

A new species of shrew (Soricomorpha: *Crocidura*) from West Java, Indonesia

JACOB A. ESSELSTYN,* ANANG S. ACHMADI, AND MAHARADATUNKAMSI

Department of Biological Sciences and Museum of Natural Science, Louisiana State University, 119 Foster Hall, Baton Rouge, LA 70803, USA (JAE)

Museum Zoologicum Bogoriense, Research Center for Biology-LIPI, Jl. Raya Jakarta–Bogor Km 46, Cibinong, Bogor, 16911 Indonesia (ASA, M)

* Correspondent: esselstyn@lsu.edu

We document the existence of a new species of shrew (Soricomorpha, Soricidae, *Crocidura*) in West Java, Indonesia, using both morphological and genetic data. Relative to other Southeast Asian *Crocidura*, the new species is medium-sized with a slender body and long tail, which together readily distinguish it from all other Javan shrews. Morphological differences between the new species and *Crocidura paradoxura*, another long-tailed shrew that is endemic to Sumatra, are subtle, but genetic differences suggest a long, independent evolutionary history. This description brings to 5 the total number of species of *Crocidura* recognized from Java. All 5 species are endemic to the island and as many as 4 occur in syntopy. Further investigation is needed to document geographical ranges of shrew species on Java, especially along the island's east–west climatic gradient, where previously proposed subspecies boundaries may be coincident with transitions in precipitation patterns.

Key words: biodiversity, new species, Soricidae, taxonomy, white-toothed shrew

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Biodiversity inventories and taxonomic revisions of Southeast Asian mammals continue to reveal the presence of undocumented lineages (e.g., Jenkins et al. 2004, 2007; Heaney et al. 2009, 2011; Achmadi et al. 2012; Esselstyn et al. 2012; Sargis et al. 2013), suggesting that a robust estimate of regional diversity remains a distant goal. The mammal fauna of Java, however, is considered relatively well known because taxonomic research started there more than a century ago (e.g., Jentink 1888, 1910b; Sody 1930). Among shrews (Soricomorpha, Soricidae), only the genus *Crocidura* is native to Java, but *Suncus murinus* also is present as a human commensal (Corbet and Hill 1992). Although some recent taxonomic changes have been made in Javan *Crocidura* (e.g., Jenkins 1982; Ruedi 1995; Esselstyn et al. 2013; Omar et al. 2013), all of the names in use today (*Crocidura brunnea* Jentink, 1888; *Crocidura maxi* Sody, 1936; *Crocidura monticola* Peters, 1870; and *Crocidura orientalis* Jentink, 1890) were reported by the time of Sody's (1936) description of *C. maxi*. Moreover, the facts that Java has long played an important role in trade and regional imperialism and is densely populated with many urban areas (Osborne 2004), suggest that the island's extant vertebrate fauna should be well documented.

Ruedi (1995), relying exclusively on morphological traits, reviewed the taxonomy of Javan *Crocidura* and recognized 3 species (*C. brunnea*, *C. monticola*, and *C. orientalis*). He placed *Crocidura brevicauda* Jentink (1890) and *Crocidura melanorhyncha* Jentink (1910a) in synonymy with *C. brunnea*, but recognized 2 subspecies: the west-Javan *C. b. brunnea* and the east-Javan *C. b. pudjonica* Sody (1936). In addition, he recognized 2 subspecies of *C. orientalis*: the western *C. o. orientalis* and the eastern *C. o. lawuana* Sody (1936). Ruedi (1995) further placed *Crocidura bartelsii* Jentink (1910a) and *C. maxi* as synonyms of *C. monticola*. Finally, based on a single specimen that did not fit any of the named species, Ruedi (1995), following Jenkins (1982), postulated the possible presence on Java of a long-tailed species similar to *Crocidura paradoxura* Dobson (1887), a species otherwise considered a Sumatran endemic.

Esselstyn et al. (2013) recently tested several of Ruedi's (1995) hypotheses in a multilocus genetic study of shrews from West and Central Java. Their analyses supported the distinction



between the small species, *C. maxi* and *C. monticola*, and between the larger *C. brunnea* and *C. orientalis*. Their former conclusion also was supported by a recent morphometric analysis (Omar et al. 2013) that primarily examined *C. monticola* complex shrews from the Malay Peninsula. In addition to the 4 described species recognized by various authors, Esselstyn et al. (2013) incorporated a single long-tailed specimen of *Crociodura* (FMNH 212794) fitting the brief characterizations (Jenkins 1982; Ruedi 1995) of the potentially undescribed species. This long-tailed specimen was genetically unique at 7 of 9 loci in the study by Esselstyn et al. (2013).

Here, we confirm the distinctiveness of this long-tailed species, distinguishing it from all known species from Java and from the Sumatran *C. paradoxura* using both morphological and molecular characters.

