Palearctic and eastern Himalayas converge with Indochina. At least 14 species of *Crocidura* occur in this area; however, the group remains poorly known, and it is likely that there are still more unrecognized species within the genus.

Much of what we know of the *Crocidura* of these regions is based on the specimens collected by historical museum expeditions. The collections available in the Natural History Museum, London (BMNH) and the American Museum of Natural History (AMNH) are logical starting points for any research on mainland Southeast Asian mammals because of the important early work that was based at these institutions. Significant collections from China held in the BMNH include those resulting from the Duke of Bedford's expeditions to Sichuan and Yunnan (Thomas, 1912a) and those collected by George Forrest in northern Yunnan (Thomas, 1922; 1923). Likewise for Indochina the BMNH houses important collections made by the Sladen-Godman Expedition (Thomas, 1925) and the four Indochina expeditions of Jean Delacour and Willoughby Lowe (Lowe, 1947). These combined with the collections of F. Kingdon Ward and Lord Cranbrook from northern Myanmar round out the BMNH collections as one of the best records of the regional fauna.

Specimens held in the AMNH are equally significant and include those collected by the first Asiatic Expedition to Yunnan and Burma [Myanmar], the third Asiatic Expedition to Sichuan and Fukien [Fujian] (Andrews, 1932) and the Vernay-Cutting Burma

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[Myanmar] Expedition (Anthony, 1941). The Kelly-Roosevelts' Expedition to Indochina of the Field Museum, Chicago (Osgood, 1932) is of similar importance.

For much of the last century, the shrews collected during these expeditions formed the basis for what little was known of the *Crocidura* of mainland Southeast Asia and for many years the only summaries of Southeast Asian *Crocidura* diversity were those included in checklists and faunal works, such as: Allen (1938), Ellerman and Morrison-Scott (1951), Van Peenan et al. (1969), and Corbet and Hill (1992). These were followed by studies concentrating specifically on Asian *Crocidura*: Jenkins (1976), Heaney and Timm (1983), Jiang and Hoffmann (2001), and Motokawa et al. (2000, 2005).

Adequately defining the various species of Southeast Asian *Crocidura* requires gathering together as many specimens as possible. Many species exhibit only subtle morphological distinctions but examined collectively, differences in size, body proportions, cranial and dental morphology, and pelage color may be recognized and associated with names fixed by holotypes. We are fortunate in having ready access to some of the most important collections of *Crocidura* in our respective institutions, including a substantial number of the holotypes. In total 267 specimens were examined including all those available from other museum collections.

Our purpose in reviewing these museum collections of historical series, type specimens and recent collections and drafting this synopsis of the morphological basis of currently known species of Southeast Asian *Crocidura*, is to provide a context for the description of three additional new species: two from small samples recently collected in Vietnam, and one from museum specimens collected long ago in northern Myanmar. These are just the latest in a string of new species descriptions in recent years (Jenkins and Smith, 1995; Jenkins et al. 2007; Lunde et al., 2003, 2004) and it is our hope that the present work will serve as a useful reference and taxonomic benchmark summarizing the currently known species diversity of *Crocidura* from SW China, northern Myanmar, and Indochina.

MATERIALS AND METHODS

INSTITUTIONS AND SPECIMENS: Specimens listed in the Species Accounts and cited by catalog number are stored in the collections of the American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Institute of Zoology, Chinese Academy of Sciences, Beijing (IZAC); Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Museum für Tierkunde, Dresden (MTD); Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia (ZIN). These acronyms preface catalog numbers referring to specimens listed in the tables, text, and figure legends. A full account of the geographic sources used to determine coordinates is given in the gazetteer in appendix 1.

ANATOMICAL DESCRIPTIONS: Descriptions of anatomical features follow Hutterer (1985) for external morphology; Meester (1963), Mills (1966), Butler and Greenwood (1979), and Dannelid (1998) for dental nomenclature; and McDowell (1958), Meester (1963), and Novacek (1993) for skull morphology (see figs. 1–4).

Abbreviations used in the text for the dental nomenclature are incisor (I/i), unicuspid (Un), premolar (P/p), molar (M/m) with premaxillary and maxillary teeth denoted by uppercase and mandibular teeth by lowercase letters.

MEASUREMENTS: Values in millimeters (mm) for lengths of tail (TL), hind foot (HF), and ear (E) are those recorded by collectors on the specimen tags. Length of head and body (HB) was obtained directly from original collectors' labels or by subtracting tail length from total length. Weights are in grams and are as recorded by the collector. We used digital calipers to measure the 31 cranial and dental dimensions listed below, which were used in the metric analyses. These include the 14 measurements illustrated in figure 4, which are the subset used in the accompanying diagnostic tables; from our experience, we

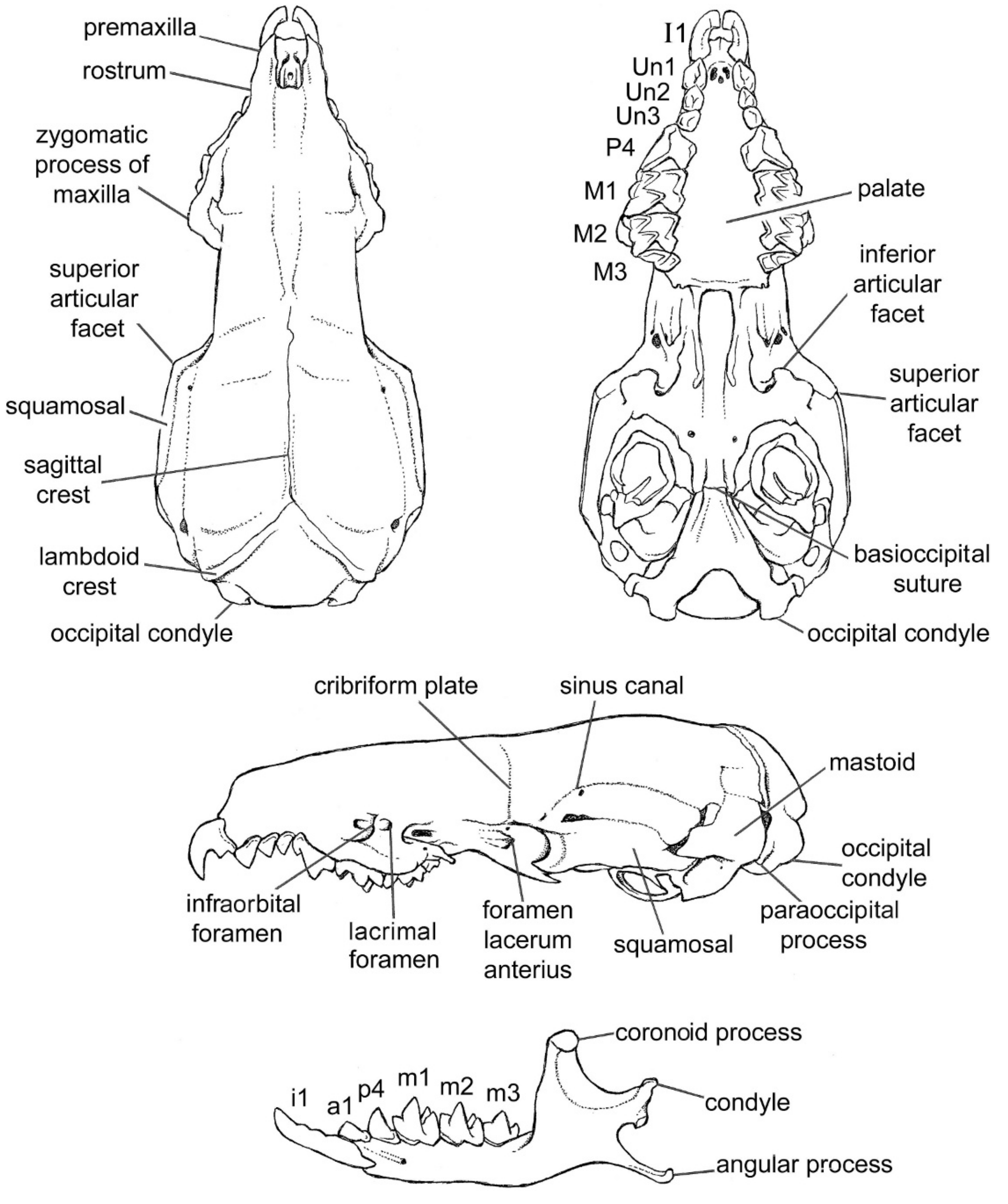

Fig. 1. Dorsal and ventral views of the cranium and lateral views of the cranium and mandible, indicating osteological features mentioned in the text.

are confident that these measurements may be taken with a good degree of consistency and are the ones most useful for identification.

Skull Measurements

Condyloincisive length (CIL): the maximum length from the anterior surfaces of the first upper

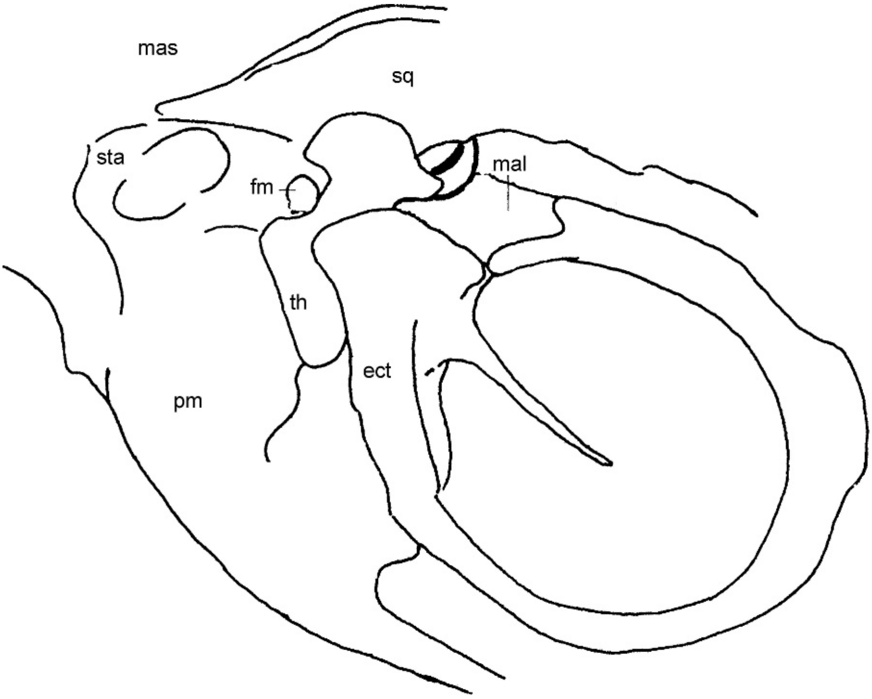

Fig. 2. Detail of the right auditory region of the skull viewed ventrolaterally, indicating osteological features mentioned in the text: **ect**, ectotympanic; **fm**, foramen mastoideum; **mal**, malleus; **mas**, mastoid; **pm**, petromastoid; **sq**, squamosal; **sta**, fossa for stapedius muscle; **th**, tympanohyal.

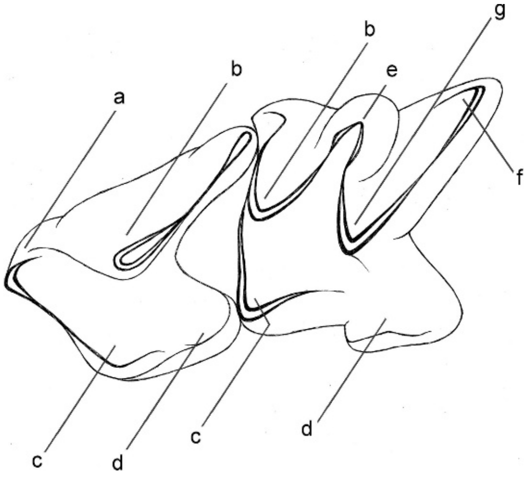

Fig. 3. Occlusal view of left P4 and M1 of *Crocidura attenuata* with cusp nomenclature indicated: **a**, parastyle; **b**, paracone; **c**, protocone; **d**, hypocone; **e**, mesostyle; **f**, metastyle; **g**, metacone.

incisors to the posterior margins of the occipital condyles, parallel to the long axis of the skull.

Condylobasal length (CBL): the maximum length from the anteriormost tips of the premaxillae to the posterior of the occipital condyles, parallel to the long axis of the skull.

Upper toothrow length (UTRL): the maximum length from the anterior face of the first upper incisor to the posterior border of the last upper molar, parallel to the long axis of the skull.

Incisor-3rd unicuspid length (I-Un3): the maximum length from the anterior face of the first upper incisor to the posterior margin of the third unicuspid.

M2-M2 breadth (M2-M2): the maximum breadth across the outer anterobuccal margins of the parastyles of the second upper molars.

Zygomatic breadth (ZB): the breadth across the zygomatic plates.

Rostral breadth (RB): the breadth across the maxillae at the level of the third upper unicuspids.

Anterior breadth of upper unicuspids (RB@Un1): the breadth across the outer margins of the first upper unicuspids.

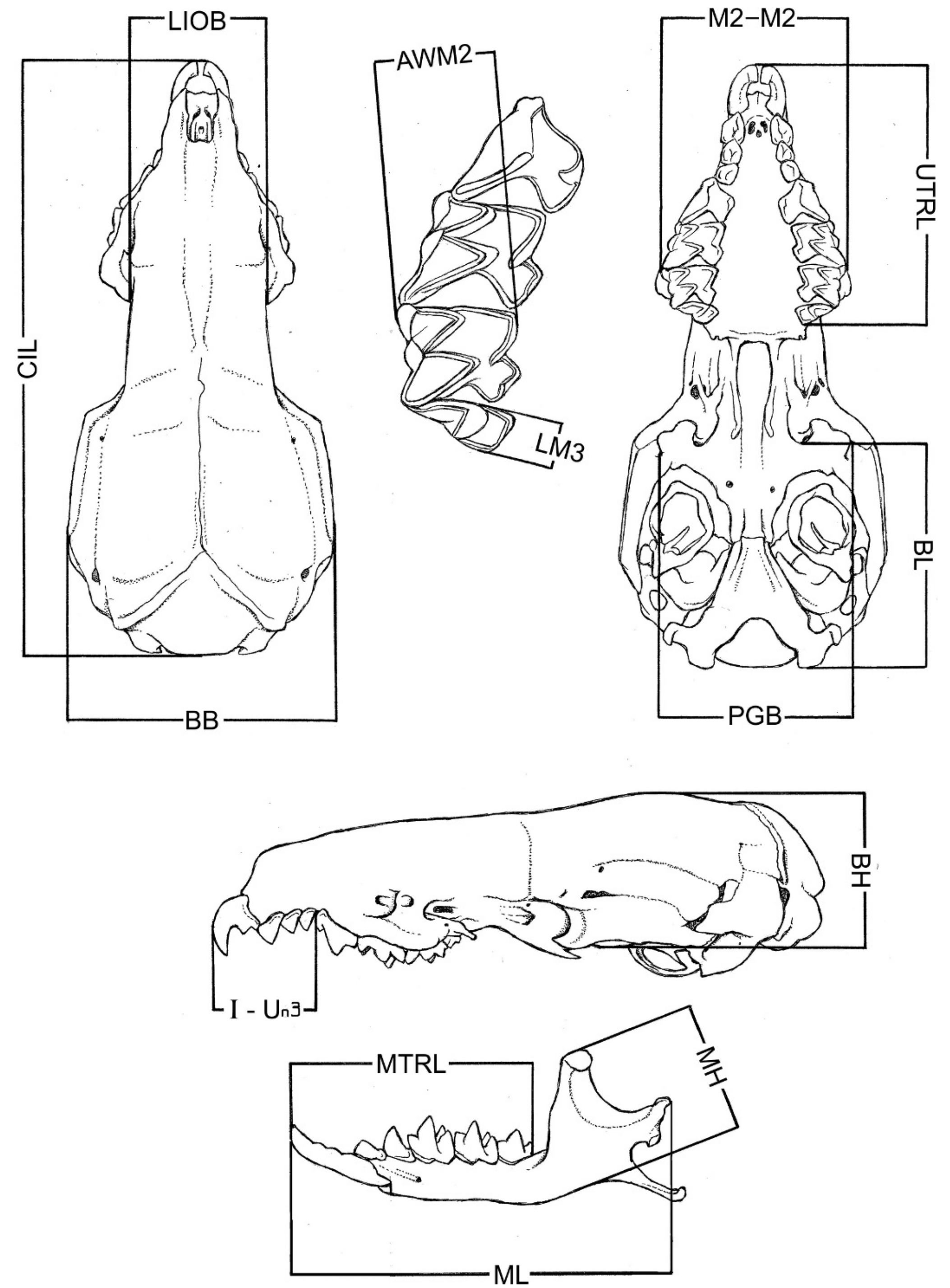

Fig. 4. Dorsal and ventral views of the cranium, lateral views of the cranium and mandible, and details of the postunicuspid dentition showing limits of cranial and dental measurements. See text for abbreviations and additional information.

Posterior breadth of upper unicuspids (RB@Un3): the breadth across the outer margins of the third upper unicuspids.

Rostral depth (RD): the depth of the rostrum from the nasals to the apices of the third upper unicuspids.

Least interorbital breadth (LIOB): the breadth across the narrowest portion of the interorbital region.

Interorbital depth (ID): the depth of the interorbital region posterior to the border of the palate.

Interorbital length (M3-PGN): the length from posterior edge of third upper molar to the postglenoid notch.

Braincase breadth (BB): the greatest breadth of the braincase measured across the junction of the most anteroventral part of the mastoid and the squamosals.

Braincase height (BH): the height of the braincase measured along the midline of the basisphenoid to the top of the skull.

Braincase length (BL): the length of the braincase from the epicondylar/postglenoid notch to the posterior margin of the occipital condyle.

Dorsal braincase length (BLdors): the length of the braincase from the superior articular facets to the posterior margin of the occipital condyle.

Postglenoid breadth (PGB): the greatest breadth across the lateral margins of the inferior articular facets.

Postglenoid depth (PGD): the depth of the braincase at the level of the inferior articular facets.

Mandible Measurements

Mandible length (ML): the length from the tip of the lower incisor to the posterodorsal facet of the condylar process.

Mandible length excluding lower incisor (ML-i): the length from the anterior of the first lower premolar to the posterodorsal facet of the condylar process.

Mandibular toothrow length (MTRL): the length from the tip of the lower incisor to the posterior border of the third lower molar.

Mandibular toothrow length excluding lower incisor (MTL-i): the length from the anterior of the first lower antemolar to the posterior border of the third lower molar.

Mandible height (MH): the vertical height of the coronoid process of the ascending ramus.

Ascending ramus length (ARL): length from the posterior border of the third lower molar to the posterodorsal facet of the condylar process.

Condyle height (CH): the height from the dorsal to the ventral facet of the condylar process.

Condyle breadth (CW): the breadth of the ventral facet of the condylar process.

Dental Measurements

Anterior width of M2 (AWM2): the greatest width of the second upper molar as measured from the anterolingual margin of the protocone to the anterobuccal margin of the parastyle.

M3 length (LM3): the greatest anterior-posterior length of the last upper molar, measured parallel to long axis of the skull.

Lower incisor length (LiL): the buccal length of the first lower incisor from the tip to the insertion.

Lower incisor height (LiH): the basal depth of the first lower incisor, anterior to the first premolar.

Metric Analyses: A total of 154 adult specimens of *Crocidura* were included in the analyses. These specimens, indicated by an asterisk against the catalog number in each species account, were categorized in 28 groups, to investigate possible relationships and the extent of variation within and among these groups. Groups were labeled by a two-letter code as indicated in table 1, with an initial capital letter followed by a lowercase letter representing, respectively, the species name and a location. For consistency and to minimize variation in measuring technique, all 31 craniodental measurements used in the metric analyses were taken by one of us (P.D.J.). The external measurements were excluded from the analyses because of the high degree of variability associated with measurements taken by different collectors. Measurement data were compiled in a spreadsheet.

Because of the nature of museum material, many of the available skulls are damaged to a greater or lesser extent, so that it is often difficult to take a complete series of measurements on every specimen. In general, analyses require a full suite of measurements for each specimen and therefore either the analysis must be restricted to a data subset (i.e., a subset of the specimens and a subset of the measurements), in which a complete matrix is available, or some means of estimating missing values must be applied

TABLE 1
Summary of Species Groups Used in the Metric Analyses

Subset	Species	Group code	Location	Group size
A	*C. fuliginosa*	Fc	Lichiang, Yunnan, China	6
A	*C. fuliginosa*	Fk	Jinsha Jiang, Yunnan, China	3
A	*C. fuliginosa*	Fo	Nam Ting, Yunnan, China	6
A	*C. fuliginosa*	Ft	Sa Pa, Vietnam	24
A	*C. fuliginosa*	Fy	Yunnan, China – other localities	6
A	*C. attenuata*	Ah	Houng Son, Vietnam	13
A	*C. attenuata*	Aq	Ngoc Linh, Vietnam	2
A	*C. attenuata*	Ar	Lang Bian, Vietnam	3
A	*C. attenuata*	As	Sichuan, China	13
A	*C. attenuata*	Av	Vietnam – other localities	6
A	*C. attenuata*	Ay	Yunnan, China	2
A	*C. sokolovi*	Sq	Ngoc Linh, Vietnam	2
A	Species 1	Cb	Myanmar	16
B	*C. vorax*	Vc	Lichiang, Yunnan, China	1
B	*C. rapax*	Rb	Myanmar	2
B	*C. rapax*	Rc	Lichiang, Yunnan, China	6
B	*C. rapax*	Rv	Vietnam – other localities	3
B	*C. rapax*	Ry	Yunnan, China – other localities	6
B	*C. indochinensis*	Ib	Myanmar	4
B	*C. indochinensis*	Iv	Vietnam	2
B	*C. indochinensis*	Iy	Yunnan, China	1
B	*C. wuchihensis*	Wh	Vietnam, northern	7
B	*C. wuchihensis*	Wt	Vietnam, southern	9
B	*C. wuchihensis*	Wv	Ba Na, Vietnam	1
B	*C. kegoensis*	Kh	Ke Go, Vietnam	1
B	*C. zaitsevi*	Zq	Ngoc Linh, Vietnam	2
B	Species 2	Dh	Houng Son, Vietnam	3
B	Species 3	Nt	Na Hang, Vietnam	4
		(28 groups)	TOTAL	154

to a ''nearly complete'' subset. Under the former, two extremes are to limit the subset to: (a) only those specimens for which the full set of measurements may be taken, which would effectively reduce the available sample size, or (b) only those measurements that are present for all specimens, thus considerably reducing the number of possible measurements.

The analysis undertaken and here reported employed a missing value estimation method applied to the data set, excluding one measurement variable which was often not available and was considered to be unreliable. A few specimens, in which the crania were particularly badly damaged, were also excluded from the analyses.

Multivariate analyses using principal components and canonical variates were used to explore the patterns of phenetic differentiation. Analyses were run on the logarithmically transformed data set of craniodental measurements. Principal component analysis (PCA) is used to assess the general appropriateness of the groupings supplied by looking at the overall variation in the log-transformed measurements. This technique is very dependent on the choice of variables. Canonical variate analysis (CVA) is used to assess the distinctiveness between groups by looking at variation between groups relative to variation within groups. This technique is more robust to choices of measurement variables.

The principal component and the canonical variate analyses were initially run on all groups to provide an overview of relationships between all species. Subsequent analyses were made to compare separate combinations of species: Subset A: the largest

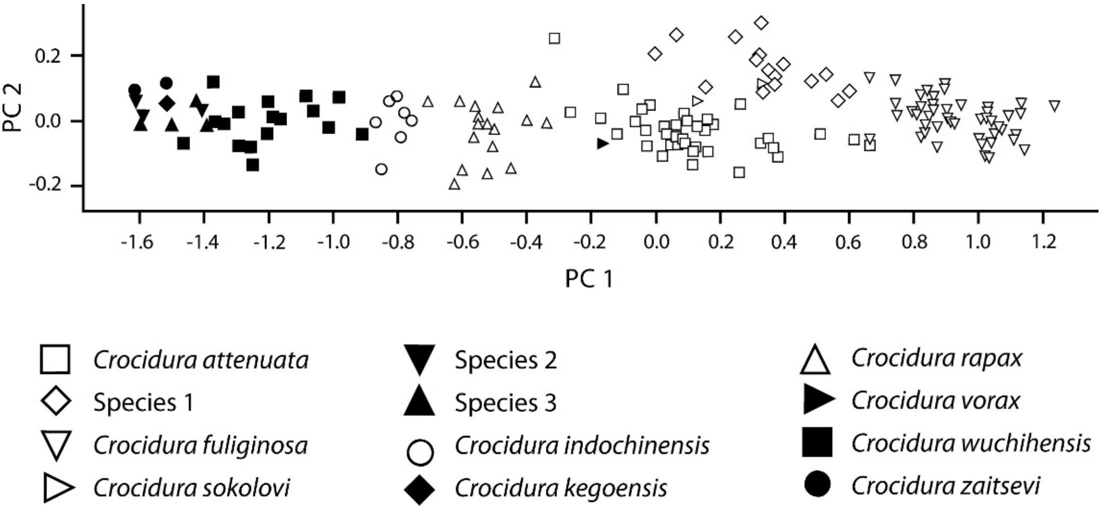

Fig. 5. Principal components plot (1st versus 2nd axes) for all specimens of Indochinese *Crocidura* included in the metric analyses. Symbols representing the species are placed at x-y locations representing the factor scores.

species *C. fuliginosa*, *C. sokolovi*, *C. attenuata*, and one undescribed species (Species 1); and Subset B: the medium- and small-sized species *C. vorax*, *C. rapax*, *C. indochinensis*, *C. wuchihensis*, *C. kegoensis*, *C. zaitsevi*, and two undescribed species (Species 2 and Species 3).

The analyses were executed using Genstat version 10 (Payne et al., 2007).

RESULTS

Metric Analyses

The first component of the PCA accounts for the greatest extent of variation (indeed, the bulk of variation [respectively 93% for analysis of all species; 81% for analysis of Subset A: *C. fuliginosa*, *C. sokolovi*, *C. attenuata*, and Species 1; 77% for analysis of Subset B: *C. vorax*, *C. rapax*, *C. indochinensis*, *C. wuchihensis*, *C. kegoensis*, *C. zaitsevi*, Species 2, and Species 3]) between individuals and consequently tends to provide visually separate groupings for the species (see fig. 5). This figure shows moderately good separation between species on this axis, which is clearly related to skull size since specimens belonging to the species with the largest skulls, *C. fuliginosa* are ranged at one extreme of this axis, while the four species with the smallest skulls, *C. kegoensis*, *C. zaitsevi*, and two undescribed species, respectively Species 2 and Species 3, are ranged toward the opposite extreme of the axis. The species with the greatest sample sizes, *Crocidura attenuata*, with fairly large-sized skulls, shows more variation on both component axes than any of the other species. The four species with the smallest skulls (all samples being of small size) are closely grouped with *C. wuchihensis*, which has slightly larger skulls but much greater sample sizes. See appendix 2 for latent roots, percentage variation and latent vector loadings.

In the CVA for all specimens, most species show good separation along the first axis when group means and confidence regions are plotted (fig. 6), and when individual specimens are plotted (fig. 7). *Crocidura fuliginosa*, *C. attenuata*, Species 1, *C. rapax*, and *C. wuchihensis* are all clearly separate from each other; however, individual specimens of *C. indochinensis* are less evidently separate from *C. rapax* and *C. wuchihensis* and individual specimens of the four very small-sized species, *C. kegoensis*, *C. zaitsevi*, Species 2, and Species 3, also intergrade with *C. wuchihensis*.

Species were divided into two groups on the basis of skull size and analyzed separately

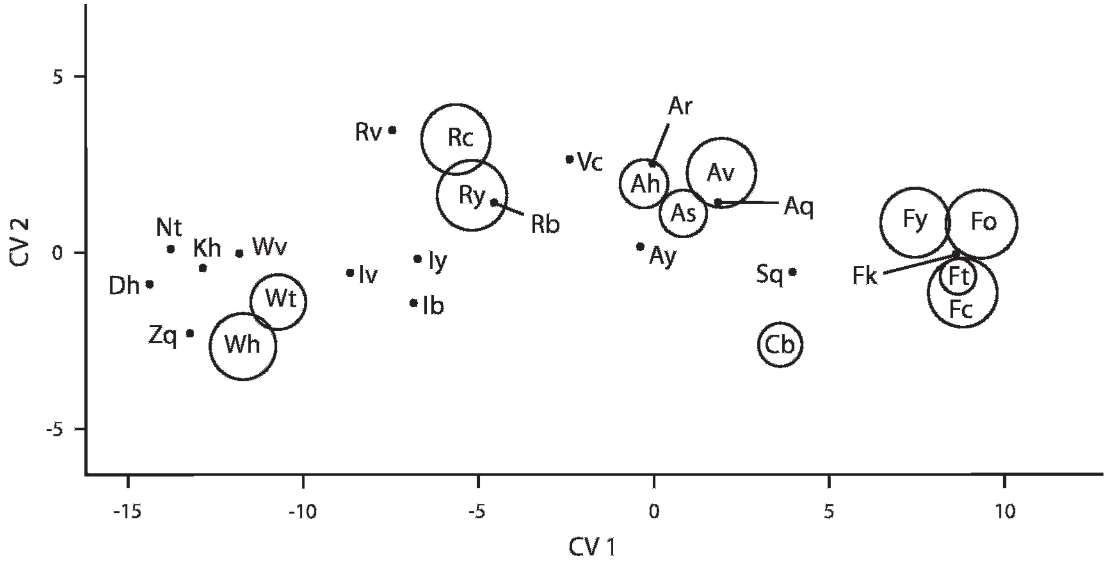

Fig. 6. Canonical variate analysis (1st versus 2nd axes) for all groups of Indochinese *Crocidura*. The means of each group are plotted and labeled and, for groups with at least six specimens, circles are plotted to indicate the 95% confidence regions of the means. Groups with the largest sample sizes have the smallest confidence regions.

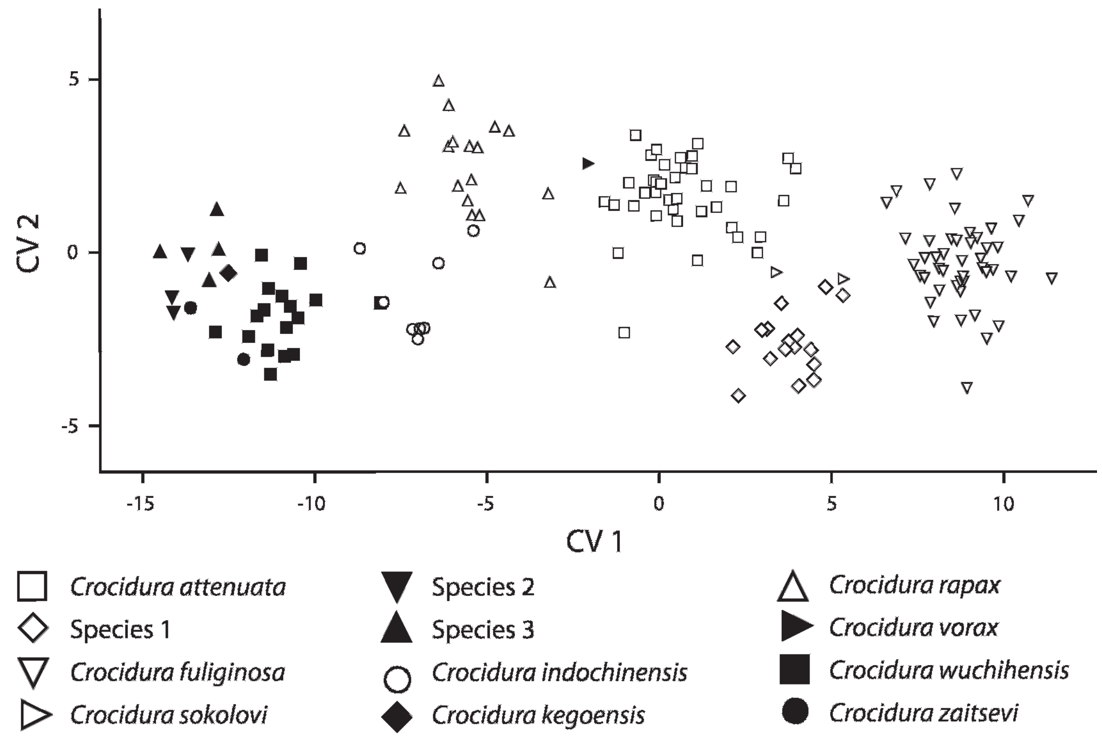

Fig. 7. Individual specimens are plotted from the CVA in the graph (above).

in order to reveal finer patterns of variation. The results of the analyses of separate combinations of species are given below.

Analysis of Subset A, combining the largest species *C. fuliginosa*, *C. sokolovi*, Species 1, and *C. attenuata*. The PCA (fig. 8) shows individual specimens distributed principally along the first axis, with *C. fuliginosa* at one extreme and *C. attenuata* distributed along the other two-thirds of the first axis but also showing some distribution on the second axis. The CVA (figs. 9 and 10) shows clear groupings of *C. fuliginosa* at one extreme and groups of *C. attenuata* at the opposite extreme of the first axis. Specimens belonging to Species 1 and *C. sokolovi* are separated from *C. fuliginosa* on both axes, most individuals are separated from other groups of *C. attenuata* on the first axis and from all but one specimen from Yunnan on the second axis.

Analysis of Subset B, combining the medium and small species *C. vorax*, *C. rapax*, *C. indochinensis*, *C. wuchihensis*, *C. kegoensis*, *C. zaitsevi*, Species 2, and Species 3. In the PCA most species are well separated mainly on the first axis, with *C. vorax* at one extreme, then *C. rapax*, *C. indochinensis*, and *C. wuchihensis* (fig. 11). At the opposite extreme and showing overlap with specimens of *C. wuchihensis* are *C. kegoensis*, *C. zaitsevi*, Species 2, and Species 3. In the CVA (figs. 12 and 13), *C. vorax*, *C. rapax*, *C. wuchihensis*, *C. zaitsevi*, and *C. kegoensis* are all well separated from each other. The few samples of *C. indochinensis* are well separated from each other on the second axis; specimens from Myanmar (Ib) grouping within the 95% confidence regions of *C. rapax* (Rc and Ry). Two groups of *C. wuchihensis* (Wh and Wt) are moderately well separated from each other. *Crocidura zaitsevi*, *C. kegoensis*, Species 2, and Species 3 are all separate from each other.

THE GENUS *CROCIDURA*

Crocidura Wagler, 1832. Isis: 275.

Musaraneus Pomel, 1848. Archives des Sciences Physiques et Naturelles, Genève 9: 249.

Rhinomus Murray, 1860. Proceedings of the Royal Philosophical Society of Edinburgh 2: 159.

Leucodon Fatio, 1869. Faune des Vertébrés de la Suisse 1: 132.

Paurodus Schulze, 1897. Helios. 14: 90.

Heliosorex Heller, 1910. Smithsonian Miscellaneous Collection 56: 6.

Praesorex Thomas, 1913. Annals and Magazine of Natural History (8) 11: 320.

Afrosorex Hutterer, 1986. Cimbebasia 8: 26.

DESCRIPTION OF SOUTHEAST ASIAN *CROCIDURA*

In contrast to the numerous and diverse species of *Crocidura* that inhabit Africa, those species that occur in Southeast Asia are remarkably conservative in morphology, differing mainly in size. The few morphological features that show some variation between these Southeast Asian species are described in the species accounts that follow. In this section we provide a description of the morphology common to the species of *Crocidura* from mainland Southeast Asia.

Dorsal pelage gray, grayish brown, or brown. Ventral pelage usually a more muted shade of the dorsal pelage and not sharply demarcated. Dorsal and ventral pelage reported to be darker in colder months among individuals from higher latitudes. Tail generally shorter than head and body, dark above, and paler below. Dorsal surfaces of hands and feet generally paler than the coloration on the back.

Skull with a broad maxillary region, constricted interorbital region and variably inflated braincase; the proportions of the interorbital region to maxillary region and of the height, depth, and length of the braincase may be specifically variable. Lambdoid crests range from poorly to well developed, meeting at a shallow angle in the midline, where a sagittal crest may be indicated in some species; superior articular facets usually well-marked in dorsal view and either rounded or somewhat angular, and leading into a shallow ridge along the lateral region of the squamosal; the anterior extension of the mastoid varies in morphology between species; sinus canal variable.

Dentition moderately robust, showing little variation except as follows. On the upper premolar (P4) the protocone is variably positioned relative to the paracone; the low hypocone and posterolingual border of the tooth may be either rounded or indented;

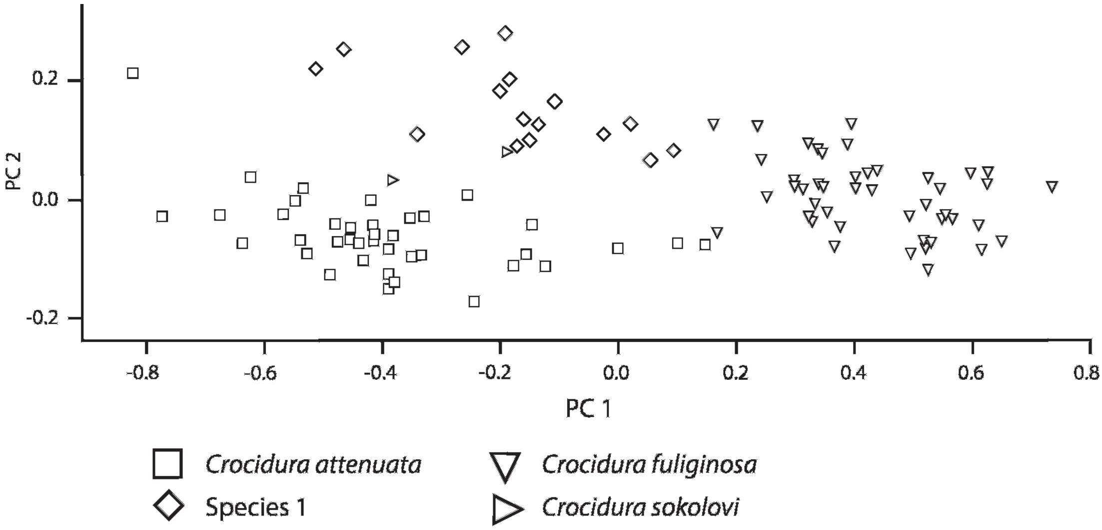

Fig. 8. Principal components plot (1st versus 2nd axes) for subset A: *Crocidura attenuata*; *Crocidura fuliginosa*; *Crocidura sokolovi*; Species 1. Symbols are placed at *x-y* locations representing the factor scores.

the talon shows variability in the degree to which it extends toward the midline of the skull, projecting further into the palatal region in some species, so that palatal distance between lingual margins of the teeth is much narrower than this distance in the succeeding molar teeth; the concave posterior border of the tooth reveals varying degrees of underlying bone in occlusal view. On the second upper molar (M2) the posterobuccal crest of paracone forms W-shaped or two V-shaped lophs in unworn dentition. On the lower third molar (m3) the entoconid, entoconid ridge, and talonid basin are present but show reduction in some species.

SPECIES ACCOUNTS

Crocidura fuliginosa (Blyth, 1855)

Sorex fuliginosus Blyth, 1855: 362.
Crocidura dracula Thomas, 1912b: 686.
Crocidura praedax Thomas, 1923: 656.
Crocidura dracula mansumensis Carter, 1942: 1.

SYNTYPES: Calcutta Museum 242a adult female body in alcohol, skull extracted and 242b adolescent male body in alcohol (253a and 253b of Blyth, 1863); presented by Major Berdmore in 1855.

TYPE LOCALITY: Schwe Gyen [Shwegyin], Pegu [Myanmar].

IDENTIFICATION AND COMPARISONS: The largest of the Indochinese species of *Crocidura* (see table 2 and fig. 14), tail 60%–91% of head and body length, pelage brownish gray. Tail thick, bicolored, bristle hairs over the proximal 50%–60% of the tail; stout, dark brown scale hairs largely obscure the underlying scales. Skull robust with a deep, broad rostrum, long and moderately broad interorbital region and a long, well-inflated braincase. Lambdoid crests well developed, meeting at a shallow angle in the midline and sometimes forming a short, weakly defined sagittal crest; superior articular facets well marked; mastoid relatively shallow, anterior portion of mastoid elongated; sinus canal rises in a shallow curve, descending gradually toward the postparietal foramen, so the distance between the canal and the squamosal ridge decreases from anterior to posterior. Upper premolar (P4) with protocone positioned posteriorly relative to the paracone; posterolingual border of the tooth rounded; posterior border of tooth deeply concave. Posterobuccal crest of paracone of M2 terminates in a conule separate from the mesostylar cusp, so that two separate V-shaped lophs are evident in unworn dentition.

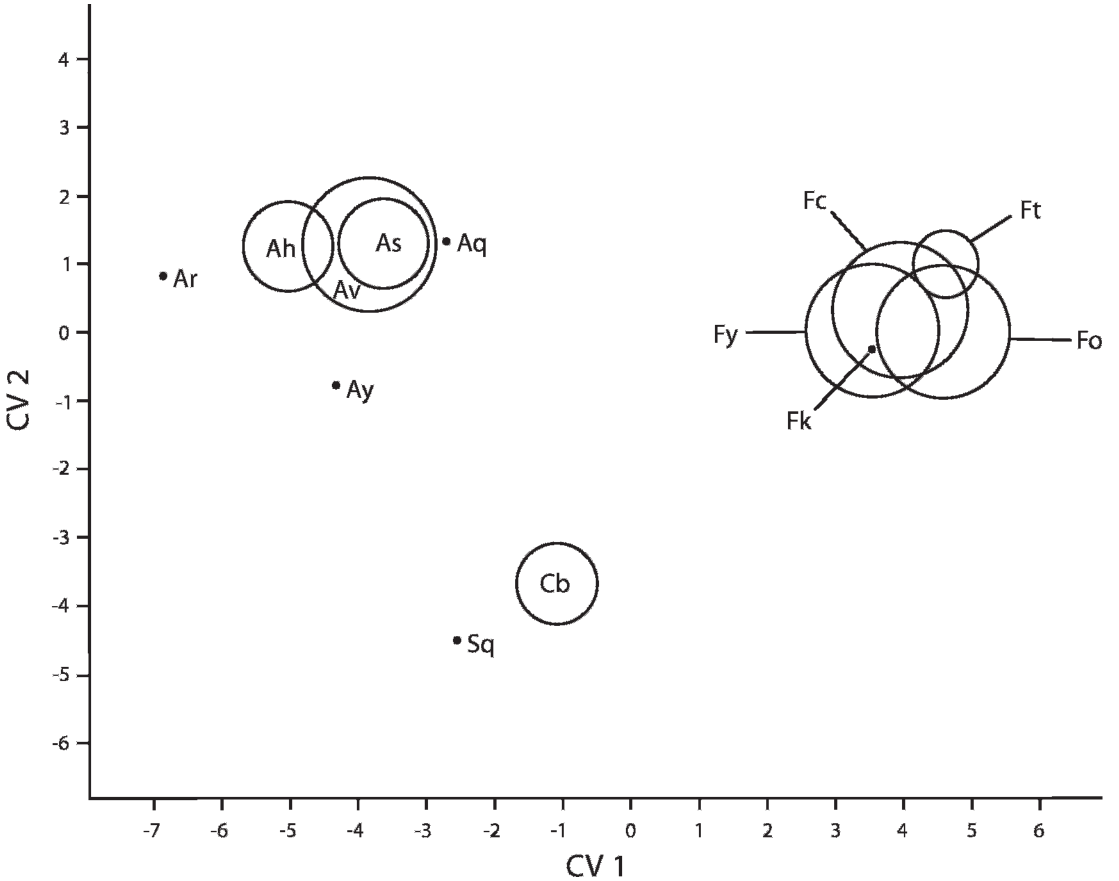

Fig. 9. Canonical variate analysis (1st versus 2nd axes) for groups of subset A: *C. attenuata*, Species 1, *C. fuliginosa*, and *C. sokolovi*. The mean of each group is plotted and labeled and, for groups with at least six specimens, circles plotted to indicate the 95% confidence regions of the means. Groups with the largest sample sizes have the smallest confidence regions.

Distinguished from all other species by its much greater body size, and larger and more robust skull. The only other species that approach *C. fuliginosa* in size are *C. attenuata*, *C. sokolovi*, and *C. cranbrooki*, the species from Myanmar described below, with which there is some overlap in external measurements (see table 2). The skull of *C. fuliginosa* is longer and broader than that of *C. sokolovi*, and is considerably larger than that of most specimens of *C. attenuata* and *C. cranbrooki*, and of those few specimens that show some overlap in size, the two smaller species are separable when the whole suite of skull length and breadth measurements are compared (see table 2). The superior articular facets of *C. fuliginosa* are less angular than in *C. attenuata*, the lambdoid crests are more well developed and the mastoid relatively shallower and more elongated anteriorly. The two species differ in the shape of the posterolingual border of P4, which is more rounded in *C. fuliginosa*. Also in contrast to *C. fuliginosa*, the lophs on the buccal region of M2 of *C. attenuata* are W-shaped, lacking a conule anterior to the mesostyle.

DISTRIBUTION: Museum specimens are recorded from NW Yunnan, the Yunnan-Myanmar border and northern Vietnam. Le Trong Trai et al. (1999) reported one specimen from Mang Xang, South of Ngoc Linh, Vietnam. One other specimen has been recorded from Nui Bi Doup, Lam Dong Province, southern Vietnam, ca. 1500 m.

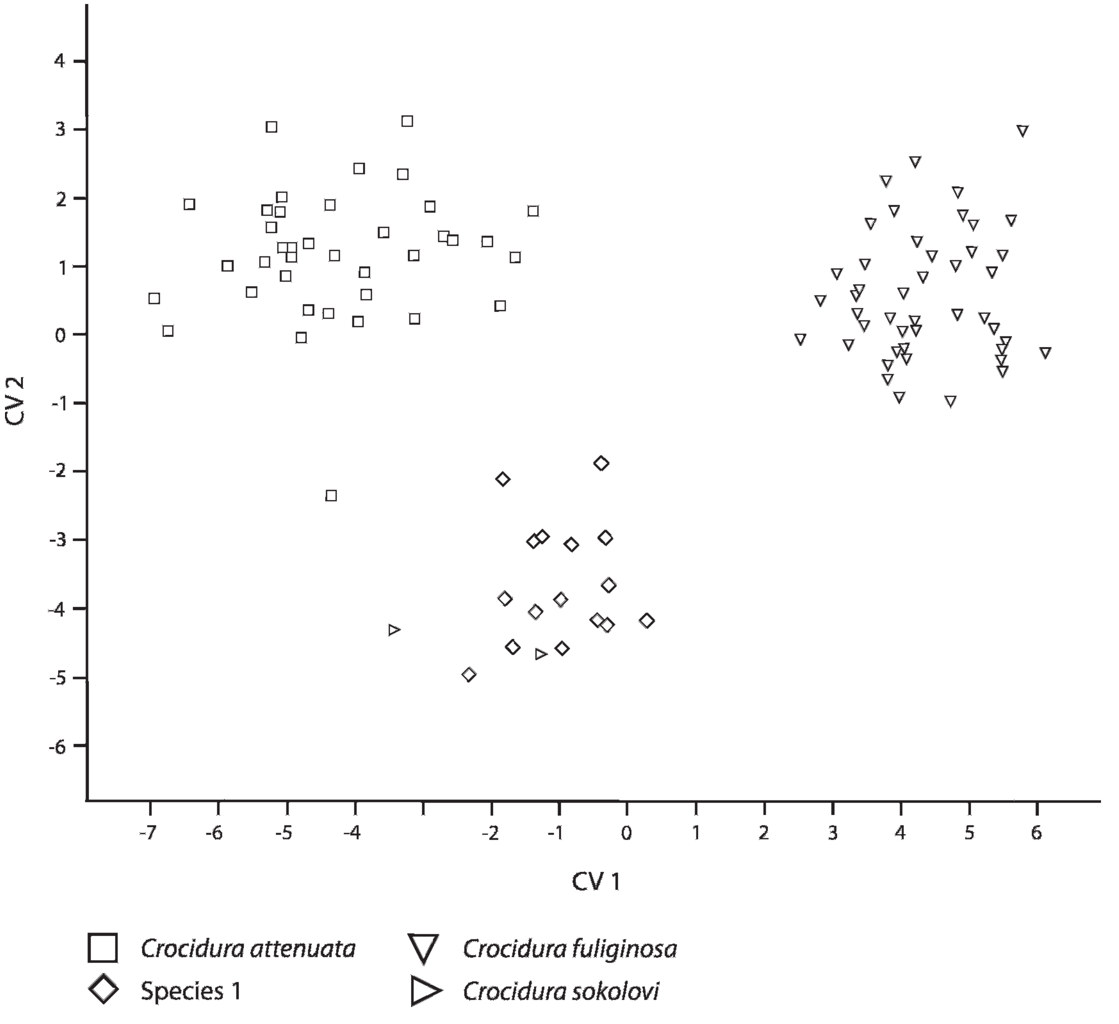

Fig. 10. Individual specimens are plotted from the graph (opposite page).