MATERIALS AND METHODS

We examined specimens of *Crociodura* collected from forests and gardens in montane areas of West Java, including samples from the vicinities of Mts. Gede and Ciremai (Fig. 1). These specimens largely correspond to the West Javan sample of Esselstyn et al. (2013), but we expanded it by the inclusion of 6 additional specimens of various Javan species (Appendix I). We restrict our examinations of specimens to those from West Java because of the more extensive collections available from this province and because questions remain regarding the appropriate taxonomic status of Central and East Javan populations relative to their putative conspecifics in West Java (Ruedi 1995; Esselstyn et al. 2013). We also examined specimens of the long-tailed Sumatran endemic, *C. paradoxura*. Most of the specimens we use herein (Appendix I) are deposited at the Museum Zoologicum Bogoriense, Bogor (MZB) or Field Museum of Natural History, Chicago (FMNH), but others are held in the collections of the American Museum of Natural History, New York (AMNH), National Museum of Natural History at the Smithsonian Institution, Washington, D.C. (USNM), and Royal Ontario Museum, Toronto (ROM).

We gathered standard external measurements from the field notes of collectors and took cranial measurements using digital calipers precise to the nearest 0.01 mm. Cranial variables are identical to those used in Esselstyn and Goodman (2010) and overlap broadly with those of Heaney and Timm (1983) and Ruedi (1995). The measurements include condylo-incisive length (CIL), braincase breadth (BB), interorbital width (IOW), rostral length (RL), rostral width (RW), postpalatal depth (PPD), postpalatal length (PPL), condyle to glenoid fossa (CGF), length of upper tooththrow (UTR), alveolar P4 to M3 (P4–M3), and labial width at M2 (M2–M2). We explored continuous variables using principal component analyses and bivariate plotting (components and raw variables) to visualize their capacity to distinguish the putative species we originally delineated from external characters noted during fieldwork. We conducted principal component analyses in R 2.13.1 (R Development Core Team 2011) using raw cranial variables and the variance–covariance matrix. We also made qualitative

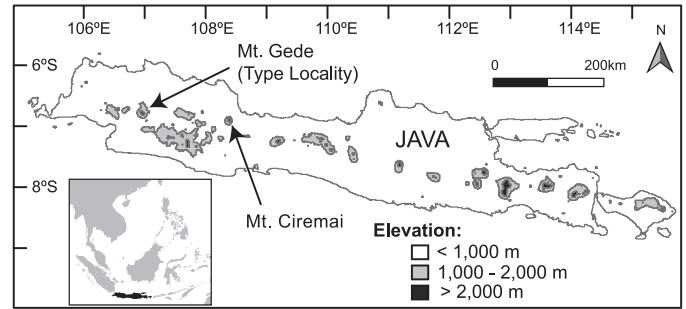


FIG. 1.—Map of Java, showing the type locality of *Crociodura absconditus*. The inset shows the position of Java among the islands of Southeast Asia.

comparisons of the cranial and external features, focusing on relative and absolute sizes and shapes of body parts and colors of the pelage and skin.

Esselstyn et al. (2013) documented the distinctiveness of the Javan long-tailed shrew (with a single specimen) from all known Javan shrew species using DNA sequences of 9 unlinked loci. Here, we add sequences of these same 9 loci from *C. paradoxura* to determine whether the Javan and Sumatran long-tailed shrews are distinct. New sequences from 17 *C. paradoxura* were collected following the protocols in Esselstyn et al. (2009, 2013). We also sequenced a fragment (684 base pairs) of mitochondrial DNA in 2 more recently obtained specimens of the new species to verify their relatedness with the single specimen available in the previous study. Hence, the loci included in our analyses are fragments of the mitochondrial protein coding cytochrome *b* (*Cytb*), the nuclear intron mast cell growth factor (*MCGF*), and the nuclear protein coding loci apolipoprotein B (*ApoB*), brain-derived neurotrophic factor (*BDNF*), breast cancer susceptibility 1 (*BRCA*), growth hormone receptor exon 10 (*GHR*), prostaglandin E4 receptor (*PTGER4*), recombination activating protein 1 (*RAG1*), and von Willebrand factor exon 28 (*vWF*). We deposited all new DNA sequences in GenBank (KF801060–KF801094).

To estimate the mitochondrial relationships of the new species, we analyzed the *Cytb* alignment from Esselstyn et al. (2013), with the addition of *C. paradoxura* and 2 new specimens of the new species. The alignment contained 1,110 nucleotides and 74 unique haplotypes (duplicate haplotypes were removed), representing most of the described species of *Crociodura* known from the islands of Southeast Asia (those islands west of Weber's line). We estimated the mitochondrial gene tree in a Bayesian phylogenetic context, using BEAST 1.6.2 (Drummond and Rambaut 2007) with an HKY + I + Γ model of sequence evolution (that favored by the Bayesian information criterion in Esselstyn et al. [2013]) with 4 Γ categories, a relaxed uncorrelated lognormal clock, and a coalescent constant population tree prior. Four runs of 3×10^7 generations were initiated with random starting trees. Parameters were sampled every 3,000 generations. We determined an appropriate burn-in by examining the trends and distributions of parameters in Tracer 1.5 (Rambaut and Drummond 2007).