REMARKS: The brief original description of the type specimen of *C. fuliginosa* (Blyth, 1855) was elaborated by Anderson (1881) and subsequently by Medway (1965), who considered that it was conspecific with *C. dracula* Thomas, 1912b. This view was followed by Jenkins (1976) and by Ruedi (1995), who cited supporting chromosomal evidence. Ruedi (1995) demonstrated that the southern distribution of this species extended no further than the Malay Penisula. Skull measurements provided by Ruedi (1995) for specimens from peninsular Malaysia are, on average, smaller than specimens from Vietnam (Heaney and Timm, 1983) and southern China (Jiang and Hoffmann, 2001) and from Vietnam and Yunnan, China, in this study. Hutterer (2005) regarded *C. fuliginosa dracula* as a valid subspecies.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate analyses). **China** – *Yunnan*: {11} Lichiang or Lichiang Range [Li-jiang, Li-kiang or Li-chiang; = Dayan] (BMNH 1923.1.1.12*, 1923.4.1.13* (holotype of *praedax*), 1923.4.1.15*, 1923.4.1.16*, 1923.4.1.17*, 1923.4.1.19*); {14} Nam Ting River, near Burma border (AMNH 44478*, 44480*, 44481*, 44485*, 44490*,

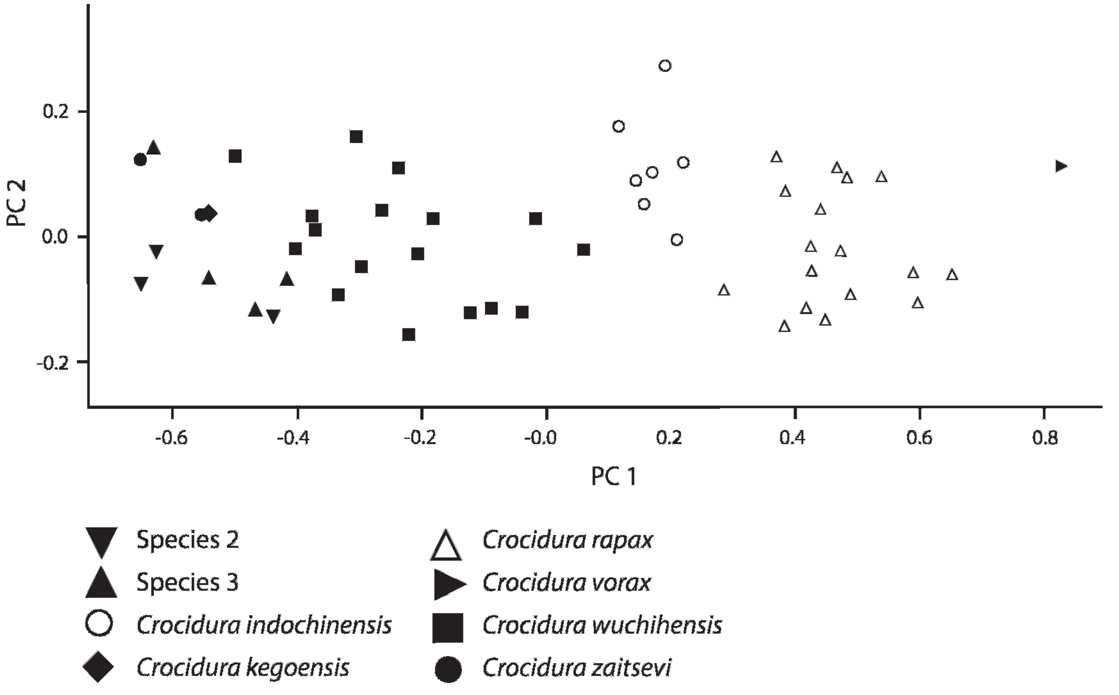

Fig. 11. Principal components plot (1st versus 2nd axes) for subset B: *Crocidura indochinensis*; *Crocidura kegoensis*; *Crocidura rapax*; *Crocidura vorax*; *Crocidura wuchihensis*; *Crocidura zaitsevi*; Species 2; Species 3. Symbols are placed at *x*-*y* locations representing the factor scores.

44494*); {15} Shang-Kuan, Talifu Lake [Xiaguan, at south end of Talifu Lake]. (AMNH 44454*); {18} Yangtze River [Jinsha Jiang], Shih-ku [Shigu] (AMNH 44474*, 44476*, 44477*); {13} Mong-Tze [Meng-Tzu, Mengzi], probably near (BMNH 1912.7.25.6*, 1912.7.25.7*, 1912.7.25.8* (holotype of *dracula*), 1912.7.25.9*, 1912.7.25.10*). **Vietnam** – *Hà Giang*: {33} Mt. Tay Con Linh II (AMNH 274180.). *Lào Cai*: {39} Chapa [Sa Pa]. (BMNH 1933.4.1.169*, 1933.4.1.170*, 1933.4.1.171*, 1933.4.1.172*, 1933.4.1.173*, 1933.4.1.174*, 1933.4.1.175*, 1933.4.1.176*, 1933.4.1.177*, 1933.4.1.178*, 1933.4.1.179*, 1933.4.1.180*, 1933.4.1.181*, 1933.4.1.182*, 1933.4.1.183*, 1933.4.1.184*, 1933.4.1.185*, 1933.4.1.186*, 1933.4.1.187*, 1933.4.1.188*, 1933.4.1.190*, 1933.4.1.191*, 1933.4.1.192*.); {40} Ngai Tio [Ngải Chồ] (BMNH 1925.1.1.25*, 1925.1.1.26*, 1925.1.1.28*).

Crocidura attenuata Milne Edwards, 1872

Crocidura attenuata Milne Edwards, 1872: 263.
Crocidura rubricosa Anderson, 1877: 280.
Crocidura kingiana Anderson, 1877: 281.
Crocidura grisea Howell, 1926: 137.
Crocidura grisescens Howell, 1928: 60.

HOLOTYPE: MNHN CG 1870-575, skin and skull, collected by Monsieur l'abbé David.

TYPE LOCALITY: Moupin, Szechuan [= Baoxing, Sichuan], China 5429 ft (1654 m).

IDENTIFICATION AND COMPARISONS: A medium-sized species of *Crocidura* (fig. 14). Dorsal pelage dark grayish brown and gradually blending into the paler, grayer ventral pelage. Tail 60%–76% head and body length, brown above, slightly paler below, and covered with fine hairs. Long bristle hairs are present on the tail along the proximal half. Skull typical of Southeast Asian *Crocidura* in overall proportions but distinguished by following combination of morphological details: superior articular facets more angular in dorsal view; mastoid relatively shallow, anterior portion of mastoid elongated. Upper premolar (P4) with protocone positioned posteriorly relative to the paracone; posterolingual border of the tooth not so rounded; posterior border of tooth deeply concave. Posterobuccal crest of paracone of M2 forming a smooth W-shaped loph in unworn dentition.

Crocidura sokolovi is similar but see the comparisons section of that species account for a differential diagnosis. One of the advantages of having such a large sample of this species is that it allows us to document size variation with age from a single population. At the most basic level, we could separate our sample into two age classes based on whether the basisphenoid-basioccipital suture was unfused and visible (juveniles), or fused and obliterated (adults) (fig. 15). Juvenile *C. attenuata* show overlapping measurements for adults of *C. wuchihensis* and *C. indochinensis*, and might be confused with these species if age were not taken into consideration (table 3).

DISTRIBUTION: A widespread and common species known throughout Vietnam, Lao PDR, and China, from eastern Xizang to Hainan and northern to southern Gansu.

REMARKS: This species has been confused with several others in the past, including *C. fuliginosa*, *C. hilliana*, and *C. tanakae*. The karyotype, supposedly of *C. attenuata* from Thailand (Tsuchiya et al., 1979), was instead demonstrated to be representative of *C. hilliana* Jenkins and Smith, 1995 (see Motokawa and Harada, 1998). *Crocidura tanakae* Kuroda, 1938, from Taiwan, long considered to be a synonym or subspecies of *C. attenuata* (Ellerman and Morrison-Scott, 1951; Jameson and Jones, 1977; Jiang and Hoffmann, 2001), was similarly shown to have a karyotype different from that of *C. attenuata* from mainland southern China by Motokawa et al. (2001), who suggested that it might represent a distinct species, a view that was accepted by Hutterer (2005). Evidence from molecular studies of cytochrome *b* by Han et al. (2002) using samples from Taiwan and by Ohdachi et al. (2006), who observed phylogenetic differentiation between the two samples they used from Taiwan and Vietnam, provides further support for the opinion that *C. tanakae* should be considered a distinct species.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate analyses). **China** – *Sichuan*: {1} Moupin [Baoxing] (MNHN CG 1870-575* (holotype of *attenuata*)); {5} Kuan Shien [Kuan-hsien; Guanxian; Guankou] (USNM 258176*); {7} Ta Cho Fu [Tacho] (USNM 260746*). *Chongqing*: {2} Chung-king [Chongqing] Mountains (BMNH 1911.12.18.1*); {3} 50 miles NE of Chung-King [Chongqing] Mountains (BMNH 1911.9.8.29*, 1911.9.8.30*, 1911.9.8.31*); {4} Chin-fu-san, near Nanchwan [Nanchuan] (BMNH 1911.9.8.26*, 1911.9.8.28*); {8} Yen-ching-kao (AMNH 56030*, 56040*, AMNH 56046/ MCZ 20717 *, AMNH 56054/ MCZ 20716 *). *Yunnan*: {14} Nam Ting River, near Burma border (AMNH 44489*); {17} Tengyueh [= Teng Chong] (BMNH 1912.7.24.1*). **Vietnam** – *Hà Tĩnh*: {31} Huong Son Camp (AMNH 272120, 272121, 272123, 272124, 272125, 272126, 272132*, 272139, 272140, 272141*, 272150*, 272152, 272171, 272172*, 272188, 272200, 272201, 272203, 272212, 272213, 272223*, 272232, 272272, 272277, 272286, 272304, 272305, 272310, 272311, 272316, 272317, 272320*, 272368, 272371*, 272372, 272421, 272433*, 272434*, 272450, 272513, 272514, 272515, 272516, 272517*, 272522, 272565, 272566, 272568, 272583, 272585, 272599*, 272600, 272601, 272602, 272612, 272613*, 272616, 272619, 272635, 272640, 272646, 272649, 272653, 272654, 272772*); *Hà Giang*: {33} Mt. Tay Con Linh II (274146, 274147, 274148, 274151, 274152, 274156, 274158, 274161, 274173, 274177, 274179, 274183, 274185, 274192, 274195, 274196, 274204, 274225, 274229, 274230, 274232, 274233, 274235, 274236, 274237, 274239, 274248, 274249, 274258, 274262, 274264, 274268, 274269, 274271, 274272, 274281, 274284, 274291, 274298, 274299, 274300, 274305, 274306, 274307, 274308, 274309, 274316, 274317, 274318, 274319, 274331, 274332, 274333, 274334, 274345, 274346, 274347, 274348); *Kon Tum*: {34} Dak To [Đăc Tô] (BMNH 1926.10.4.45*); *Lâm Đồng*: {35} Langbian Peak [Lang Bian] (FMNH 46641*); {37} Mt Lang Bian (USNM 320505*, 320506*, 320508*); *Quảng Nam*: {42} Ba Na (BMNH 1997.639*); {43} Ngoc Linh Nature Reserve (ZIN 91229*, 91230*); *Quảng Tri*: {44} Thon Ke Tri Peak

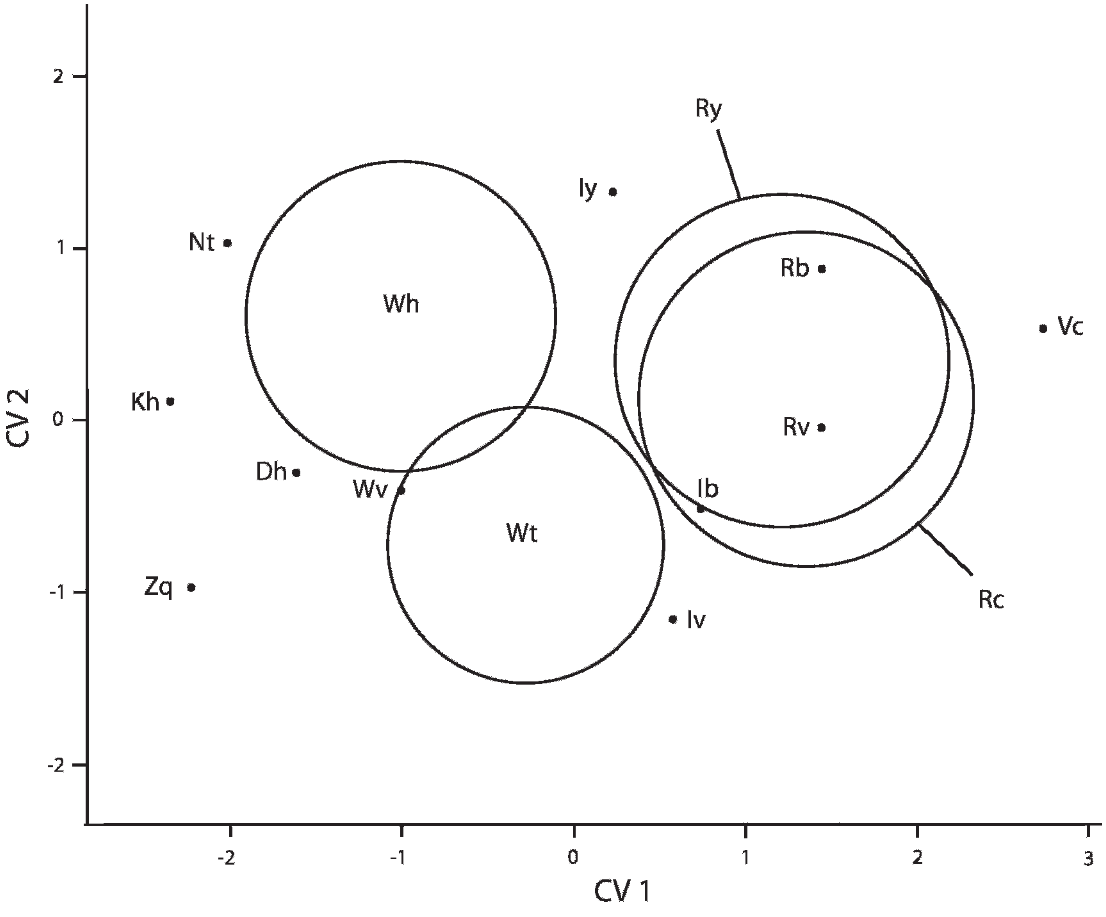

Fig. 12. Canonical variate analysis (1st versus 2nd axes) for groups of subset B: *C. annamitensis*, *C. guy*, *C. indochinensis*, *C. kegoensis*, *C. rapax*, *C. vorax*, *C. wuchihensis*, and *C. zaitsevi*. The mean of each group is plotted and labeled and, for groups with at least six specimens, circles plotted to indicate the 95% confidence regions of the means. Groups with the largest sample sizes have the smallest confidence regions.

(USNM 357630*); *Thu'a Thiên*: {45} 9.1 kilometers W of, 3.6 km N of Nui Ke, Thua Thien Province, altitude 30 m. (USNM 357577*, 357578*).

Crocidura sokolovi Jenkins, Abramov, Rozhnov and Makarova, 2007

Crocidura sokolovi Jenkins et al., 2007: 63.

HOLOTYPE: ZIN 91232; male; body in ethanol, skull extracted; collector's number 11; collected 5 April 2004 by A.V. Abramov.

TYPE LOCALITY: Ngoc Linh Mountain, west slope, 1–2 km west of the apex, Central Highlands, Kon Tum Province, Vietnam, 15°05′ N, 107°57′ E, altitude 2400 m.

IDENTIFICATION AND COMPARISONS: First upper incisor small, principal cusp slender, talon small; protocone and anterior portion of talon of P4 positioned closer to the midline of the skull than the mid and posterior portion of the talon.

Smaller than *C. fuliginosa* (see table 2). Similar in body size to *C. attenuata*, but pelage brown and with a proportionately longer tail relative to head and body length (87%–93%) than Vietnamese populations of *C. attenuata* (47%–78%). The skull of *C. sokolovi* is similar in overall size to that of *C. attenuata* but differs in shape and proportions (see fig. 14 and table 2). The maxillary region of *C. sokolovi* is narrower relative to

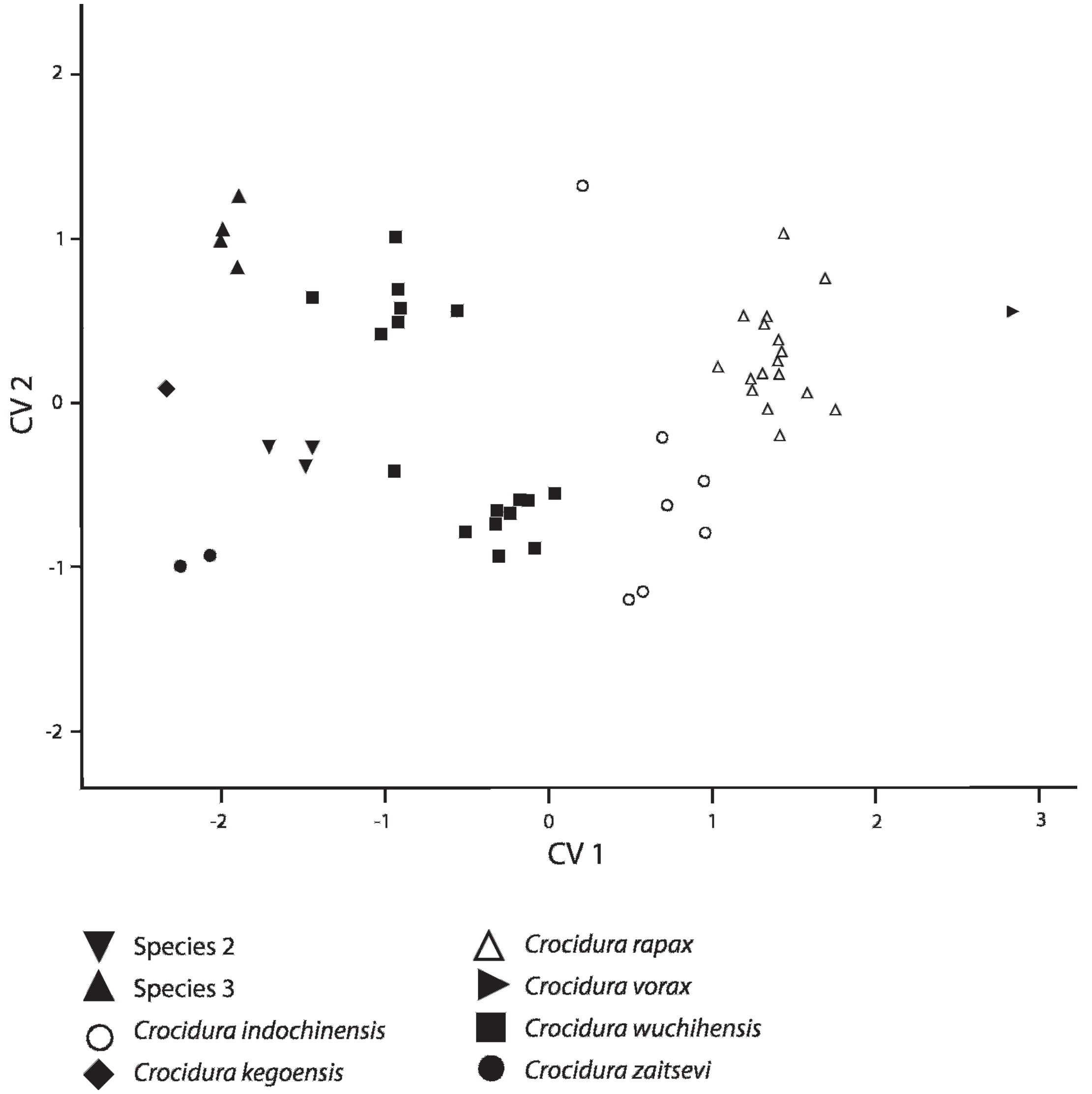

Fig. 13. Individual specimens are plotted from the graph (opposite page).

interorbital breadth and braincase breadth than that of *C. attenuata* and the braincase is deep, relatively shorter, and more rounded in appearance than the angular, comparatively narrower, shallower, and long braincase of *C. attenuata*. The small, slender first upper incisor of *C. sokolovi* differs from that of *C. attenuata* which has a large principal cusp and talon. The anterior face of P4 lies at a shallow angle relative to the midline of the palate in *C. sokolovi* in contrast to the steeper angle in *C. attenuata*. The talon of P4 of *C. sokolovi* is suboblong in shape with a shallowly concave posterior margin, unlike *C. attenuata* in which the hypocone is set further toward the midline, the lingual edge is more curved and the posterior border of the tooth is markedly concave.

DISTRIBUTION: Recorded only at high altitudes of 2300–2400 m from the type locality of Ngoc Linh Mountain in the Southern Annamites, Vietnam.

TABLE 2

Comparative Measurements of *Crocidura sokolovi*, *C. attenuata*, *C. cranbrooki*, and *C. fuliginosa*

Measurements in millimeters are presented as mean, standard deviation, and range, with number of specimens in parentheses.

	Crocidura sokolovi	*Crocidura attenuate* Sichuan	*Crocidura cranbrooki* Myanmar	*Crocidura fuliginosa*
HB	72.67	71.4 ± 6.64	76.13 ± 7.77	91.48 ± 6.51
	70–78 (3)	63–82 (10)	65–86 (8)	78–107 (40)
TL	66	53.7 ± 3.57	74.13 ± 7.16	72.04 ± 5.44
	65–68 (3)	48–60 (10)	65–88 (8)	60–88 (39)
HF	14 ± 0	14 ± 1.06	14.94 ± 0.64	16.33 ± 1.12
	14 (3)	12–15.5 (10)	14–16 (9)	14–19 (40)
E	6.0 ± 1.73		–	–
	5–8 (3)	10 (2)		
CIL	20.22	20.55 ± 0.66	21.38 ± 0.67	23.55 ± 0.65
	19.4–21.0 (3)	19.6–21.7 (9)	19.9–22.2 (14)	22.1–24.9 (30)
UTLR	8.75	8.72 ± 0.38	9.29 ± 0.29	10.27 ± 0.30
	8.32–9.2 (3)	8.2–9.5 (11)	8.6–9.8 (17)	9.7–11.1 (45)
1-Un3	3.86	4.0 ± 0.23	4.36 ± 0.17	4.67 ± 0.17
	3.6–4.2 (3)	3.8–4.5 (11)	3.9–4.7 (16)	4.2–5.0 (45)
M2-M2	5.91	6.09 ± 0.22	6.09 ± 0.25	6.97 ± 0.17
	5.8–6.02 (3)	5.8–6.5 (11)	5.4–6.5 (18)	6.7–7.3 (44)
LIOB	4.74	4.43 ± 0.18	4.74 ± 0.12	4.94 ± 0.13
	4.6–4.9 (3)	4.1–4.7 (9)	4.4–4.9 (17)	4.7–5.3 (40)
PGB	6.14	6.38 ± 0.27	6.35 ± 0.20	7.17 ± 0.23
	6.0–6.3 (3)	6.0–6.7 (9)	5.9–6.7 (17)	6.7–7.7 (40)
BB	9.53	9.17 ± 0.24	9.31 ± 0.2	10.23 ± 0.23
	9.4–9.7 (3)	8.7–9.4 (8)	9.0–9.6 (14)	9.8–10.7 (32)
BH	5.2	4.91 ± 0.1	5.14 ± 0.13	5.41 ± 0.17
	5.1–5.3 (3)	4.8–5.1 (8)	5.0–5.3 (14)	5.1–5.7 (30)
BL	7.63	8.01 ± 0.37	8.27 ± 0.22	8.78 ± 0.29
	7.5–7.8 (3)	7.6–8.8 (8)	7.8–8.7 (14)	8.0–9.2 (30)
AWM2	2.03	2.03 ± 0.07	2.11 ± 0.09	2.33 ± 0.11
	1.95–2.09 (3)	1.94–2.16 (11)	1.97–2.3 (16)	2.1–2.6 (45)
LM3	0.72	0.62 ± 0.04	0.71 ± 0.05	0.77 ± 0.05
	0.71–0.73 (3)	0.55–0.68 (11)	0.63–0.8 (16)	0.7–0.89 (45)
ML	12.73	12.76 ± 0.62	13.35 ± 0.45	14.9 ± 0.43
	11.9–13.4 (3)	11.7–13.9 (11)	12.2–13.9 (16)	13.8–15.8 (30)
MTRL	8.14	8.22 ± 0.36	8.68 ± 0.28	9.67 ± 0.26
	7.7–8.6 (3)	7.7–8.9 (11)	8.0–9.2 (16)	9.0–10.3 (30)
MH	4.76	4.82 ± 0.19	4.94 ± 0.19	5.62 ± 0.21
	4.5–4.9 (3)	4.5–5.2 (11)	4.6–5.3 (18)	5.2–6.0 (43)
TL (% of HB)	0.91 ± 0.03	0.76 ± 0.08	0.98 ± 0.1	0.79 ± 0.08
	0.87–0.93 (3)	0.65–0.94 (10)	0.81–1.08 (8)	0.59–0.92 (39)
TL : CIL	3.27 ± 0.06	2.64 ± 0.09	3.47 ± 0.3	3.06 ± 0.22
	3.21–3.35 (3)	2.55–2.77 (7)	2.99–3.96 (7)	2.5–3.57 (29)
IOB : M2-M2	0.8 ± 0.01	0.73 ± 0.02	0.77 ± 0.02	0.71 ± 0.02
	0.79–0.82 (3)	0.69–0.76 (9)	0.72–0.8 (17)	0.67–0.75 (40)
M2-M2 : BB	0.62 ± 0.001	0.67 ± 0.02	0.66 ± 0.02	0.68 ± 0.02
	0.62 (3)	0.63–0.68 (8)	0.64–0.69 (14)	0.64–0.71 (32)
BL : BB	0.8 ± 0.01	0.87 ± 0.02	0.88 ± 0.02	0.86 ± 0.03
	0.78–0.81 (3)	0.84–0.9 (8)	0.86–0.92 (14)	0.79–0.90 (29)
BH : BL	0.68 ± 0.02	0.62 ± 0.02	0.62 ± 0.019	0.62 ± 0.02
	0.66–0.7 (3)	0.58–0.64 (8)	0.60–0.67 (14)	0.58–0.66 (30)

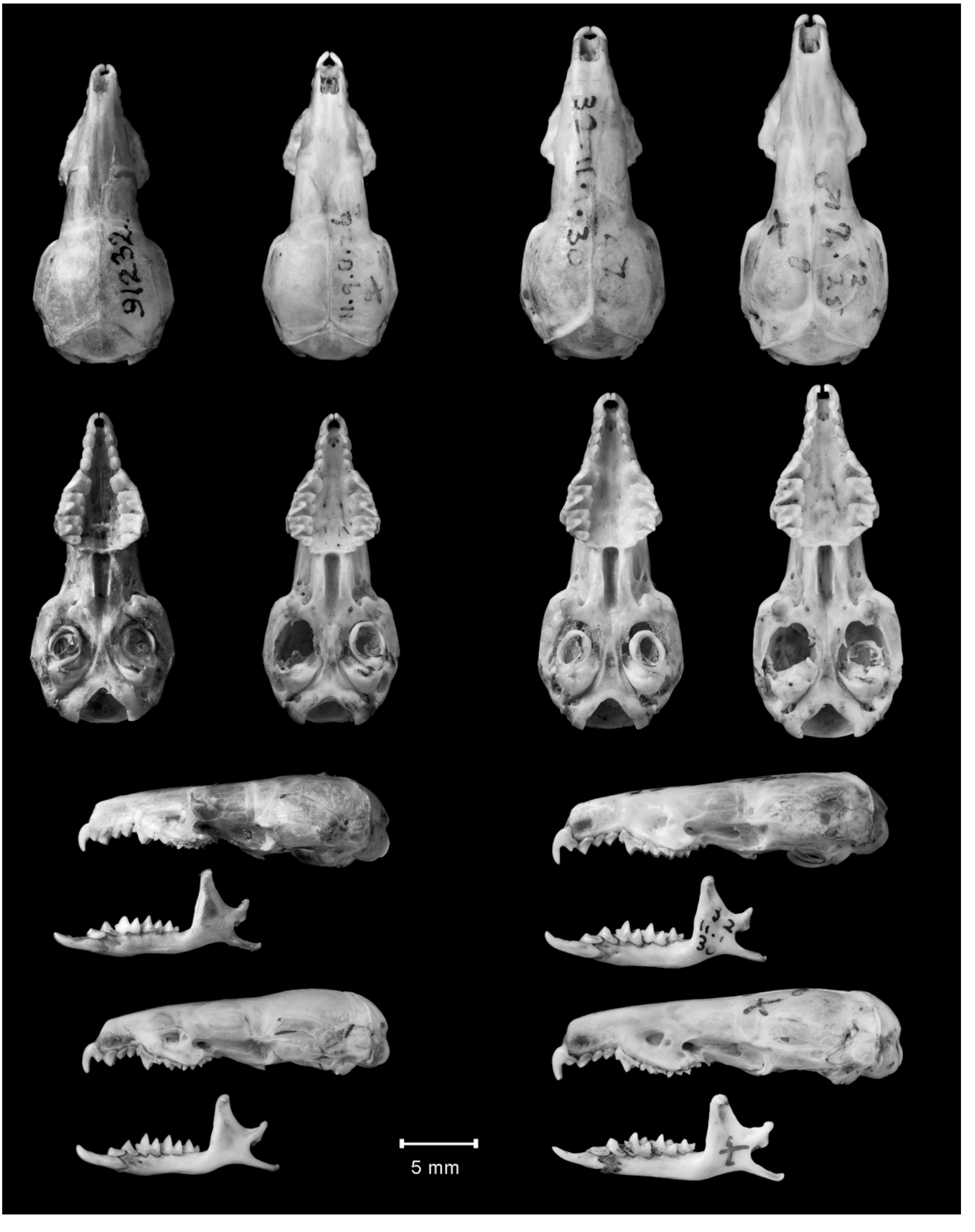

Fig. 14. Large species. Top row from left to right: dorsal views of the skulls of *C. sokolovi* (the holotype ZIN 91232), *C. attenuata* from Sichuan (BMNH 1911.9.8.26), *C. cranbrooki* (a paratype BMNH 1932.11.1.30), and *C. fuliginosa* (the holotype of *C. dracula* BMNH 1912.7.25.8); second row: ventral views of skulls in the same order; third and fourth rows: left lateral views of the skulls and mandibles of (above left) *C. sokolovi*; (below left) *C. attenuata*; (above right) *C. cranbrooki*; and (below right) *C. fuliginosa*.

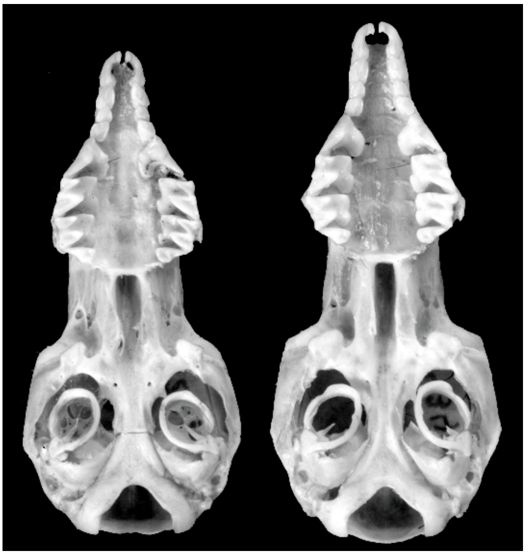

Fig. 15. Ventral view of juvenile skull of *C. attenuata* AMNH 272310 showing unfused basioccipital suture and adult skull of AMNH 272434 in which the suture is fully fused.

REMARKS: This species may be endemic to Ngoc Linh Mountain.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22). (* = specimens included in multivariate analyses) **Vietnam** – *Quảng Nam*: {43} Ngoc Linh Nature Reserve (ZIN 91232* (holotype of *sokolovi*), 91234*).

Crocidura cranbrooki, sp. nov.

HOLOTYPE: BMNH 1932.11.1.27 adult female, skin and skull, collector's number 137, collected 17 January 1931 by the fourth Earl of Cranbrook and F. Kingdon Ward.

TYPE LOCALITY: Nam Tamai Valley, Upper Burma (Myanmar) 3,500 feet (1068 m) 27°42′N 98°01′E.

PARATYPES: BMNH 1932.11.1.24 adult male skin and skull, collected 8 January 1931; BMNH 1932.11.1.25 adult male skin and skull, collected 15 January 1931; BMNH 1932.11.1.26 adult male skin and skull, collected 15 January 1931; BMNH 1932.11.1.28 adult female skin and skull, collected 18 January 1931; BMNH 1932.11.1.29 adult skin and skull, collected 12 January 1931; BMNH 1932.11.1.178 adult male skull; BMNH 1932.11.1.179 adult male skull; BMNH 1932.11.1.180 male skull; BMNH 1932.11.1.194 adult male skull; BMNH 1932.11.1.195 adult male skull; BMNH 1932.11.1.196 adult male skull; BMNH 1932.11.1.197 adult male skull. All from Nam Tamai Valley, Myanmar 3,000–3,500 feet (915–1068 m). BMNH 1932. 11.1.30 adult skin and skull, collected 6 January 1931, from [Nam] Tisang – [Nam] Tamai Divide, 4,000 feet (1220 m); BMNH 1932.11.1.31 adult skin and skull, collected 6 January 1931, in hills E. of Nam Hat, 4,000 feet (1220 m). BMNH 1932.11.1.32 adult skin and skull, collected 29 December 1930, in hills 10 miles E. of Fort Hertz [Putao], 4,000 feet (1220 m) (27°21′N 97°24′E). All collected by the fourth Earl of Cranbrook and F. Kingdon Ward.

DIAGNOSIS: Intermediate in size between the larger *C. fuliginosa* and the smaller *C. attenuata* and *C. sokolovi*. Tail long and thin, scales visible, scale hairs pale, short, and thin. Third upper unicuspid elongated; P4 with a broad talon; M3 large with a bicuspid mesostyle and broad talon.

DESCRIPTION: Dorsal pelage brown, individual hairs with gray bases and brown tips, ventral pelage dark gray brown, paler than dorsum, individual hairs with gray bases and buff tips. Tail long and thin, 81%–108% of head and body length; light in color with dark patches over length of tail; bristle hairs on proximal 30%; scale hairs pale, short, and thin, so that underlying scales are readily visible. Hands and feet light buff with darker stripe along inner lateral border of limb and digits.

Skull (see fig. 14) with a long, deep rostrum, broad zygomatic plate, comparatively narrow maxillary and broad interorbital regions; braincase long and deep with rounded superior articular facets, moderately well-developed sagittal and lambdoid crests; anterior region of sinus canal arched; anterior of mastoid elongated, subtriangular, posterior region deep.

First upper incisor with a large principal cusp and low, broad talon approximately same height as Un2. Unicuspids longer than broad, with well-marked, broad cingula, moderately well spaced, Un2 just overlapping the posterior cingulum of Un1; Un3 markedly longer than broad, with cingula united

TABLE 3

Comparative Measurements of Young and Adult *Crocidura attenuata* Based on Measurements of Large Series of Specimens from Two Localities in Vietnam

Measurements in millimeters are presented as mean, standard deviation, and range, with number of specimens in parentheses.

	Huong Son juveniles	Huong Son adults	Tay Con Linh II juveniles	Tay Con Linh II adults
HB	69.9 ± 4.6 60–80 (26)	79.2 + 5.1 65–91 (30)	75.3 ± 5.6 66–89 (33)	78.2 ± 5.2 70–87 (20)
TL	47.9 ± 3.4 43–54 (26)	47.7 + 2.8 43–52 (30)	50.6 ± 4.0 41–56 (33)	52.9 ± 3.0 45–58 (20)
HF	13.4 ± 0.8 11–15 (27)	13.5 + 0.7 12–14 (30)	14.5 ± 0.8 13–16 (33)	14.8 ± 1.0 13–16 (20)
E	8.4 ± 1.1 6–10 (27)	8.3 ± 1.4 5–11 (30)	8.8 ± 1.0 6–11 (33)	9.1 ± 0.8 7–10 (20)
CIL	18.4 ± 0.5 17.1–19.5 (26)	19.2 ± 0.4 18.6–20.3 (29)	19.8 ± 0.5 18.9–20.7 (33)	20.2 ± 0.4 19.2–20.7 (20)
UTRL	8.6 ± 0.2 8.0–9.0 (31)	8.6 ± 0.2 8.2–9.1 (29)	8.7 ± 0.5 18.9–20.7 (33)	8.8 ± 0.2 8.5–9.1 (20)
I-Un3	3.8 ± 0.1 3.5–4.1 (31)	3.8 ± 0.2 3.4–4.1 (29)	4.0 ± 0.1 3.7–4.3 (33)	4.1 ± 0.1 3.8–4.4 (20)
M2-M2	4.3 ± 0.1 3.9–4.5 (31)	6.0 ± 0.2 5.7–6.5 (29)	5.9 ± 0.2 5.6–6.3 (33)	6.0 ± 0.2 5.7–6.3 (20)
LIOB	4.3 ± 0.1 3.9–4.5 (31)	4.4 ± 0.2 4.1–4.8 (30)	4.4 ± 0.2 4.2–5.0 (33)	4.5 ± 0.1 4.3–4.8 (20)
PGD	6.1 ± 0.3 5.4–6.6 (31)	6.3 ± 0.2 5.9–6.7 (30)	6.2 ± 0.2 5.7–6.6 (33)	6.3 ± 0.2 6.2–6.7 (20)
BB	8.7 ± 0.2 8.1–9.1 (24)	9.0 ± 0.3 8.2–9.8 (29)	8.9 ± 0.2 8.5–9.4 (33)	9.0 ± 0.2 8.6–9.4 (20)
BH	4.6 ± 0.2 4.2–5.0 (25)	4.7 ± 0.1 4.5–5.0 (29)	4.9 ± 0.2 4.5–5.1 (33)	5.0 ± 0.2 4.7–5.3 (20)
BL	7.1 ± 0.3 6.6–7.5 (27)	7.5 ± 0.1 7.2–7.8 (29)	7.4 ± 0.2 7.0–8.1 (33)	7.8 ± 0.3 7.2–8.2 (20)
AWM2	2.1 ± 0.1 1.9–2.3 (31)	2.1 ± 0.1 2.0–2.3 (30)	2.1 ± 0.1 1.9–2.2 (33)	2.1 ± 0.1 2.0–2.2 (20)
LM3	0.7 ± 0.0 0.5–0.8 (31)	0.7 ± 0.1 0.6–0.8 (30)	0.6 ± 0.0 0.6–0.7 (33)	0.7 ± 0.0 0.6–0.7 (20)
ML	12.2 ± 0.3 11.4–13.1 (31)	12.4 ± 0.2 12.0–12.9 (30)	12.5 ± 0.4 11.8–13.1 (32)	12.7 ± 0.3 11.9–13.1 (19)
MTRL	7.9 ± 0.2 7.5–8.4 (31)	8.0 ± 0.2 7.6–8.4 (30)	8.1 ± 0.2 7.6–8.5 (32)	8.1 ± 0.2 7.8–8.4 (19)
MH	4.6 ± 0.2 4.2–4.9 (31)	4.8 ± 0.1 4.5–5.1 (29)	4.7 ± 0.2 4.4–5.0 (32)	4.8 ± 0.1 4.5–5.0 (19)
Weight	7.4 ± 1.4 4.0–10.5 (23)	10.7 ± 2.1 6.6–15 (21)	8.2 ± 1.1 5.5–10.5 (33)	10.1 ± 1.4 7.5–13 (20)

posteriorly to form a small raised ridge. Talon of P4 broad, proportion of talon to trigon high, midregion of talon closest to midline of skull; posterolingual portion of P4 and anterolingual region of M1 nearly in contact, so that P4 overlapped by M1 in occlusal view, small crescent of underlying bone visible; protocone medial or posterior relative to paracone; a well-marked cingulum present from hypocone along posterolingual border of the tooth. Third upper molar (M3) large, mesostyle bicuspid.

COMPARISONS: Smaller on average than *C. fuliginosa* with a narrower skull (compare breadth of maxillary region and braincase in table 2). Tail thin unlike the thick tail of *C. fuliginosa*, in which the scales are more obscured by the stout, dark brown scale hairs.

The dorsal pelage is browner than that of *C. attenuata*, in which the tail is more pilose with stout dark brown scale hairs. Larger on average than *C. attenuata* and *C. sokolovi*, with a longer tail relative to condyloincisive length than *C. attenuata* and with a longer braincase than *C. sokolovi* (see table 2). The braincase of *C. sokolovi* is short, relatively narrow anteriorly in the region of the articular facets, flaring toward the junction of the squamosal and mastoid, differing markedly in shape from that of *C. cranbrooki* (see fig. 14). The skull of *C. attenuata* is more angular than that of *C. cranbrooki*, the maxillary region of *C. attenuata* is flared laterally and the superior articular facets are angular, in contrast to the more rounded appearance of the skull in *C. cranbrooki*. First upper incisor larger than that of *C. sokolovi*. Unicuspids more elongated and well spaced than those of *C. attenuata*, in which Un2 overlaps the posterolingual cingulum of Un1. The upper premolar of *C. cranbrooki* differs from that of *C. attenuata* (see fig. 16), in which the talon is short and the proportion of the talon to the trigon is low; the parastyle is angled anteriorly from the paracone and talon, accentuating the small size of the talon in *C. attenuata*, whereas the parastyle lies closer to the paracone and is more integral with the talon in *C. cranbrooki*. The posterolingual border of P4 and the anterolingual border of M1 of *C. attenuata* are well separated and P4 is not overlapped by M1 in occlusal view, so that a large, deep portion of the underlying bone is visible in contrast to the condition in *C. cranbrooki*. The hypocone of *C. attenuata* is low and the cingulum is low and poorly defined, unlike that of *C. cranbrooki*.

DISTRIBUTION: Recorded from the high river valleys and surrounding hills of the extreme north of Myanmar, near the borders with Tibet and Yunnan, China.

ETYMOLOGY: This species is named for John David Gathorne-Hardy, the fourth Earl of Cranbrook who, together with the renowned plant hunter Frank Kingdon Ward, participated in an expedition to explore the sources of the river Irrawady (Ward, 1932). Lord Cranbrook was responsible for collecting mammals on the expedition and his diaries provide an intriguing glimpse of the hardships, endurance and sheer sense of adventure attendant on expeditions to such remote regions at that period.

REMARKS: This species was collected in a little explored area of high endemicity for mammals. These specimens were originally identified as *C. attenuata* (see Ellerman and Morrison-Scott, 1951), and Jenkins (1976) suggested that they represented a separate subspecies. The results of the metric analyses, however provide clear evidence at the 95% confidence level that this is a species distinct from *C. attenuata*. The species is reported as Species 1 in the results of the metric analyses and indicated by the letter C and the symbol ◇ in the accompanying figures.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate analyses). **Myanmar** – *Kachin*: {20} Fort Hertz (BMNH 1932.11.1.32); {24} Nam Hat or Nam Hut (BMNH 1932.11.1.31*); {25} Nam Tamai (BMNH 1932.11.1.24*, 1932.11.1.25*, 1932.11.1.26*, 1932.11.1.27* (holotype of *cranbrooki*), 1932.11.1.28*, 1932.11.1.29*, 1932.11.1.178*, 1932.11.1.179*, 1932.11.1.180*, 1932.11.1.194*, 1932.11.1.195*, 1932.11.1.196*, 1932.11.1.197*, 1950.489, 1950.490, 1976.1229*); {26} Nam Tisang (BMNH 1932.11.1.30*).

Crocidura vorax G. Allen, 1923

Crocidura vorax G. Allen, 1923: 8.

HOLOTYPE: AMNH 44383; male; skin and skull; collector's number 432; collected 15 October 1916 by R.C. Andrews and E. Heller.

TYPE LOCALITY: Ssu-Shan (Snow Mountain), Li-chiang, Yunnan, China, 12,000 feet (3660 m), timberline forest.

IDENTIFICATION AND COMPARISONS: A medium-sized species. Dorsal pelage pale brown, ventral pelage pale gray-brown. Tail approximately 71% of the length of head and body, sharply bicolored brown above, pale below. Long bristlelike hairs extend along 80% of the proximal portion of the tail. Skull robust; with angular superior articular facets, well-developed lambdoid crests, and deep mastoids. Dentition: protocone of P4 even with paracone in lateral view, posterolingual border of P4 rounded and deeply concave

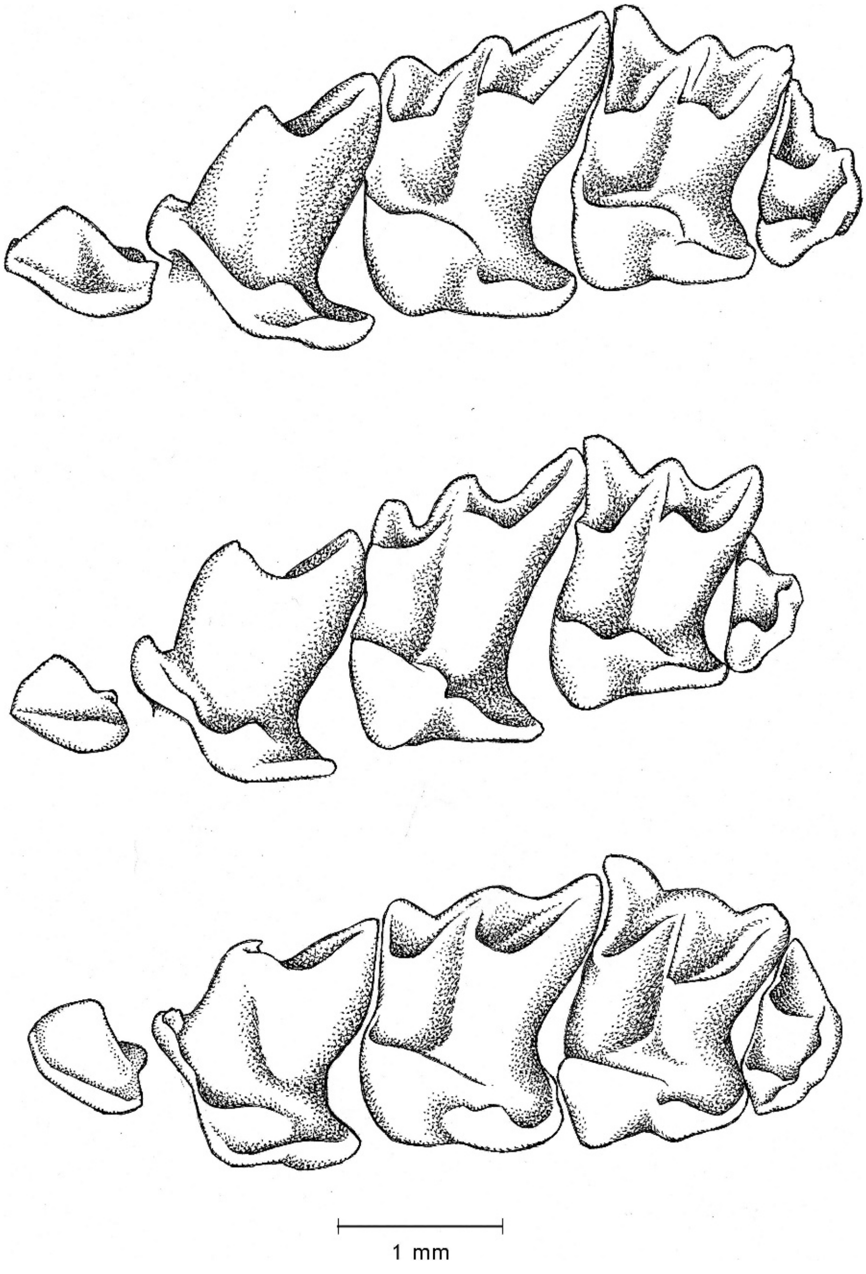

Fig. 16. Lingual view of left upper tooth rows from third unicuspid to third molar to show differences in shape of the parastyle and talon of P4. Upper *Crocidura cranbrooki* BMNH 1932.11.1.197; middle *Crocidura attenuata* BMNH 1911.9.8.29 from Sichuan, China; below *Crocidura sokolovi* ZIN 91232.

such that it exposes a deep crescent of bone. Buccal lophs of M2 terminate in a conule separate from the mesostylar cusp, so that two separate V-shaped lophs are evident in unworn dentition.

Similar in size to *C. attenuata* but generally smaller and with a more brownish pelage and a sharply bicolored tail. Superficially similar to *C. rapax* but larger, and with a more sharply bicolored tail that is covered with long pilose hairs extending over 80% of its proximal length as opposed to only 50% in *C. rapax*. The skull of *C. vorax* is more robust in appearance compared to both *C. attenuata* and *C. rapax* (see fig. 17) and differs from both species in that the buccal lophs of M2 terminate in a conule separate from the mesostylar cusp, so that two separate V-shaped lophs are evident in unworn dentition, whereas in both *C. attenuata* and *C. rapax* the lophs are continuous and W-shaped. *Crocidura vorax* is further distinguished from *C. attenuata* in that the posterolingual border of P4 is rounded (indented in *C. attenuata*); and *C. vorax* is further distinguished from *C. rapax* in that the crescent of bone posterior to P4 is more pronounced, than the moderate crescent present in *C. rapax*.

DISTRIBUTION: Known only from the holotype collected in the Snow Mountains of western Yunnan China at 12,000 ft.

REMARKS: The original specimen tag on the holotype indicates that the specimen was taken in timberline forest and that it was "seen devouring an *Apodemus* in a trap."

Regarded variously as a subspecies of *C. russula* (Hermann, 1780) (Ellerman and Morrison-Scott, 1951) or a synonym of *C. pullata* Miller, 1911 (Hutterer, 1993), this species was revised by Jiang and Hoffmann (2001) who found that it was not readily distinguished from other Chinese species in their PCA but was distinguished by their discriminant analysis.

Our metric analyses show some differences in discrimination of *C. vorax* and *C. rapax*. In the metric analyses of all species and of all the small- to medium-sized species, *C. vorax* is separate from *C. rapax*. In an analysis of *C. rapax*, *C. vorax*, and *C. indochinensis*, *C. vorax* is clearly separate from *C. rapax* on both axes in the PCA, but in the CVA the holotype of *C. vorax* is included within the 95% confidence region of the Rc group of *C. rapax*.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered locality (in curly brackets {}) and map (fig. 22). (* = specimen included in multivariate analyses) **China** – *Yunnan*: {11} Lichiang or Lichiang Range [Li-jiang, Li-kiang or Li-chiang; = Dayan] (AMNH 44383* (holotype of *vorax*)).

Crocidura rapax G. Allen, 1923

Crocidura rapax G. Allen, 1923: 9.
Crocidura horsfieldii kurodai Jameson and Jones, 1977: 461.
Crocidura tadae Tokuda and Kano, 1936 15: 429.
Crocidura tadae lutaoensis Fang and Lee, 2002: 150.

HOLOTYPE: AMNH 44321; male; skin and skull; collectors number 1258; collected 25 December 1916 by R.C. Andrews and E. Heller.

TYPE LOCALITY: Ying-pan-kai, Mekong River, southern Yunnan, 9000 feet (2745 m).

IDENTIFICATION AND COMPARISONS: A medium-sized species. Dorsal pelage brown, ventral pelage pale gray-brown. Tail length ranges between 63%–69% the length of head and body and is faintly bicolored brown above, pale below. Long bristlelike hairs extend along 50% of the proximal portion of the tail. Skull with angular superior articular facets, somewhat well-developed lamboidal crests, and deep, slightly inflated mastoids. Dentition: protocone of P4 posterior to the paracone in lateral view, posterolingual border rounded and concave such that it exposes a moderately deep crescent of bone. Buccal lophs of M2 terminate continuously such that they form a continuous W-shaped loph in unworn dentition. A well-developed talonid is present on m3. Posterolingual cuspid absent on p4.

Most similar to *C. vorax*, but see that account for comparisons. From *C. attenuata*, *C. rapax* is distinguished by its paler brown dorsal pelage, its faintly bicolored tail, and details in the dentition as follows: the posterior margin of P4 is not so severely concave, exposing less of a crescent of bone; protocone posterior to paracone of P4 (medial in *C. attenuata*); posterolingual border of P4 rounded (indented in *C. attenuata*).

DISTRIBUTION: Reported from NE India, northern Myanmar, and throughout southern China, with isolated records from Vietnam, Taiwan, and offshore islands.

REMARKS: In the original description Allen (1923) expressed some reservations over the distinction of *C. vorax* and *C. rapax*,

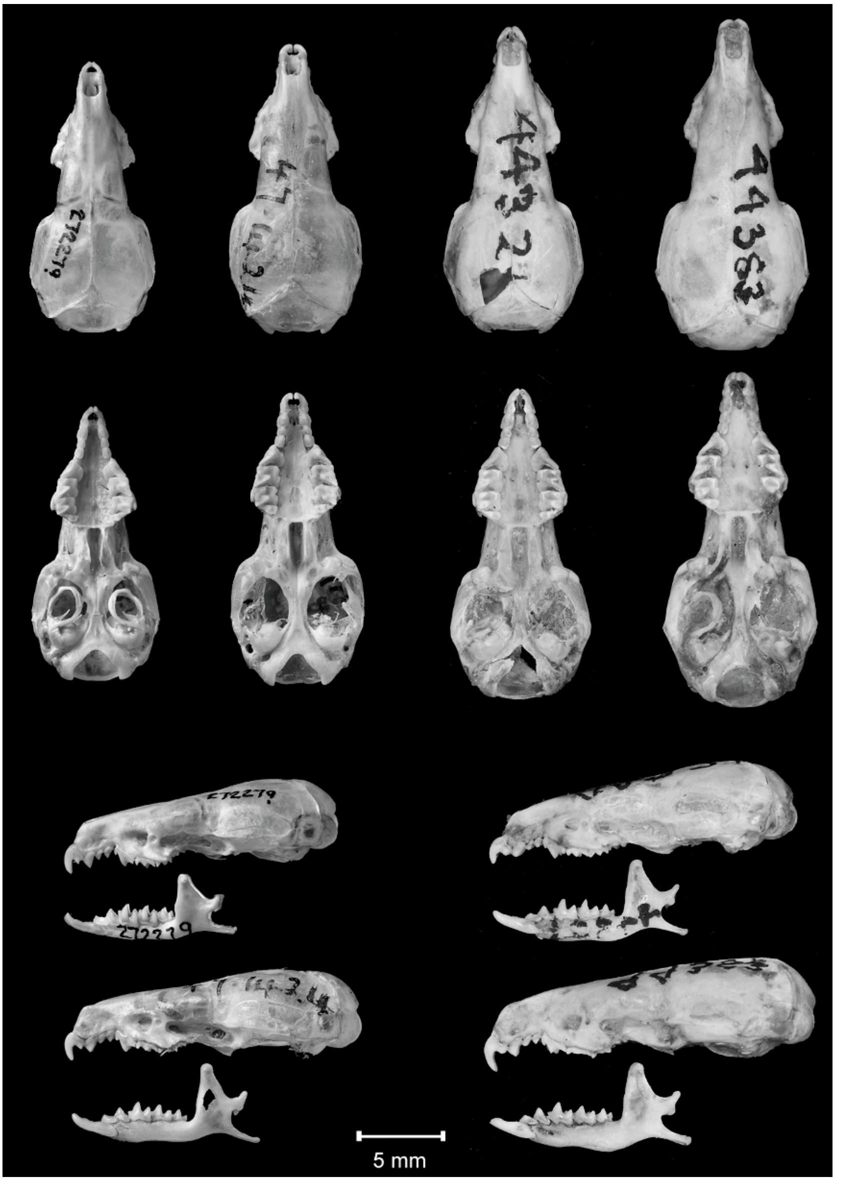

Fig. 17. Medium species. Top row from left to right: dorsal views of the skulls of *C. wuchihensis* (AMNH 272279), *C. indochinensis* (the holotype BMNH 1947.1424), *C. rapax* (the holotype AMNH 44321), and *C. vorax* (the holotype AMNH 44383); second row: ventral views of skulls in the same order; third and fourth rows: lateral views of the skulls and mandibles of (above left) *C. wuchihensis* (left lateral view); (below left) *C. indochinensis* (left lateral view); (above right) *C. rapax* (photograph of right lateral view transposed); and (below right) *C. vorax* (photograph of right lateral view of skull transposed, left lateral view of mandible).

which he suggested might be geographical representatives of the same species. Both species have been considered either subspecies of *C. russula* (Ellerman and Morrison-Scott, 1951) or synonyms of *C. pullata* (Hutterer, 1993). Jiang and Hoffmann (2001) in their revision of Chinese *Crocidura* regarded it as a distinct species. Fang and Lee

(2002) and Motokawa et al. (2005) considered *C. tadae* a distinct species with subspecies *C. t. kurodai* and *C. t. lataoensis*, however, Hutterer (2005) synonymized these taxa with *C. rapax*.

Specimens from An Khe and Mount Lang Bian formerly considered to belong to *C. indochinensis* (Heaney and Timm, 1983) are here identified as examples of *C. rapax*.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate analyses). **China** – *Sichuan*: {6} Nien Yuen Fu (FMNH 32545*); *Yunnan*: {9} Chi-tien, Yangtse River [Judian, Yangtze, Jinsha Jiang]. (AMNH 44388*); {11} Lichiang or Lichiang Range [Li-jiang, Li-kiang or Li-chiang; = Dayan] (AMNH 44381*, 44384*, AMNH 44382/MCZ 20719*; BMNH 1922.9.1.29*, 1922.9.1.30*, 1923.4.1.18*); {12} Mekong-Salwin [Salween] Divide (BMNH 1922.9.1.28*); {16} Taku [= Daju] Ferry, W bank of Yangtse R. [Yangtse, Jinsha Jiang] (AMNH 44387/MCZ 20720*); {17} Tengyueh [= Teng Chong] (BMNH 1911.8.6.2*); {19} Yin Pan Kai, Mekong River (AMNH 44321* (holotype of *rapax*)). **Myanmar** – *Kachin*: {28} 12 miles N of Myitkina (USNM 277598*); *Shan*: {29} Chin Hills (BMNH 1997.647*). **Vietnam** – *Gia Lai*: {30} An Khe [= An Túc] (USNM 357761*, 357862*); *Lâm Đồng*: {37} Mt. Lang Bian (USNM 320507*).

Crocidura indochinensis Robinson and Kloss, 1922

Crocidura indochinensis Robinson and Kloss, 1922: 88.

Crocidura horsfieldii indochinensis: Ellerman and Morrison Scott, 1951: 76

HOLOTYPE: BMNH 1947.1424, adult male, skin and skull, collected 7 April 1918 by C. Boden Kloss; collector's number 3359/CBK.

TYPE LOCALITY: Dalat, Langbian Plateau, South Annam, 5000 feet.

IDENTIFICATION AND COMPARISONS: A moderately small shrew intermediate in size between the smaller *C. wuchihensis* and larger *C. vorax*, averaging smaller than *C. rapax* (see table 4). Pelage dark brownish gray, darker and grayer than *C. rapax*, tail slender, 63%–85% of head and body length, longer on average than that of *C. rapax* (40%–76% of head and body length).

The skull of *C. indochinensis* is broader than that of *C. wuchihensis*, the maxillary region is broader, the interorbital region averages broader and the braincase is broader, deeper and longer. The skull of *C. rapax* is generally longer than that of *C. indochinensis* with a proportionately broader maxillary to interorbital region but with a comparatively narrow braincase relative to skull length and maxillary breadth (see fig. 17 and table 4).

DISTRIBUTION: From museum records, this species has an apparently disjunct distribution.

REMARKS: This species, poorly represented in museum collections, was regarded as a subspecies of *Crocidura horsfieldii* (Tomes, 1856) by Ellerman and Morrison-Scott (1951) and this classification was followed by subsequent authors (Jenkins, 1976; Jameson and Jones, 1977; Heaney and Timm, 1983; Hutterer, 1993; Corbet and Hill, 1992 with a query on its status; Jiang and Hoffmann, 2001). It was recognized as a distinct species but without explanation by Van Peenan et al. (1969) and Hutterer (2005). The two species are very difficult to separate on size but differ slightly in dental morphology. On biogeographical grounds *C. horsfieldii* is thought to be restricted to Sri Lanka and peninsular India (Lunde et al., 2003).

In the metric analyses of all species (figs. 6, 7) and the combined analysis of all the small- to medium-sized species (figs. 11–13), *C. indochinensis* groups nearest to *C. rapax* and *C. wuchihensis*; separating from both on the first axis in the PCAs. In the CVA of *C. rapax*, *C. vorax*, and *C. indochinensis* (fig. 12), the holotype and one other specimen of *C. indochinensis* from Vietnam (Iv) lie close to *C. rapax* but are well separated from the small sample of *C. indochinensis* from Myanmar (Ib) and the single specimen from Yunnan (Iy). Sample sizes are too small for conclusions to be drawn; however, it is probable that three distinct taxa are represented by these biogeographically disparate samples from Vietnam, Myanmar and Yunnan.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate

TABLE 4

Comparative Measurements of *Crocidura wuchihensis*, *C. indochinensis*, *C. rapax*, and *C. vorax*

Measurements in millimeters are presented as mean, standard deviation, and range, with number of specimens in parentheses.

	Crocidura wuchihensis	*Crocidura indochinensis*	*Crocidura rapax*	*Crocidura vorax*
HB	58.46 ± 4.18	60.5 ± 6.35	64.36 ± 6.05	
	52–65 (13)	53–71 (6)	55–72 (11)	72
TL	38.62 ± 2.66	45.3 ± 3.77	41.6 ± 2.12	
	35–44 (13)	40–50 (6)	38–45 (10)	51
HF	11.15 ± 0.80	11.53 ± 1.24	11.82 ± 0.68	
	10–13 (13)	10–13 (6)	11–13 (11)	13
E	7.5 ± 0.97			
	6–9 (10)	9 (1)	9 (1)	-
CIL	16.25 ± 0.43	17.31 ± 0.21	18.21 ± 0.36	
	15.78–17.1 (13)	17.0–17.6 (6)	17.8–18.8 (7)	19.4
UTRL	6.82 ± 0.29	7.24 ± 0.13	7.75 ± 0.23	
	6.4–7.2 (15)	7.1–7.5 (7)	7.3–8.1 (14)	8.2
I-Un3	3.09 ± 0.15	3.26 ± 0.10	3.55 ± 0.16	
	2.8–3.3 (15)	3.1–3.4 (7)	3.2–3.8 (14)	3.7
M2-M2	4.74 ± 0.14	5.05 ± 0.13	5.46 ± 0.11	
	4.5–5.0 (15)	5.0–5.3 (7)	5.3–5.7 (14)	5.6
LIOB	3.69 ± 0.14	4.00 ± 0.09	3.91 ± 0.12	
	3.5–3.9 (15)	3.9–4.2 (7)	3.8–4.1 (12)	4.2
PGB	5.2 ± 0.20	5.50 ± 0.1	5.70 ± 0.18	
	4.7–5.4 (15)	5.4–5.6 (7)	5.4–6.0 (9)	6.1
BB	7.55 ± 0.20	8.11 ± 0.22	8.17 ± 0.13	
	7.1–7.8 (14)	7.8–8.4 (6)	7.9–8.4 (7)	9.1
BH	3.99 ± 0.12	4.46 ± 0.08	4.64 ± 0.10	
	3.7–4.1 (14)	4.4–4.6 (6)	4.5–4.8 (7)	5
BL	6.77 ± 0.16	7.24 ± 0.10	7.32 ± 0.19	
	6.4–7.0 (14)	7.1–7.4 (6)	7.0–7.5 (6)	8.3
AWM2	1.58 ± 0.07	1.69 ± 0.04	1.84 ± 0.05	
	1.47–1.67 (15)	1.62–1.73 (7)	1.74–1.94 (14)	1.94
LM3	0.54 ± 0.07	0.59 ± 0.06	0.61 ± 0.03	
	0.44–0.65 (15)	0.54–0.68 (6)	0.57–0.64 (14)	0.66
ML	9.78 ± 0.33	10.45 ± 0.23	11.14 ± 0.26	
	9.4–10.4 (15)	10.2–10.8 (7)	10.7–11.5 (14)	11.5
MTRL	6.38 ± 0.23	6.73 ± 0.11	7.25 ± 0.20	
	6.0–6.8 (15)	6.6–6.9 (7)	7.0–7.6 (14)	7.5
MH	3.72 ± 0.15	4.02 ± 0.19	4.23 ± 0.14	
	3.4–4.0 (15)	3.8–4.4 (7)	3.9–4.4 (13)	4.5

analyses). **China** – *Yunnan*: {10} Ho Mu Shu Pass (AMNH 44356*). **Myanmar** – *Kachin*: {21} Gangfang [Kangfang] (AMNH 114711*, 114713*, 114714*); {27} Rawngaw [Rawngtsaw] (AMNH 114790*). **Vietnam** – *Lâm Đồng*: {36} DaLat [Dà Lat] (BMNH 1947.1424* (holotype of *indochinensis*)); *Lào Cai*: {39} Chapa [Sa Pa] (FMNH 39029*).

Crocidura wuchihensis Shaw, Wang, Lu and Chang, 1966

Crocidura wuchihensis Shaw et al., 1966: 275.

HOLOTYPE: IZAC 13874; male; skin and skull; collected 16 April 1957.

TYPE LOCALITY: Shui-Man, western slope of Wuchih Mountain, Hainan Island, China.

IDENTIFICATION AND COMPARISONS: A medium-sized species. Dorsal pelage dark gray with dark brown tinges. Ventral pelage slightly paler than dorsal pelage, gray brown. Tail approximately 68% head and body length and faintly bicolored. Long bristlelike hairs extend along 20% of the proximal portion of the tail. Skull small and delicate (fig. 17). Dentition: posterior margin of P4 only slightly concave and exposing only a shallow crescent of bone. P4 with protocone somewhat anterior to the paracone, and with the posterolingual border rounded. Buccal lophs of M2 form a continuous W-shaped cusp in unworn dentition. Talonid of m3 well developed. Posterolingual cuspid absent on p4.

Four very small species overlap the lower end of the size range of this species, but each is distinguishable based on a suite of qualitative morphological characters. See the individual accounts of *C. annamitensis*, *C. zaitsevi*, *C. guy*, and *C. kegoensis* for further details. *Crocidura indochinensis* is slightly larger than *C. wuchihensis*, but the two share a number of external characteristics, and so are very likely to be confused. Both are small dark gray-brown shrews with the tail averaging about 70% the length of head and body and with approximately 20%–30% of the proximal tail length having long bristles. However, *C. wuchihensis* is distinguished by its more rounded superior articular facets and by the position of the protocone on P4, which is situated anterior to the paracone.

DISTRIBUTION: In addition to the type locality on Hainan Island, additional specimens have been identified from W Yunnan, N Lao PDR, and N Vietnam.

REMARKS: Long considered a synonym of *C. horsfieldii* (along with *C. indochinensis*) until Lunde et al. (2003) restricted *horsfieldii* to Sri Lanka and peninsular India (based on both observed morphological differences and biogeographic considerations) and reinstated the name *wuchihensis* for a valid species that was distinct from *C. indochinensis*.

The CVA (fig. 12) shows that the two groups of *C. wuchihensis* (Wh and Wt) respectively from northern Vietnam and the southern Annamites are moderately well separated from each other. Specimens from northern Vietnam are larger on average (CIL 15.7–17.1, mean 16.4) than those from the southern Annamites (CIL 15.8–16.4, mean 16.0).

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered localities (in curly brackets {}) and map (fig. 22) (* = specimens included in multivariate analyses). **China** – *Hainan*: IZAC 13874 (holotype of *wuchihensis*). **Vietnam** – *Hà Tĩnh*: {31} Huong Son Camp (AMNH 272127*, 272128*, 272129*, 272133*, 272233*, 272279*); *Hà Giang*: {33} Mt. Tay Con Linh II (AMNH 273209*, 274153*, 274162*, 274167*, 274168*, 274182*); *Lạng Sơn*: {38} Pa Kha [Pak Ha; Bac Hà] (BMNH 1933.4.1.168); *Lào Cai*: {40} Ngai Tio [Ngải Chồ] (BMNH 1925.1.1.24*, 1925.1.1.27*); {41} Thai Nien (BMNH 1925.1.1.29*); *Quảng Nam*: {42} Ba Na (BMNH 1997.640*, 1997.641*).

Crocidura kegoensis Lunde, Musser and Ziegler, 2004

Crocidura kegoensis Lunde et al., 2004: 27–36.

HOLOTYPE: MTD B 23389. "Ky Anh – Ke Go" (= "Ke Go" or "Ho Ke Go") Nature Reserve (vicinity of 18°04′N, 105°58′E), Ha Tinh Province, Vietnam, at an altitude of about 200 m.

IDENTIFICATION AND COMPARISONS: A diminutive brown *Crocidura* with short tail, short feet, and conspicuous blackish mystacial patches on the muzzle above the upper lips. Skull small, the rostrum short and broad; braincase broad and flattened. Upper premolar (P4) with a small but well-defined anterior parastyle and a tall thin paracone. The protocone is only slightly more prominent than the barely perceptible hypocone. Posterior border of P4 deeply concave, exposing a crescent of underlying bone between it and the anterior margin of the first upper molar (fig. 18). Strong emargination on M1 and M2 define crescentic posterior margins, but these are less marked than in P4.

Crocidura kegoensis has a relatively short tail in comparison to head and body length (56%), similar to that of *C. annamitensis* (56%–61%), shorter than that of *Crocidura zaitsevi* (61%–81%) and *C. guy* (68%–77%), and is similar in condyloincisive length (see table 5). *Crocidura kegoensis* has a broader maxillary region and longer braincase than *C. annamitensis*, *C. guy*, and *C. zaitsevi*. The talon of P4 in *C. kegoensis* is smaller and has a more deeply concave posterior border than any of the other three species. The talonid of m3 is similar to that of *C. guy*, less reduced than that of *C. annamitensis*, but more reduced than that of *C. zaitsevi*. *Crocidura wuchihensis* has a longer condyloincisive and braincase length and averages larger than *C. kegoensis* in all other external and cranial measurements (see tables 4 and 5).

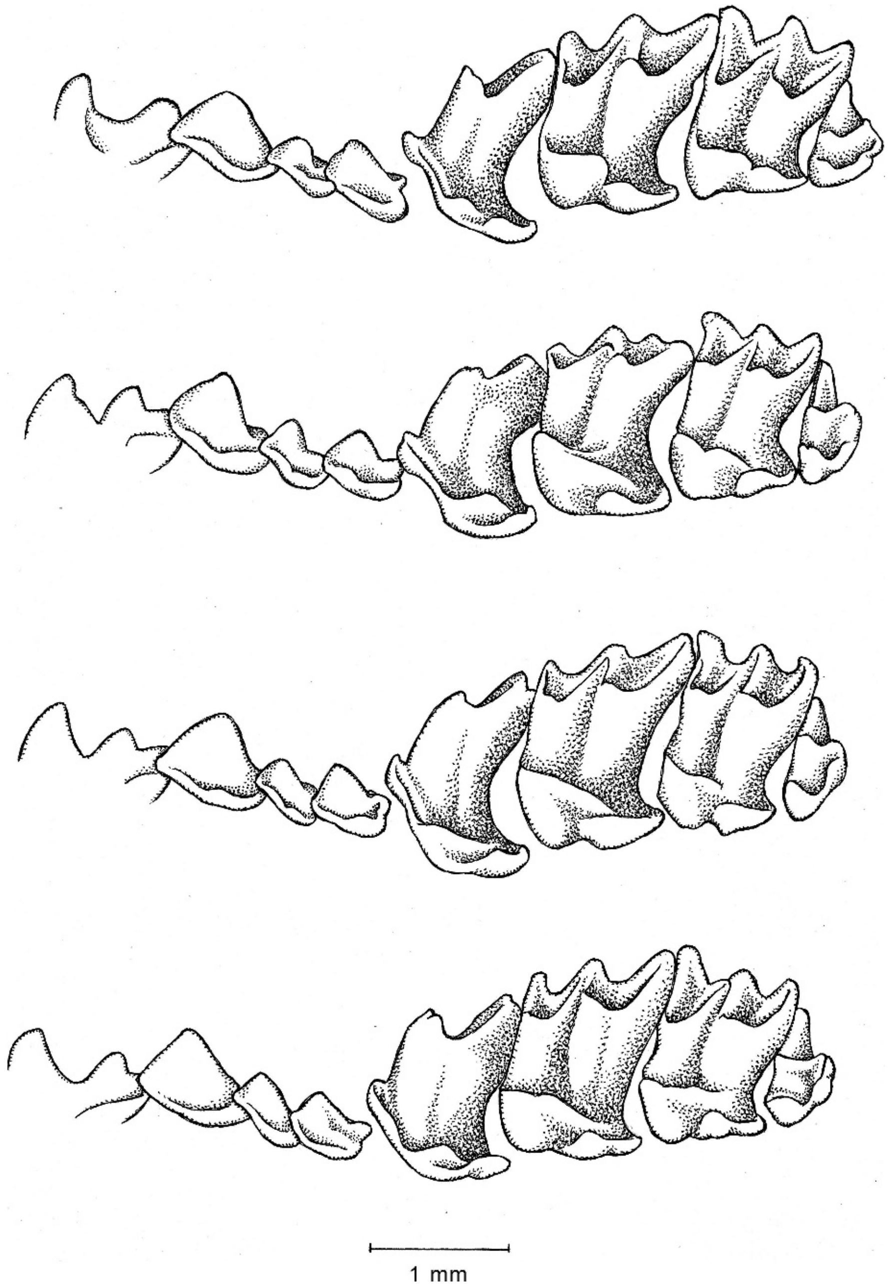

Fig. 18. Lingual view of left upper tooth rows to show differences in the proportions of the talon of P4 in relation to M1. First incisor partially obscured by right incisor. Top row: *Crocidura kegoensis* MTD B23389; second row: *Crocidura zaitsevi* ZIN 91224; third row: *Crocidura annamitensis* AMNH 272329; bottom row: *Crocidura guy* BMNH 1997.643.

DISTRIBUTION: Currently known only from the type locality.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered locality (in curly brackets {}) and map (fig. 22). (* = specimen included in multivariate analyses) **Vietnam** – *Hà Tĩnh*: {32} Ky Anh - Ke Go Nature Reserve (MTD 23389* (holotype of *kegoensis*)).

TABLE 5

Comparative Measurements of *Crocidura kegoensis*, *C. zaitsevi*, *C. annamitensis*, and *C. guy*

Measurements in millimeters are presented as mean, standard deviation, and range, with number of specimens in parentheses. All measurements taken by P.J., with the exception of those for *C. zaitsevi*, which are taken from the original description.

	Crocidura kegoensis	*Crocidura zaitsevi*	*Crocidura annamitensis*	*Crocidura guy*
HB		53 ± 3	54	49.5 ± 2.27
	48	48–58 (12)	49–58 (3)	47–52.5 (4)
TL		37 ± 2	32	35.85 ± 1.40
	27	33–41 (12)	30–33 (3)	34–37.4 (4)
HF		10 ± 1	9.33	9.5 ± 0.41
	10	8–11 (12)	9–10 (3)	9–10 (4)
E		7 ± 1	6.33	6.48 ± 0.41
	5	5–8 (12)	5–8 (3)	6–7 (4)
CIL		15.40 ± 0.38	15.27	15.37 ± 0.05
	15.3	14.8–15.8 (12)	15.1–15.4 (3)	15.3–15.4 (4)
UTRL		6.51 ± 0.16	6.48	6.49 ± 0.14
	6.4	6.2–6.8 (12)	6.6–6.6 (3)	6.4–6.7 (4)
I-Un3		2.79 ± 0.08	2.85	2.77 ± 0.07
	2.8	2.6–3.0 (12)	2.8–2.9 (3)	2.7–2.8 (4)
M2-M2		4.38 ± 0.11	4.46	4.53 ± 0.14
	4.7	4.2–4.6 (12)	4.4–4.6 (3)	4.4–4.7 (4)
LIOB		3.64 ± 0.1	3.4	3.53 ± 0.10
	3.6	3.4–3.8 (12)	3.3–3.5 (3)	3.4–3.6 (4)
PGB		4.78 ± 0.14	4.89	4.96 ± 0.24
	5.2	4.5–5.0 (12)	4.6–5.1 (3)	4.7–5.3
BB		7.51 ± 0.18		7.23 ± 0.17
	7.3	7.2–7.8 (6)	7.2	7.0–7.4 (4)
BH		3.75 ± 0.12		3.58 ± 0.1
	3.7	3.5–4.0 (11)	3.7	3.5–3.8 (4)
BH		6.16 ± 0.16		6.30 ± 0.05
	6.4	5.9–6.5 (11)	6.1 (2)	6.2–6.4 (4)
AWM2		1.44 ± 0.05	1.55	1.58 ± 0.08
	1.61	1.36–1.56 (12)	1.49–1.58 (3)	1.48–1.66 (4)
LM3		0.54 ± 0.04	0.55	0.53 ± 0.04
	0.54	0.47–0.59 (12)	0.52–0.6 (3)	0.49–0.58 (4)
ML		9.29 ± 0.21	9.28	9.5 ± 0.16
	9.3	8.8–9.6 (12)	9.1–9.5 (3)	9.3–9.6 (4)
MTRL		6.06 ± 0.14	6.14	6.14 ± 0.11
	6.1	5.7–6.2 (12)	6.1–6.2 (3)	6.0–6.3 (4)
MH		3.49 ± 0.12	3.44	3.53 ± 0.06
	3.6	3.3–3.7 (12)	3.4–3.5 (3)	3.4–3.6 (4)
TL (% HB)	56.25	69.66 ± 6.31	59.37 ± 1.82	72.49 ± 3.36
		61.82–81.25 (12)	56. 9–61.22 (3)	68.68–76.6 (4)
TL: CIL	1.77	2.39 ± 0.18	2.10 ± 0.11	2.33 ± 0.09
		2.14–2.72 (12)	1.95–2.19 (3)	2.22–2.43 (4)
IOB : M2-M2	0.76	0.83 ± 0.02	0.76 ± 0.00	0.78 ± 0.02
		0.80–0.86 (12)	0.76–0.77 (3)	0.77–0.81 (4)
AWM2 : M2-M2	0.34	0.33 ± 0.01	0.35 ± 0.01	0.35 ± 0.01
		0.31–0.34 (12)	0.34–0.36 (3)	0.34–0.36 (4)

C. zaitsevi Jenkins, Abramov, Rozhnov and Makarova, 2007

C. zaitsevi Jenkins et al., 2007: 59.

HOLOTYPE: ZIN 91224; collector's number 31; female, body in ethanol, skull extracted, collected 11 April 2004 by A.V. Abramov.

TYPE LOCALITY: Ngoc Linh Mountain, west slope, 1–2 km west of apex, Central Highlands, Kon Tum Province, Vietnam, 15°05′N, 107°57′E, altitude 2300 m.

IDENTIFICATION AND COMPARISONS: A very small, gray shrew with a slightly brownish hue and with a moderately long tail, ranging from 62%–81% of head and body length. The interorbital region is broad relative to maxillary breadth (fig. 19). The parastyle of P4 is well defined, the paracone is broad and the posterior border of cusp is short and sloping, the talon is moderately large, the protocone is large and anteromedial in position, the hypocone is posterior in position and the posterior border is concave. The talonid of m3 is complete, with a low cusp anterobuccal to the hypoconid evident in the unworn dentition, a well marked entoconid ridge, a small entoconid and well marked talonid basin.

Crocidura zaitsevi is smaller on average than *C. wuchihensis*; it is comparable in size to the other three very small shrews, *C. kegoensis*, *C. annamitensis*, and *C. guy*, from which it is distinguished by a combination of characters. It has a longer tail relative to head and body length than that of *C. kegoensis* (56.3%) and *C. annamitensis* (56.9%–61.2%) and the tail is also longer relative to condyloincisive length than in *C. kegoensis* and averages longer than in *C. annamitensis* (see table 5). *Crocidura zaitsevi* is narrower than *C. kegoensis* in maxillary and postglenoid breadth, has a shorter braincase, and M2 is narrower. The interorbital region is broader relative to maxillary breadth in *C. zaitsevi* than in *C. kegoensis* and *C. annamitensis* and averages greater than in *C. guy*. The ratio of the anterior width of M2 to maxillary breadth averages less than in *C. kegoensis*, *C. annamitensis*, and *C. guy*. *Crocidura zaitsevi* differs from *C. kegoensis* in the shape of the paracone of P4, the broad talon and relative positions of the protocone and hypocone. The posterior border of the talon of P4 is concave as in *C. annamitensis* unlike the deeply concave border in *C. kegoensis* or the shallowly concave border in *C. guy* (see fig. 18). The talonid of m3 in *C. zaitsevi* is large and well developed, more so than *C. guy* and *C. kegoensis* in which the entoconid is small with a small shallow talonid basin, or *C. annamitensis* in which the talonid is reduced to a hypoconid and slight entoconid ridge (see fig. 20). *Crocidura wuchihensis* has a longer braincase and averages larger than *C. zaitsevi* in all other external and cranial measurements (see tables 4 and 5).

DISTRIBUTION: Recorded only from the type locality of Ngoc Linh Mountain in the Southern Annamites, Vietnam at high altitudes, 1650–2300 m.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered locality (in curly brackets {}) and map (fig. 22). (* = specimens included in multivariate analyses). **Vietnam** – *Quảng Nam*: {43} Ngoc Linh Nature Reserve (ZIN 91218*, 91224* (holotype of *zaitsevi*)).

Crocidura annamitensis, sp. nov.

HOLOTYPE: AMNH 272329. Adult collected May 12, 1998 by D.P. Lunde (DPL 1244). The specimen was fixed whole in formalin and is now stored in ethanol. The skull was subsequently removed and cleaned in a dermestid beetle colony.

TYPE LOCALITY: Vietnam: Ha Tinh; Huong Son Camp, 920 m.

PARATYPES: AMNH 272614, 272648.

DIAGNOSIS: A very small brown shrew with a relatively short tail measuring a little more than half the length of head and body; talonid of m3 reduced to a hypoconid and slight entoconid ridge; a large portion of the incus and head of the malleus visible below the dorsal limb of the tympanohyal, ventral limb long.

DESCRIPTION: Size small (head and body length 49–58) with a moderately short tail (57–61% head and body length). Dorsal pelage light brown. Individual hairs pale gray at the bases and pale brown at the tips. Ventral color grayish buff. Individual hairs pale grayish brown at base, buff toward the tip. No demarcation between dorsal and ventral color. Tail dark brown above, pale

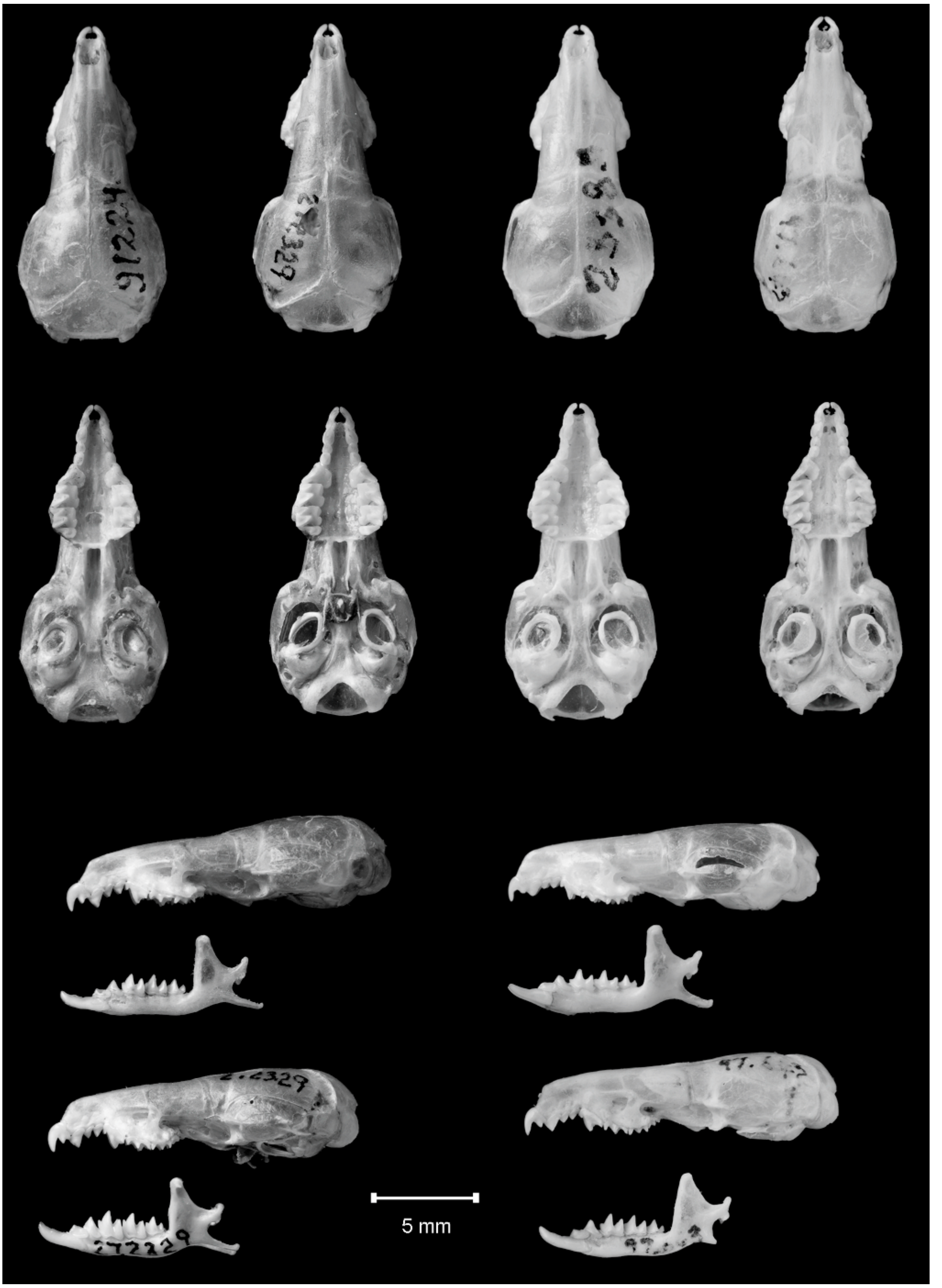

Fig. 19. Small species. Top row from left to right: dorsal views of the skulls of *C. zaitsevi* (the holotype ZIN 91224), *C. annamitensis* (the holotype AMNH 272329), *C. kegoensis* (the holotype MTD B 23389), and *C. guy* (the holotype BMNH 1997.643); second row: ventral views of skulls in the same order; third and fourth rows: left lateral views of the skulls and mandibles of (above left) *C. zaitsevi*; (below left) *C. annamitensis*; (above right) *C. kegoensis*; and (below right) *C. guy*.

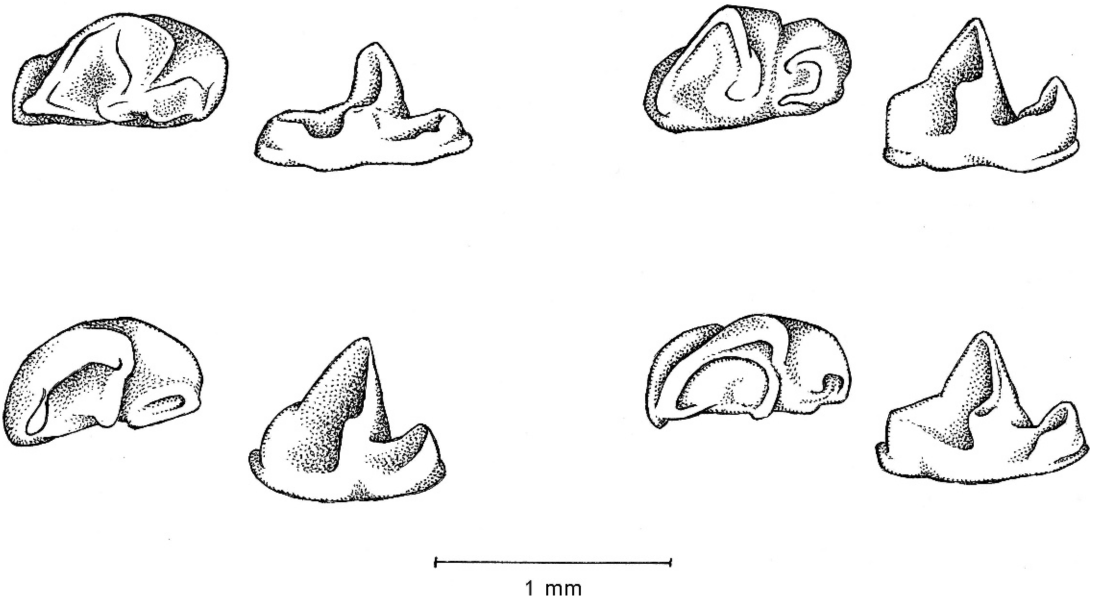

Fig. 20. Occlusal (left) and lingual (right) views of right lower third molar to show differences in development of the talonid. Upper row: (left) *Crocidura kegoensis* MTD B23389 (dentition very worn); (right) *Crocidura zaitsevi* ZIN 91224; lower row: (left) *Crocidura annamitensis* AMNH 272329; (right) *Crocidura guy* BMNH 1997.643.

brown below. Long pilose hairs present on the proximal half of the tail. Dorsal surfaces of hands pale buffy brown. Dorsal surfaces of feet pale buffy brown with darker brown pigmentation laterally. Skull small (fig. 19). Rostrum narrow, increasing gradually in breadth through the interorbital region and through the well-rounded braincase such that in dorsal view the skull approximates a rather evenly shaped wedge. First upper incisor (I1) pro-odont, projecting well beyond the anterior border of the premaxillary, talon well developed and approximately half the height of Un1. First unicuspid very large, equal to or slightly less in height than the principal cusp of I1 but less than the height of the paracone of P4. Second upper unicuspid approximately half the height of Un1 but only slightly smaller than Un3. Parastyle of P4 well defined, shorter than Un3. Paracone robust, protocone and hypocone moderately prominent. Posterior border of P4 concave. The talon of P4 projects to but not beyond the protocone of M1. The first lower incisor (i1) has two low cusps and a well-marked posterobuccal cingulum. The first lower premolar (p1) is elongated, approximately half the lower border of the tooth is in contact with i1, and its posterior border is slightly overlapped by the second lower premolar (p4). Lower m3 with talonid reduced to a hypoconid and slight entoconid ridge (fig. 20).

COMPARISONS: *Crocidura annamitensis* has a relatively short tail in comparison to head and body length (56%–61%), similar to that of *C. kegoensis* (56%), shorter than that of *C. guy* (68%–77%) and averaging shorter than that of *Crocidura zaitsevi* (61%–81%), and similarly in comparison to condyloincisive length (see table 5). The skull of *C. annamitensis* is narrower than that of *C. kegoensis*, which also has a slightly longer braincase. The interorbital region of *C. annamitensis* is narrower relative to maxillary breadth and the ratio of the anterior width of M2 to maxillary breadth averages greater than in *C. zaitsevi*. The talon of P4 of *C. annamitensis* is larger than that of *C. kegoensis* and the posterior border is concave as in *C. zaitsevi* but unlike the deeply concave border in *C. kegoensis* or the shallowly concave border in *C. guy*. The talonid of m3 in *C. annamitensis* is more reduced than in *C. guy* and *C.*

kegoensis in which the entoconid is small with a shallow talonid basin or *C. zaitsevi*, which has a large and well-developed talonid. *Crocidura wuchihensis* has a longer condyloincisive and braincase length and averages larger than *C. annamitensis* in all other external and cranial measurements (see tables 4 and 5).

DISTRIBUTION: Currently known only from elevations between 920–1240 m at the type locality, and likely occurring at higher elevations throughout the northern Annamite (or Truong Son) mountain range.

ETYMOLOGY: Annamite refers to an older, colonial name for the range of mountains defining the border between much of central Vietnam and Lao PDR.

REMARKS: The species is reported as Species 2 in the results of the metric analyses and indicated by the letter D and the symbol ▼ in the accompanying figures.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered locality (in curly brackets {}) and map (fig. 22). (* = specimens included in multivariate analyses). **Vietnam** – *Hà Tĩnh*: {31} Huong Son Camp (AMNH 272329* (holotype of *annamitensis*), 272614*, 272648*.

Crocidura guy, sp. nov.

HOLOTYPE: BMNH 1997.643 adult female, body in alcohol, skull extracted. Collected July–September 1996. Society for Environmental Exploration.

TYPE LOCALITY: Vietnam, Tuyen Quang Province, Na Hang Nature Reserve, Tat Ke Sector, ca. 22°30′N 105°30′E.

PARATYPES: BMNH 1997.642 adult male, 1997.644 adult male, 1997.645 adult male, 1997.646 juvenile; all bodies in alcohol, skulls extracted, all with the same locality data as the holotype.

DIAGNOSIS: very small; silvery gray venter; P4 with large talon; m3 with slightly reduced talonid; dorsal limb of tympanohyal broad, largely concealing the underlying head of the malleus; ventral limb long.

DESCRIPTION: Very small in size (see table 5) with a moderately long tail 68%–77% of head and body length. Dorsal pelage brownish gray, individual hairs with gray bases and brown tips; ventral color silvery gray, individual hairs with gray bases, light gray and light buff tips. No demarkation between dorsal and ventral color. Tail pale brown dorsally, paler ventrally, moderately stout with bristle hairs on the proximal half of the tail; tail scales visible beneath the short scale hairs. Feet pale brown, with a slightly darker stripe on the outer lateral surface; foot pads small, rounded and well spaced. Males with prominent lateral glands, with a central portion of short brown hairs surrounded by longer silvery hairs. Female with three pairs of inguinal mammae.

Skull (see fig. 19) with a moderately broad and deep rostrum. Interorbital region moderately straight, increasing gradually in breadth from anterior to posterior. Braincase narrow to moderately broad, somewhat flat in profile and moderately long; anterior region of sinus canal steeply curved; mastoid broad and deep. Auditory region with dorsal limb of tympanohyal moderately deep, subrectangular, mainly concealing incus and head of malleus, and ventral limb of tympanohyal long (see fig. 21).

First upper incisor moderately robust. Premolars large, with robust parastyle; paracone moderately robust and tall with steep but short posterior border, posterobuccal portion of trigon short and slender; talon large, anterior portion projecting well into palate; protocone anteromedial in position; hypocone posterior in position; posterior border of tooth shallowly concave. Second upper molar (M2) with double V-shaped buccal lophs evident in unworn dentition. Mandibular dentition robust. Cuspid present on posterolingual border of p4. Protoconid of m3 broad; talonid slightly reduced; no trace of cusp anterobuccal to hypoconid; talonid with entoconid ridge, low entoconid and small, shallow talonid basin.

COMPARISONS: This species is in the same size group as the very small *C. annamitensis*, *C. kegoensis* and *C. zaitsevi* and so readily distinguished from all other species, with the possible exception of *C. wuchihensis*, with which there may be slight overlap in some measurements. The brownish gray dorsal colour of the pelage of *C. guy* is unlike that of the grayer *C. zaitsevi* and the browner *C. kegoensis* and *C. annamitensis* and the silvery gray venter is distinctive and unlike that of

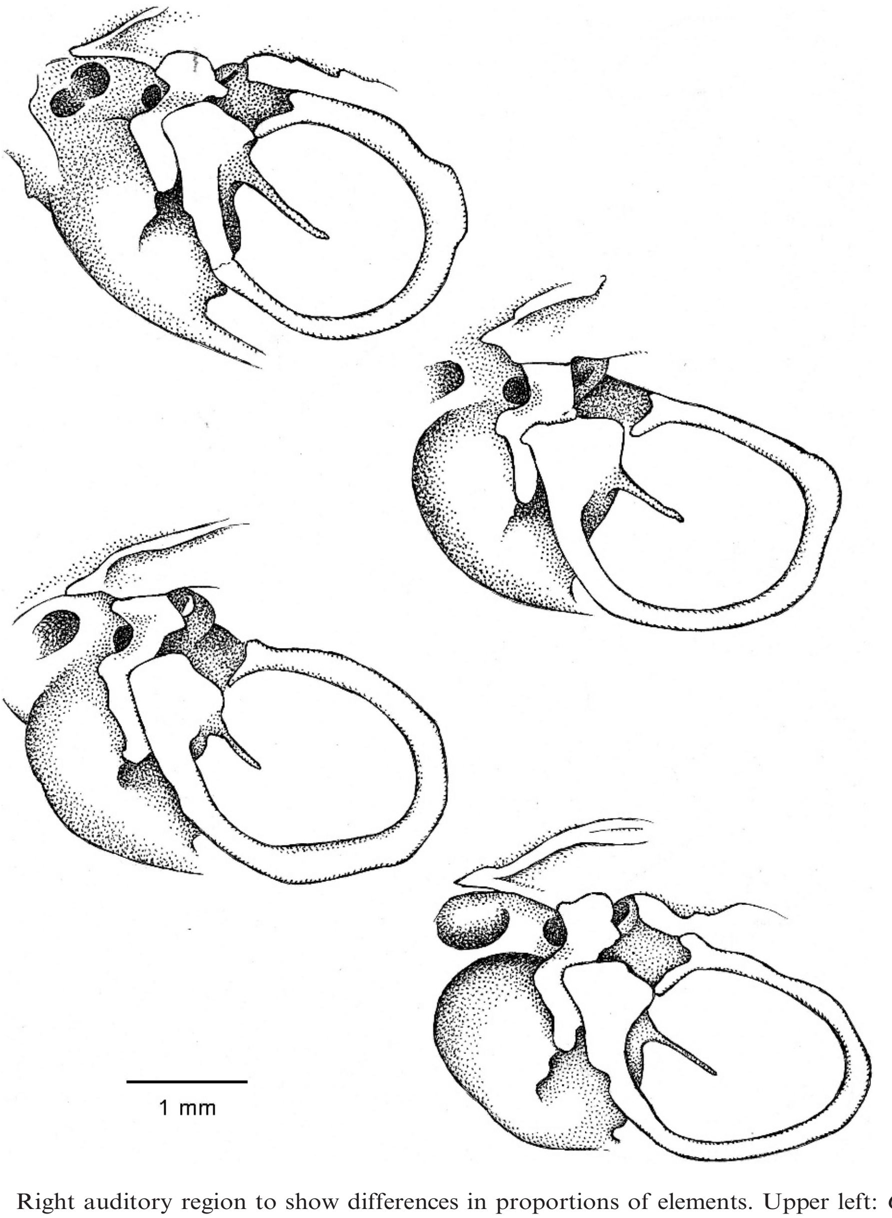

Fig. 21. Right auditory region to show differences in proportions of elements. Upper left: *Crocidura kegoensis* MTD B23389 (tympanic ring broken); middle right: *Crocidura zaitsevi* ZIN 91224; middle left: *Crocidura annamitensis* AMNH 272329; lower right: *Crocidura guy* BMNH 1997.643.

the other three species. The long tail relative to head and body length is similar to that of *C. zaitsevi* (61%–81%) but unlike the shorter tail of *C. annamitensis* (57%–61%) or *C. kegoensis* (56%). The ratio of interorbital breadth to maxillary breadth averages slightly greater than *C. kegoensis* and *C. annamitensis* but less than *C. zaitsevi* (see table 5). The braincase is longer than that of *C. annamitensis* but shorter than that of *C. kegoensis*, and the rostrum is shallower than that of *C. kegoensis*. The anterior region of the sinus canal forms a steeper curve than in *C. zaitsevi* and is unlike the shallowly curved canals of *C. kegoensis* and *C. annamitensis*. The tympanohyal and the degree of exposure

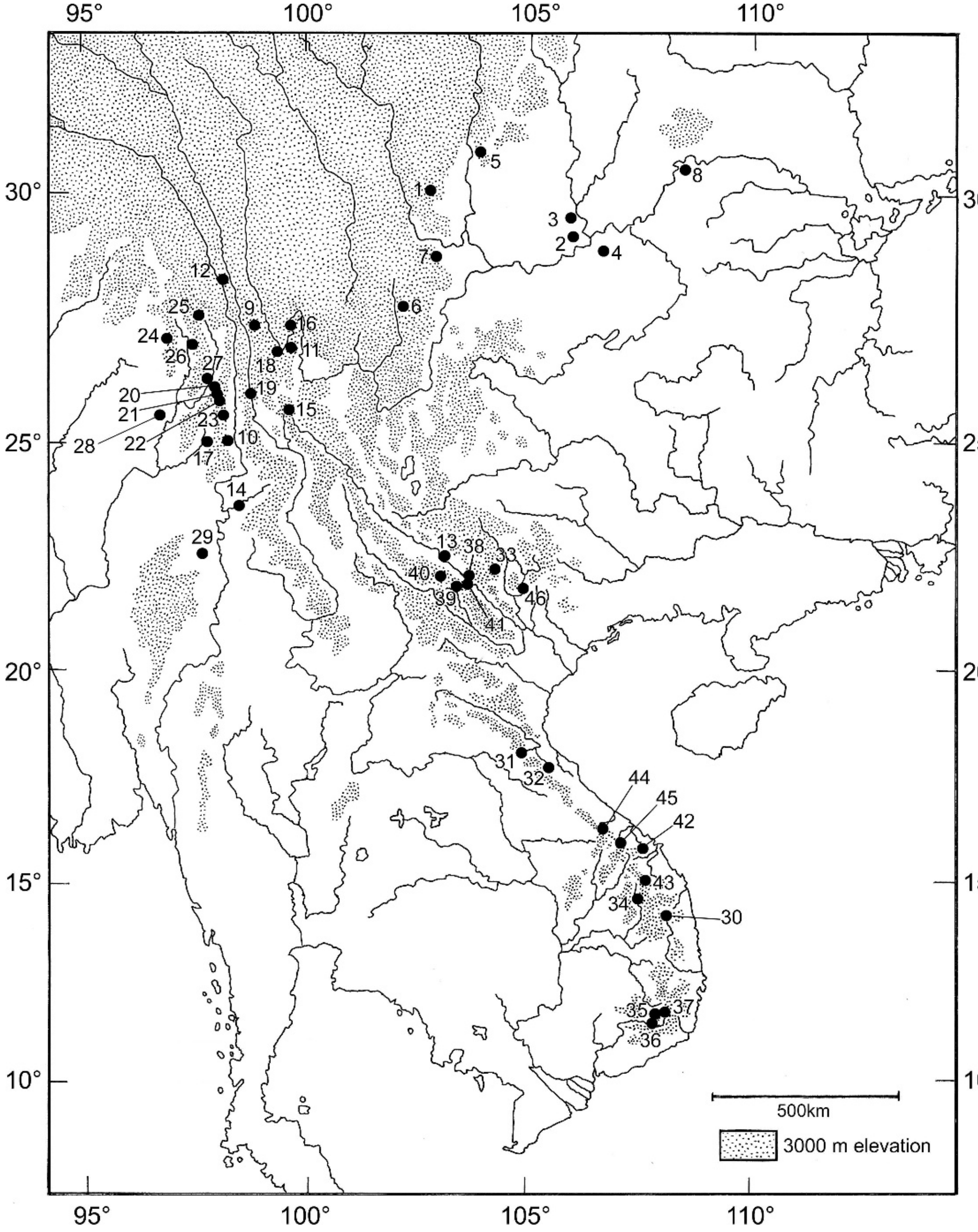

Fig. 22. Map of Southeast Asia. Numbers indicate localities listed in the gazetteer.

of the head of the malleus differ in all four species (see fig. 21). The dorsal limb of the tympanohyal of *Crocidura kegoensis* is compressed, the junction with the squamosal is domed, the ventral limb is short, the incus and head of malleus is small and largely concealed by the tympanohyal. The dorsal limb of the tympanohyal of *Crocidura zaitsevi* is broad, the ventral limb thin and short. The ventral limb of the tympanohyal of *Crocidura annamitensis* is long, and a large portion of the incus and head of the malleus is visible below the dorsal limb of the tympanohyal.

The ratio of the anterior width of M2 to maxillary breadth averages greater than that of *C. zaitsevi*. The upper premolar, particularly the talon, is more robust than that of the other species in this size group and the posterior border of the tooth is less concave. Lower m3 with somewhat reduced talonid unlike *C. zaitsevi*, in which all elements of the talonid are complete, or *C. annamitensis*, in which the talonid is reduced to a hypoconid and slight entoconid ridge (see fig. 20).

Externally *C. guy* is distinguished on pelage colour from the considerably darker grayish brown *C. wuchihensis*. *Crocidura guy* averages smaller than *C. wuchihensis* in external and cranial measurements (see tables 4 and 5) and has a shorter skull, shown by the shorter condyloincisive, rostral and braincase lengths.

DISTRIBUTION: Recorded only from the northern wilderness section Tat Ke Sector of the Na Hang Nature Reserve, Vietnam. This is an area of rugged limestone hills 300–800 m, consisting of forest and land cleared for cultivation.

ETYMOLOGY: The specific epithet is treated as a noun in apposition. This new species is named in honor of our inspirational colleague and mentor Guy Musser. He has spent many weeks as an occasional and most welcome visitor to BMNH, quietly and painstakingly working through the small mammal collections, measuring, comparing, reidentifying and often recurating the collections, discussing and exchanging views. He has always been generous in making his deep and wide-ranging knowledge of mammalogy freely available to all who seek his advice. Our choosing this particular taxon to honor Guy is based on his having joined one of us (DPL) on a mammal field survey to the stunningly beautiful Viet Bac limestone region of northeastern Vietnam (see Lunde et al. 2007), within which the new species is apparently endemic.

REMARKS: The species is reported as Species 3 in the results of the metric analyses and indicated by the letter N and the symbol ▲ in the accompanying figures.

SPECIMENS EXAMINED: See gazetteer (appendix 1) for details of numbered locality (in curly brackets {}) and map (fig. 22). (* = specimens included in multivariate analyses). **Vietnam** – *Tuyên Quang*: {46} Na Hang Nature Reserve, Tat Ke sector (BMNH 1997.642*, 1997.643* (holotype of *guy*), 1997.644*, 1997.645*, 1997.646).

BIOGEOGRAPHY

Two main sources were used for the determination of the biogeographical regions in Indochina: Zhang et al. (1997) for Sichuan and Yunnan, China, and Wikramanayake et al. (2002) for Vietnam and Myanmar. Wikramanayake et al. (2002) use the political boundary with China as the northern boundary for the Indo-Pacific region that is the subject of their study; however, they indicate where the biologically based ecoregions overlap the boundaries with China. For southwestern China, we have therefore used both publications to determine biogeographic units.

All collection localities in China in this study occur within the Oriental realm (Zhang et al, 1997). *Crocidura attenuata* was the only species collected from the four localities in Chongqing that lie within the Western Mountain Subregion, Central China Region of the Oriental Realm, a subregion of subtropical shrubforest and grass. This subregion extends east and west of the Min Jiang and north and south of the Chang Jiang (Yangtze River), which is evidently no barrier to this species of *Crocidura*. Four species, *C. attenuata*, *C. fuliginosa*, *C. rapax* and *C. vorax* occur within the Southwest Mountain Subregion, Southwest China Region of the Oriental Realm. Alpine forest steppe, and subtropical shrub forest and grass occur in this subregion, which is drained by the Nu Jiang (Salween), Lancang Jiang (Mekong), and the Jinsha Jiang (Yangtze) rivers.

The South China Region of the Oriental Realm is the only one where there is correspondence between the classification system used by Zhang et al. (1997) and that of Wikramanayake et al. (2002). The Southern Yunnan Mountain Subregion, an area of subtropical shrub forest and grass is broadly equivalent to Ecoregion 74 Northern Indochina Subtropical Forests of Wikramanayake et al. (2002), characterized as a tropical and subtropical moist broadleaf forests biome. Wikramanayake et al. (2002) state that "This large ecoregion extends across the highlands of northern Myanmar, Laos and Vietnam and also includes most of southern Yunnan Province." The region is drained by the Nu Jiang and Lancang Jiang and lies to the west of the Sông Hông (Red River). *Crocidura attenuata*, *C. fuliginosa*, *C. indochinensis*, *C. rapax*, and *C. wuchihensis* are recorded from localities in this large ecoregion.

Ecoregion 75 South China–Vietnam Subtropical Evergreen Forests, classed as a tropical and subtropical moist broadleaf forests biome, lies NE of the Sông Hông and is geologically separate from the remainder of SE Asia (Wikramanayake et al., 2002) and the fauna has mixed affinities with southern China and Indochina (Lunde et al., 2003). Four species occur in this ecoregion, *C. attenuata*, *C. guy*, *C. fuliginosa*, and *C. wuchihensis*. There is no evidence to suggest that the Sông Hông forms a barrier to species, since *C. attenuata*, *C. fuliginosa*, and *C. wuchihensis* occur in localities on either side of this river.

Three species, *C. annamitensis*, *C. attenuata*, and *C. wuchihensis* have been recorded from localities within the Northern Annamites Rain Forests Ecoregion 54, an area of tropical and subtropical moist broadleaf forests. The same biome is characteristic of the Southern Annamites Montane Rain Forests Ecoregion 57, although Wikramanayake et al. (2002) used the Hai Van Pass (16°12′N 108°08′E) as the boundary between the northern and the southern Annamites based on differences between the northern and southern flora. Both ecoregions are famous for their high levels of biodiversity and endemism; however, as far as *Crocidura* is concerned, the Southern Annamites are apparently more faunistically diverse than any of the other ecoregions with six species recorded: *C. attenuata*, *C. indochinensis*, *C. rapax*, *C. wuchihensis*, and two endemics, *C. sokolovi* and *C. zaitsevi*. In contrast a single endemic species, *C. kegoensis*, has been recorded from the Northern Vietnam Lowland Rain Forests Ecoregion 56, also an area of tropical and subtropical moist broadleaf forests.

Crocidura rapax has been recorded from two localities in the tropical and subtropical moist broadleaf forests of the Mizoram-Manipur-Kachin Rain Forests Ecoregion 50. The same biome occurs in the Northern Triangle Subtropical Forests Ecoregion 73, where *C. indochinensis* and *C. cranbrooki* occur and the latter species occurs also in the bordering temperate broadleaf and mixed forests of Ecoregion 76 Northern Triangle Temperate Forests.

Crocidura attenuata is by far the most commonly collected species, occuring at 39% of collection localities and has the widest distribution, being found in 70% of ecotones and subregions. *Crocidura rapax* was collected at 24% of localities and was found in 40% of the ecotones and subregions. *Crocidura fuliginosa* was more commonly collected (22%) than *C. wuchihensis* (13%) or *C. indochinensis* (11%), but *C. wuchihensis* was found in 40% of ecotones, whereas the other two species occurred only in 30% of ecotones and subregions. At localities where two or more species were collected, *C. attenuata* occurred in sympatry in 70% of localities, *C. fuliginosa* at 50% of localities, *C. wuchihensis* at 40% of localities, and *C. rapax* at 30% of localities.

DISCUSSION

Knowledge of the mammalian fauna of Indochina is based on specimens in museum collections from a mosaic of sources, ranging from the serendipitous acquisition of occasional specimens, through small-scale collections by amateurs, often as an adjunct to their careers in the military or commerce, escalating to a number of professionally organized large-scale collecting expeditions as recorded in the Introduction. These expeditions used conventional trapping techniques, resulting in the collection of mainly large- and medium-sized shrews that give a distorted idea of the shrew fauna. It was only the relatively recent introduction of pitfall trapping, which allows the collection of smaller animals, that has resulted in a more balanced view.

The ongoing critical examination of historical specimens in museums and collecting in the field continue to yield new species of *Crocidura* from mainland southeast Asia. At the time of writing, including the three species described herein, there are now at least 14 species (the 12 in this study, plus *C. hilliana* from Thailand and the recently described *C. phuquocensis* Abramov et al., 2008) known from the region, half of which were described in the current decade. Efforts to frame the known distributions of these species into some biogeographic context are hampered by small sample sizes and spotty geographic coverage (see fig. 22): many species are still known from only one or very few specimens (*C. sokolovi*, *C. vorax*, *C. indochinensis*, *C. wuchihensis*, *C. kegoensis*, *C. zaitsevi*, *C. annamitensis*, *C. guy*), while those that are represented in museums by larger numbers of specimens were collected from such broadly distributed localities as to provide little insight into their biogeography.

Even with these limitations, a number of patterns are emerging. One such pattern is the discovery of an apparent limestone karst endemic. *Crocidura guy* is known only from karstic habitats within the Viet Bac karst formation of northeastern Vietnam—a region from which an apparently endemic rodent, *Tonkinomys daovantieni*, was recently described (Musser et al. 2006).

Another biogeographic pattern is the emergence of what may be a series of high-altitude Annamite endemics, namely *C. annamitensis*, *C. sokolovi*, and *C. zaitsevi*, all of which are currently known only from isolated high-elevation localities within the Annamite mountain chain, an area that also supports a number of other endemic mammal species including the Saola (*Pseudoryx nghetinhensis* Dung et al., 1993) and Annamite Striped Rabbit (*Nesolagus timminsi* Averianov et al., 2000) and three different species of douc langur (*Pygathrix nemaeus* (Linnaeus, 1771), *P. cinerea* Nadler, 1997, and *P. nigripes* (Milne Edwards, 1871)) (see Sterling et al., 2006).

Clearly, further collecting is needed to clarify the full extent of each species' distribution, and the likely biogeographic history behind their distributions.

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APPENDIX 1

Gazetteer

We were able to determine coordinates (noted below) for most of the named localities in Vietnam, southwestern China, and northern Myanmar from which specimens of *Crocidura* were examined. For some recently collected specimens, place names and their coordinates were recorded from original specimen labels or the collector's original field notes; however, most were determined by researching published expedition summaries (Andrews and Andrews, 1918; Anthony, 1941; Legendre, 1936); and a variety of unpublished, primary sources such as field journals and original annotated maps. When not recorded by the original collector, coordinates were obtained from either the U.S. Board on Geographic Names (USBGN) or by using original descriptions of geographic landmarks to pinpoint collecting localities in Google Earth (http://earth.google.com). In some instances we used the USBGN coordinates to determine the general vicinity of a collecting locality and Google Earth to further pinpoint the coordinates of the collecting site.

The number preceding each place corresponds to the like numbered locality on the map in figure 19. Italicized proper names in the list below are the largest administrative units recognized within each country (province); boldface identifies locality names as they are used on original museum specimen labels and in the text of this report. Latitude and longitude are given after place names. Elevation, in feet or meters, is given exactly as recorded on original museum tags, but we provide meter equivalents in brackets.

The spelling of place names in southwest China and northern Myanmar is complicated by the fact that the original English spellings were based on the phonetics of the native name, and so several spellings may be encountered for the same place. For example the base camp of the Vernay Cutting Burma expedition that was named "Gangfang" on specimen labels is also spelled on some maps as "Kangfang" (Anthony 1941: 43). In cases where we encountered more than one place name for a locality, alternate spellings or names are given in parentheses following the name used in this report.

CHINA

1. *Sichuan*: **Moupin** [Mupin, Mu-p'ing, Pao-shing, Pao-hsing, Pao-hsing-hsien, Baosin, Baoxing]. Baoxing (30°23′N 102°50′E USBGN) is the accepted name according to Hutterer (2005) [*C. attenuata*].
2. *Chongqing*: **Chung-king** [Chongqing] **Mountains**. Not located but apparently near the city of Chongqing (29°34′N 106°35′E USBGN), formerly within the administrative division of Sichuan, currently within the Chongqing municipality [*C. attenuata*].
3. *Chongqing*: **50 miles NE of Chung-King Mts**. Not located but apparently near the city of Chongqing (29°34′N 106°35′E USBGN) [*C. attenuata*].
4. *Chongqing*: **Chin-fu-san, near Nan-chwan** [Nanchuan]. Not located but described as "a mountain near the city of Nan-chwan, south of Chung-king, not far north of the Sze-chwan [Sichuan] – Kwei-chow [Guizou] border." (Thomas 1912a: 128). The city of Nanchuan is at 29°10′N 107°05′E Google Earth. The nearest Guizhou border is at 28°57′N 107°03′E Google Earth. [*C. attenuata*].
5. *Sichuan*: **Kuan Shien** [Kuan-hsien, Guanxian; Guankou], 3000 ft [915m]. (31°00′N 103°37′E USBGN) A population on the east bank of the Min Jiang. [*C. attenuata*].
6. *Sichuan*: **Nien Yuen Fu** [Ningyuanfu, Hsi-ch'ang, Xichang] (27°53′N 102°18′E USBGN). [*C. rapax*].
7. *Sichuan*: **Ta Cho Fu**. Not located but listed in Jiang and Hoffmann (2001) as Tacho (29°12′N 103°18′E) [*C. attenuata*].
8. *Chongqing*: **Yen-ching-kao**. Mapped in Andrews (1932) where it is indicated SE of Wanhsien [Wan Xian] (30°49′N 108°22′E Google Earth) on the east bank of the Yangtze River [Chang Jiang] [*C. attenuata*].
9. *Yunnan*: **Chi-tien, Yangtse River** [Judian, Yangtze, Jinsha Jiang] (27°18′N 99°40′E USBGN). From a specimen collected on December 10th as the AMNH Asiatic expedition traveled up the trade route on the western side of the Yangtze just before turning westward through Li-tien [Ludian] while on their way through Wei-hsi [Wei-xi] to the Mekong River (Andrews and Andrews 1918: 182–189). Chi-tien is not specifically mentioned in Andrews and Andrews (1918), but its synonymy with Judian is determined from the published map and narrative, and from dates associated with this place name in the original AMNH specimen ledger. The nearby population of Li-tien [Ludian], a homonym of Chi-tien [Judian], is situated approximately midway between Chi-tien [Judian] and Wei-hsi [Wei-xi], and is documented in the AMNH ledger as having been visited by the expedition on December 11th, and further corroborates Judian as the appropriate modern place-name for 'Chi-tien, Yangtze River' [*C. rapax*].
10. *Yunnan*: **Ho Mu Shu Pass** (24°55′N 98°45′E Google Earth). From a specimen collected on 7 April 1917 as the AMNH Asiatic Expedition traveled west toward Teng-yueh [Teng Chong]. "A tiny village built into the mountain-side with hardly fifty yards of level ground about it, but commanding a magnificent view over the Salween valley." Elevation approximately 8000 ft [2440 m]. (Andrews and Andrews 1918: 283). [*C. indochinensis*].
11. *Yunnan*: **Lichiang** or **Lichiang Range** [Li-jiang, Li-kiang or Li-chiang; = Dayan] (26°48′N 100°16′E USBGN; 26°52′24″N 100°13′53″E Google Earth), 9000–12,000 ft [2745–3660 m]. This collecting locality and its three alternative spellings refer to the modern-day city of Dayan, however, depending on the expedition, specimens bearing this place name may have been collected from the outskirts of the city itself, to as far as several

miles to the north. The AMNH Asiatic Expedition based their expedition from an active temple (the temple of the flowers) within the city itself, where they trapped animals, and purchased specimens from locals (Andrews and Andrews 1918:108–109). From here they traveled 12 miles to the north of the city into the snow mountain range where they based their efforts from "a tiny temple nestled into a grove of spruce trees on the out-skirts of a straggling village" somewhere [not located] just south of the highest mountain peak at 18,235 ft [5562 m] (27°05′59.42″ N 100°10′33.92″ E Google Earth). Andrews and Andrews (1918: 113) give us some clues to their exact location in their description of this camp: "To the north the Snow Mountain rose almost above us, and on the east and south a grassy rock-strewn plain rolled away in gentle undulations to a range of hills which jutted into the valley. …" From this locality the AMNH expedition made collecting forays up toward the summit of Snow Mountain and from a subsequent camp in a meadow at a higher elevation before shifting their base camp to "the other side of Snow Mountain at 'White Water'" camping on a broad terrace at the edge of spruce forest. From here the AMNH expedition returned to the temple of the flowers at Lichiang via a different route, presumably the regular trade route running along the eastern slopes of the Snow Mountains.
All of these places are too far south for the coordinates given by Thomas (1922) for NHM specimens collected by Forrest from Li-kiang at 27°40′N, 9000–13000 ft [2745–3965 m]. In a later paper, Thomas (1923) discussing additional specimens collected by G. Forrest from the Li-kiang Range gives coordinates as 27°N 100°30′E [holotype of *C. praedax* 1923.4.1.13 at 9500 ft [2898 m]]. Based on this historical information, and if Thomas' coordinates for specimens collected by George Forrest are accurate, it clear that specimens identified as being from Lichiang, or any one of its alternate spellings may have been collected anywhere from the outskirts of the city itself to points as far as 12 or more miles to the north and east. [*C. fuliginosa*, *C. rapax*, *C. vorax*].

12. *Yunnan*: **Mekong-Salwin** [Salween] **Divide** (ca. 28°20′N 98°44′E). Elevation 12,000 ft [3660 m]. From a specimen collected by G. Forrest. Coordinates are those recorded in Thomas (1922). [*C. rapax*].
13. *Yunnan*: Mong-Tze [Meng-Tzu, Mengzi, Wenlan] (23°22′N 103°24′E USBGN). Reported by Thomas (1912b) as the probable locality for the original series of specimens of *C. dracula*. [*C. fuliginosa*].
14. *Yunnan*: **Nam Ting River, near Burma border** (ca. 23°36′N 99°26′E) (actual collecting locality for AMNH 44489 may have been in Myanmar, just west of the Yunnan border, according to a notation on the original label). [*C. attenuata*, *C. fuliginosa*].
15. *Yunnan*: **Shang-Kuan, Talifu Lake**. [Xiaguan, at south end of Talifu Lake] (ca. 25°34′N 100°14′E USBGN.) [*C. fuliginosa*].
16. *Yunnan*: **Taku** [= Daju] **Ferry, W bank of Yangtse R**, [Yangtse, Jinsha Jiang] (ca. 27°18′N 100°14′E USBGN), 6000 ft [1830 m]. Apparently a transliteration of *Daju*, precisely the locality indicated for Taku Ferry on the map in Andrews and Andrews (1918). [*C. rapax*:].
17. *Yunnan*: **Tengyueh** [= Teng Chong] (25°00′N 98°28′E USBGN). A town presumably on a trade route as the collector's address was Custom House, Tengyueh [*C. attenuata*, *C. rapax*].
18. *Yunnan*: **Yangtze River** [Jinsha Jiang], **Shih-ku** [Shigu] (26°52′N 99°57′E USBGN). A population on the south bank of the Yangtze River and crossing point (Shih-ku ferry) on the main caravan route used by the AMNH Asiatic expedition. [*C. fuliginosa*].
19. *Yunnan*: **Yin Pan Kai, Mekong River** [possibly Ying-p'an-chieh, = Yingpan 26°27′N 99°09′E USBGN; or La-chi-ching at same coordinates in Google Earth]. The single *Crocidura* specimen collected from this named locality was procured on December 25, five days after the AMNH Asiatic expedition "turned away from the Mekong valley and began to march southeast by east across an unmapped region toward Ta-li Fu (Andrews and Andrews 1918:193). The locality is probably the "very dirty Chinese town in a deep valley near some extensive salt wells" that the expedition mentions having passed through on Christmas Day (Andrews and Andrews 1918: 196). [*C. rapax*].

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20. *Kachin*: **Fort Hertz** [Putao], 10 miles E. of (27°21′N 97°24′E USBGN) [*C. cranbrooki*].
21. *Kachin*: **Gangfang** [Kangfang] (26°08′42″N 98°34′59″E; Google Earth). Anthony (1941) explained how some maps show two villages by this name, one on the east bank of the Ngawchang River and one on the west. These are respectively identified as Gangfang (26°08′N 98°36′E) and Kang fang (26°08′N 98°34′E) in Google Earth, but Anthony (1941) goes on to explain that their base camp was situated at the trading post located at the precise junction of the Ngawchang and Hpawte Rivers at an elevation of 5403 ft [1648 m]. [*C. indochinensis*].
22. *Kachin*: **Hkamkawn** [Gamhkawn; Kham Kham] (25°59′00″N 98°23′59″E; Google Earth). An agricultural village in the valley of the Ngawchang River near the junction of the Munglang River, 4080 ft [1244 m]. Judging from original expedition maps in the AMNH Department of Mammalogy archives, and published maps and descriptions in Anthony (1941), this locality may be synonymous with Ba-le. [*C. fuliginosa*].
23. *Kachin*: **Htawgaw** (not located, vicinity of 25°55′N 98°21′E). A military police post located along the crest of a ridge lying between Ngawchang and Hkaingshang rivers at 6025 ft [1838 m]. [*C. fuliginosa*].

24. *Kachin*: **Nam Hat** or **Nam Hut**, hills E. of. Not located [27°N 97°–98°E]. This locality lies between the rivers Nam Tisang and Nam Tamai but is not shown on the sketch-map in Ward (1932) nor listed in the USBGN gazetteer. [*C. cranbrooki*].
25. *Kachin*: **Nam Tamai** 27°42′N 98°01′E [USBGN]. A river shown on the sketch-map in Ward (1932). This locality was visited during the 1931–1932 expedition of F. Kingdon Ward and Lord Cranbrook. [*C. cranbrooki*].
26. *Kachin*: **Nam Tisang**, Nam Tamai Divide [Nam Tisang 27°05′N 97°49′E USBGN]. The Nam Tisang is a river shown on the sketch-map in Ward (1932). A single specimen of *Crocidura* was collected on the journey between the two rivers. [*C. cranbrooki*].
27. *Kachin*: **Rawngaw** [Rawngtsaw] (26°18′57″N 98°19′47″E); 4200 ft [1281 m]. [*C. indochinensis*].
28. *Kachin*: **12 miles N of Myitkina** (25°24′N 97°25′E) [*C. rapax*].
29. *Shan*: **Chin Hills** (approximately 22°30′N 93°30′E) [*C. rapax*].

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30. *Gia Lai*: **An Khe** [= An Túc] (14°26′N 108°33′E; Google Earth). A military base at approximately 600 m elevation. This locality is placed in Bình Đinh Province by Heaney and Timm (1983) and on the USNM online database but the military base is situated just NE of the city of An Khê in Gia Lai Province [*C. rapax*].
31. *Hà Tĩnh*: **Huong Son Camp** (18°21′53″N 105°13′13″E; Lunde); elevations 230–1270 m. Collecting locality of Lunde 1998, 1999. [*C. annamitensis*, *C. attenuata*, *C. wuchihensis*].
32. *Hà Tĩnh*: **Ky Anh - Ke Go Nature Reserve** (18°04′N 105°58′E); elevation 200 m. [*C. kegoensis*].
33. *Hà Giang*: **Mt. Tay Con Linh II** (22°45′47″N 104°49′49″E; Lunde). Collecting locality of Lunde 2001. [*C. attenuata*, *C. fuliginosa*: 274180, *C. wuchihensis*].
34. *Kon Tum*: **Dak To** [Đăc Tô]; (14°42′N 107°51′E; USBGN); Collecting locality of W. Lowe during the Delacour Exploration of French Indo-China. Described as south of Hue, about 100 km from the coast, and at about 14°30′N, 108°0′E at an elevation of 3000 ft [915 m] (Thomas 1927). Locality shown on the sketch-map in Lowe (1947). [*C. attenuata*].
35. *Lâm Đồng*: **Langbian Peak** [Lang Bian]; (12°03′N 108°26′E); elevation 2167 m. [*C. attenuata*].
36. *Lâm Đồng*: **DaLat** [Dà Lat]; (11°56′N 108°25′E); elevation ca. 1500 m. [*C. indochinensis*].
37. *Lâm Đồng*: **Mt Lang Bian**; (12°05′N 108°30′E). [*C. attenuata*, *C. rapax*].
38. *Lang Sơn*: **Pa Kha** [Pak Ha; Bac Hà] (22°33′N 104°16′E). [*C. wuchihensis*].
39. *Lào Cai*: **Chapa** [Sa Pa] (22°21′N 103°50′E). [*C. fuliginosa*, *C. indochinensis*].
40. *Lào Cai*: **Ngai Tio** [Ngải Chồ] (22°36′N 103°40′E). Collecting locality of H. Stevens of the Sladen-Godman Expedition to Tonkin, and described by Thomas (1925: 495 and 496) as "the highest part of Tonkin… at an elevation of 4800 ft [1464 m], just beyond the Col des Nuages…" and "approximately at 22°40′N 103°30′E some 50 miles S of Mong-tsze."] [*C. fuliginosa*, *C. wuchihensis*].
41. *Lào Cai*: **Thai Nien** (22°24′N 104°05′E). Collecting locality of H. Stevens. (Thai- Nien, on the Song-Koi or Red River at 300 ft [915 m] (see Thomas, 1925: 496). [*C. wuchihensis*].
42. *Quảng Nam*: **Ba Na** [Ba Na Nature Reserve, Quang Nam-Da Nang Provinces] (15°57′–16°03′N 107°5′–108°03′E). [*C. attenuata*, *C. wuchihensis*].
43. *Quảng Nam*: **Ngoc Linh Nature Reserve** (15°05′N 107°57′E) [*C. attenuata*, *C. sokolovi*, *C. zaitsevi*].
44. *Quảng Tri*: **Thon Ke Tri Peak** (2.3 km E and 8 km S of Quang Tri at ca. 16°40′N 107°12′E). [*C. attenuata*].
45. *Thừa Thiên*: **Nui Ke**. Not located but apparently near Mt. Nui Ke (16°19′N 107°34′E; USBGN) Specimen label: 9.1 kilometers W of, 3.6 km N of Nui Ke, Thua Thien Province, altitude 30 m. [*C. attenuata*].
46. *Tuyên Quang*: **Na Hang Nature Reserve, Tat Ke sector** (22°16′–22°31′N 105°22′–105°29′E) [*C. guy*].

APPENDIX 2

LATENT ROOTS, PERCENTAGE VARIATION AND LATENT VECTOR LOADINGS FOR THE PRINCIPAL COMPONENT AND CANONICAL VARIATE ANALYSES

PCA of all species				
Trace	Latent roots			
	1	2	3	4
110.0	102.49	1.20	1.03	0.81
Percentage variation				
	1	2	3	4
	93.22	1.09	0.93	0.74
Latent vectors				
	1	2	3	4
CIL	0.1749	0.0804	−0.0160	0.0182
CBL	0.1759	0.0800	0.0073	0.0478
URTL	0.1914	0.1596	−0.0522	−0.1220
I-Un3	0.2014	0.2223	−0.0127	−0.0693
M2-M2	0.1786	−0.0906	0.0482	−0.0263
LIOB	0.1431	0.1315	0.0945	0.1578
BB	0.1435	0.0016	0.0608	0.1176
BH	0.1486	0.0961	0.1567	0.3024
BL	0.1284	0.0071	0.1899	0.1581
BL-dors	0.1449	0.0344	0.0986	0.1384
PGB	0.1511	−0.1259	0.0796	0.0808
AWM2	0.1767	−0.0534	0.0153	−0.0400
LM3	0.1518	0.2360	0.1753	−0.3314
ML	0.1950	0.0874	−0.1179	−0.0173
ML-i	0.1913	0.0965	−0.1324	0.0148
MTRL	0.1926	0.1545	−0.0647	−0.0989
MTL-i	0.1911	0.1680	−0.0466	−0.0599
MH	0.1935	−0.0717	−0.0036	0.0590
LiL	0.1941	0.1673	−0.0481	−0.4787
LiH	0.2030	−0.3704	0.1147	−0.5471
CH	0.1793	−0.3425	−0.4803	0.1638
CW	0.1793	−0.6204	0.0955	0.0025
ARL	0.1998	−0.0002	−0.2082	0.0659
RB	0.2028	−0.0758	0.1570	0.1439
M3-PGN	0.2522	0.0988	−0.5834	0.1032
ZB	0.1545	−0.0088	0.0780	0.0947
ID	0.1567	0.0653	0.2426	0.1227
PGD	0.1498	0.0598	0.2226	0.2239
RD	0.2010	0.0491	0.1597	0.0208
RB@Un3	0.1915	−0.0402	0.1334	0.0398
RB@Un1	0.1735	−0.1814	0.1222	−0.0170
PCA of SubsetA				
Trace	Latent roots			
	1	2	3	4
22.16	18.025	0.931	0.548	0.430
Percentage variation				
	1	2	3	4
	81.33	4.20	2.47	1.94
Latent vectors				
	1	2	3	4
CIL	0.1787	0.0820	−0.0105	0.0881
CBL	0.1793	0.0972	0.0155	0.0722
UTRL	0.1905	0.1220	−0.1391	−0.0105
I-Un3	0.1936	0.2116	−0.0967	−0.0152

APPENDIX 2
(Continued)

M2-M2	0.1648	−0.0929	0.0544	−0.1833
LIOB	0.1313	0.1707	0.1091	−0.0178
BB	0.1385	0.0189	0.0916	0.0097
BH	0.1308	0.1995	0.1911	0.1061
BL	0.1414	0.1041	0.1912	0.1016
BL-dors	0.1541	0.0928	0.1421	0.0969
PGB	0.1597	−0.1080	0.1323	−0.0428
AWM2	0.1382	−0.0867	0.0602	−0.2301
LM3	0.1702	0.2161	−0.1358	0.1525
ML	0.1878	0.0525	−0.1017	0.1194
ML-i	0.1780	0.0457	−0.0972	0.1512
MTRL	0.1956	0.1113	−0.1159	−0.0036
MTL-i	0.1912	0.1442	−0.1238	−0.0308
MH	0.1845	−0.0759	0.0774	0.0005
LiL	0.2043	0.1109	−0.2670	−0.2577
LiH	0.2769	−0.3267	−0.4065	−0.4164
CH	0.1577	−0.3478	−0.3393	0.2636
CW	0.1890	−0.6048	0.3703	0.2492
ARL	0.1773	−0.0623	−0.0782	0.3569
RB	0.2043	−0.0460	0.2726	−0.1085
M3-PGN	0.1927	−0.0504	−0.2462	0.4142
ZB	0.1505	0.0134	0.1202	−0.0751
ID	0.1801	0.1803	0.1892	0.0172
PGD	0.1591	0.1557	0.1837	0.0628
RD	0.2127	0.1179	0.0851	−0.1691
RB@Un3	0.2007	−0.0372	0.1319	−0.1275
RB@Un1	0.1819	−0.1748	0.1476	−0.2623

PCA of Subset B				
Trace	Latent roots			
	1	2	3	4
11.81	9.079	0.522	0.449	0.338
Percentage variation				
	1	2	3	4
	76.87	4.42	3.80	2.86
Latent vectors				
	1	2	3	4
CIL	0.1591	0.0035	−0.0372	0.0127
CBL	0.1593	0.0383	−0.0115	0.0297
UTRL	0.1698	−0.1287	−0.0603	0.0998
I-Un3	0.2049	−0.1723	−0.0962	−0.0509
M2-M2	0.1891	−0.0473	0.1064	0.0062
LIOB	0.1154	0.1425	0.0813	−0.0324
BB	0.1239	0.1538	0.0723	−0.0300
BH	0.2074	0.1549	0.0576	−0.1415
BL	0.1514	0.1257	0.1351	−0.1147
BL-dors	0.1537	0.0921	0.0150	−0.0710
PGB	0.1387	0.0691	0.0985	−0.1182
AWM2	0.1907	−0.1211	0.1305	0.1446
ML3	0.1660	−0.2817	0.2348	0.6378
ML	0.1695	−0.0491	−0.0771	0.0751
ML-i	0.1592	−0.0298	−0.0493	0.0961
MTRL	0.1567	−0.1324	−0.0754	0.0714
MTL-i	0.1521	−0.0502	−0.0194	0.1251
MH	0.1965	0.0313	0.0227	0.0157

APPENDIX 2
(Continued)

LiL	0.2072	−0.6443	−0.2205	−0.2895
LiH	0.2066	0.3128	0.0946	0.1134
CH	0.2192	0.3463	−0.5410	−0.0448
CW	0.2188	−0.1916	0.2015	−0.5162
ARL	0.1713	−0.0559	−0.0148	0.0373
RB	0.2021	0.0538	0.1761	0.0819
M3-PGN	0.2197	0.0252	−0.5727	0.1996
ZB	0.0934	0.1298	0.1859	−0.0279
ID	0.1966	0.0630	0.0631	−0.1078
PGD	0.2112	0.1805	0.0369	−0.0882
RD	0.1966	0.0572	0.0986	−0.1371
RB@Un3	0.1771	0.0407	0.1673	0.0807
RB@Un1	0.1976	0.0057	0.1268	0.1006

CVA of all species				
Trace	Latent roots			
	1	2	3	4
92.07	70.87	3.94	3.12	2.76
Percentage variation				
	1	2	3	4
	76.98	4.28	3.39	3.00
Latent vectors				
	1	2	3	4
CIL	−35.04	17.92	56.08	−68.28
CBL	23.29	−11.70	−6.25	−7.20
UTRL	2.79	12.58	−23.72	27.99
I-Un3	−1.08	−2.28	−12.86	11.05
M2-M2	12.84	19.90	−5.42	−17.22
LIOB	−1.00	−4.86	1.98	17.55
BB	21.68	−5.25	16.92	20.62
BH	−0.30	4.62	−12.88	11.30
BL	−0.05	25.92	−16.30	15.28
BL-dors	−0.57	−36.74	−20.86	4.91
PGB	−3.81	2.45	2.01	−21.14
AWM2	−2.16	10.79	3.95	12.09
LM3	0.48	0.52	−3.93	−2.29
ML	19.62	−47.08	−37.38	43.65
ML-i	−3.17	8.37	−6.06	0.93
MTRL	11.63	10.91	36.30	−53.00
MTL-i	5.35	−15.46	6.07	10.66
MH	−3.87	−1.56	−1.70	14.49
LiL	0.84	−2.69	−0.36	1.47
LiH	−0.31	−1.00	−4.13	−4.10
CH	0.10	8.89	1.38	−1.09
CW	−3.88	5.02	2.83	1.45
ARL	−2.39	1.20	12.24	−10.60
RB	−10.32	−0.22	3.14	1.46
M3-PGN	1.70	11.93	3.12	9.96
ZB	6.23	−18.42	11.36	4.15
ID	0.06	2.51	−10.24	−11.71
PGD	9.81	−2.02	−6.17	−2.19
RD	1.92	−8.11	4.61	−8.64
RB@Un3	7.27	−2.16	2.82	4.25
RB@Un1	−3.94	14.76	−2.86	−4.89

APPENDIX 2
(Continued)

CVA of Subset A				
Trace	Latent roots			
	1	2	3	4
40.39	24.301	4.986	2.892	2.679
Percentage variation				
	1	2	3	4
	60.17	12.35	7.16	6.63
Latent vectors				
	1	2	3	4
CIL	−9.38	82.18	55.42	60.71
CBL	19.07	−22.15	−42.10	20.81
UTRL	5.99	−3.99	12.59	−4.71
I-Un3	−12.47	−19.78	−0.01	10.86
M2-M2	16.49	19.06	−21.99	−4.25
LIOB	−9.45	−14.96	3.84	−15.17
BB	15.81	4.00	27.33	−8.93
BH	−15.67	−8.11	11.64	−11.15
BL	−10.35	−3.57	8.39	10.52
BL-dors	15.96	−27.42	−31.20	−46.17
PGB	10.92	17.47	−22.81	2.72
AWM2	−12.09	−1.34	13.85	14.63
LM3	4.84	−4.63	2.68	7.01
ML	−31.74	−66.93	45.23	−75.09
ML-i	−1.90	−7.38	−5.65	7.53
MTRL	46.71	37.81	−43.57	−1.80
MTL-i	6.98	2.51	−5.96	12.21
MH	−5.29	−18.21	2.59	−0.56
LiL	−3.59	−3.65	−2.52	−4.96
LiH	2.37	−0.23	3.52	−1.61
CH	−0.29	7.48	4.61	−7.31
CW	−8.84	2.02	5.02	4.20
ARL	4.45	28.01	−32.05	8.99
RB	−3.52	−0.33	−4.35	8.26
M3-PGN	0.94	−5.39	5.89	−2.81
ZB	7.57	−6.93	4.23	−0.53
ID	5.09	4.12	−11.91	−9.42
PGD	18.51	−2.36	9.74	2.38
RD	6.61	1.89	−9.78	15.97
RB@Un3	−11.32	−2.19	18.00	7.34
RB@Un1	−3.88	11.07	10.22	−9.13
CVA of Subset B				
Trace	Latent roots			
	1	2	3	4
163.2	89.65	22.11	12.62	11.54
Percentage variation				
	1	2	3	4
	54.93	13.54	7.73	7.07
Latent vectors				
	1	2	3	4
CIL	−8.212	6.816	3.651	−10.599
CBL	21.013	10.291	12.894	35.733
UTRL	−13.206	−3.914	−24.383	−16.277
I-Un3	4.511	−15.663	1.782	7.299
M2-M2	−0.580	−2.919	−7.575	−3.463

APPENDIX 2
(Continued)

LIOB	−3.112	−0.724	1.990	1.142
BB	4.925	5.518	3.774	4.530
BH	1.609	9.959	−3.900	−7.326
BL	−3.037	13.646	2.190	−12.588
BL-dors	−2.263	−22.330	−4.086	−1.486
PGB	−2.344	0.229	−1.394	1.006
AWM2	1.904	4.806	0.339	1.201
LM3	1.411	−3.236	3.468	0.110
ML	−1.627	13.585	14.219	−9.431
ML-i	0.225	−6.987	−5.815	2.085
MTRL	10.329	0.329	13.641	−9.162
MTL-i	−3.341	−3.049	−3.304	4.498
MH	−2.325	4.262	−2.166	−2.968
LiL	0.954	7.394	0.443	3.064
LiH	2.654	−3.808	−0.972	0.792
CH	1.630	−2.080	1.366	1.855
CW	1.265	−4.990	−3.488	1.867
ARL	2.535	−1.004	4.252	5.480
RB	−5.581	8.252	−6.163	6.136
M3-PGN	−2.494	4.503	−1.866	−1.778
ZB	0.242	5.424	4.389	−2.327
ID	2.128	−1.162	−2.220	−2.634
PGD	1.473	−6.587	4.649	8.354
RD	0.317	2.127	−4.917	−1.201
RB@Un3	6.940	−7.366	3.745	−1.244
RB@Un1	−0.867	−6.168	3.444	−4.860