TABLE 1.—Cranial and external measurements from all known Javan species of *Crocidura* and *C. paradoxura* from Sumatra. Abbreviated cranial dimensions are defined in the “Materials and Methods.” Hind-foot length (HF) includes the claw. Numbers are means \pm standard deviations. Exceptions to stated sample sizes (n) are provided as footnotes. All measurements are in millimeters except mass (g).

Variable	<i>C. brunnea</i> ($n = 10$)	<i>C. maxi</i> ($n = 7$)	<i>C. monticola</i> ($n = 9$)	<i>C. orientalis</i> ($n = 5$)	<i>C. paradoxura</i> ($n = 8$)	<i>C. absconditus</i> ($n = 4$)
CIL	23.80 \pm 0.81	17.71 \pm 0.25	16.02 \pm 0.23	23.68 \pm 0.42	21.22 \pm 0.49	19.95 \pm 0.35
BB	10.19 \pm 0.18	8.34 \pm 0.22	7.38 \pm 0.15	10.09 \pm 0.14	9.03 \pm 0.27	8.78 \pm 0.23
IOW	4.84 \pm 0.18	4.06 \pm 0.07	3.55 \pm 0.07	5.03 \pm 0.21	4.65 \pm 0.21	4.47 \pm 0.04
RL	9.69 \pm 0.44	6.99 \pm 0.14	6.14 \pm 0.20	9.98 \pm 0.29	8.27 \pm 0.20	7.84 \pm 0.19
PPD	4.21 \pm 0.16	3.29 \pm 0.09	2.97 \pm 0.10	4.16 \pm 0.10	3.91 \pm 0.17	3.84 \pm 0.05
RW	3.26 \pm 0.20	2.67 \pm 0.25	2.31 \pm 0.20	2.94 \pm 0.26	2.93 \pm 0.09	2.56 \pm 0.08
PPL	10.56 \pm 0.39	8.14 \pm 0.13	7.34 \pm 0.08	10.66 \pm 0.22	9.64 \pm 0.21	9.13 \pm 0.29
CGF	9.03 \pm 0.24	7.29 \pm 0.13	6.62 \pm 0.05	8.77 \pm 0.17	8.47 \pm 0.16	7.93 \pm 0.10
UTR	10.65 \pm 0.39	7.66 \pm 0.13	6.86 \pm 0.17	10.52 \pm 0.24	9.16 \pm 0.26	8.67 \pm 0.15
P4–M3	5.88 \pm 0.19	4.36 \pm 0.14	3.89 \pm 0.08	5.88 \pm 0.16	5.18 \pm 0.16	4.72 \pm 0.06
M2–M2	6.74 \pm 0.21	5.06 \pm 0.14	4.48 \pm 0.15	6.66 \pm 0.42	5.82 \pm 0.21	5.62 \pm 0.16
Total	142.7 \pm 8.96	120.6 \pm 3.82	98.3 \pm 4.5	160.4 \pm 12.18	185.0 \pm 6.19	161.8 \pm 4.11
Tail	53.9 \pm 3.11	51.9 \pm 3.8	38.1 \pm 2.03	75.4 \pm 5.41	107.3 \pm 5.23	88.3 \pm 3.50
HF	15.9 \pm 0.74	12.4 \pm 0.53	10.9 \pm 0.60	17.0 \pm 0.71	16.8 \pm 0.89	16 ^a
Mass	14.42 ^b \pm 2.81	5.86 \pm 0.72	4.07 \pm 0.55	14.58 ^c \pm 3.5	8.39 \pm 0.98	7.5 \pm 0.87

^a $n = 1$.

^b $n = 6$.

^c $n = 3$.

All runs appeared to converge within the 1st million generations, but we discarded the first 50% of each run, leaving 2×10^4 trees in the posterior. The effective sample sizes of all parameters were $> 2,000$.

Because there was substantial uncertainty regarding the relationships of the new species and *C. paradoxura* in the mitochondrial gene tree, we also estimated a species tree for the new species and its closest relatives, as inferred in the mitochondrial gene tree. This analysis included species of *Crocidura* from the Sunda Shelf (*C. brunnea*, *C. foetida*, *C. lepidura*, *C. maxi*, *C. monticola*, *C. orientalis*, and *C. paradoxura*), Sulawesi (*C. nigripes*), and the Philippines (*C. beatus*, *C. grayi*, *C. mindorus*, *C. negrina*, *C. ninoyi*, *C. palawanensis*, and *C. panayensis*), along with the new species. We estimated the species tree in *BEAST version 1.7.4 (Heled and Drummond 2010) using sequences of all 8 nuclear loci (mitochondrial DNA excluded), taken from 1 or 2 individuals per species. All genes were analyzed with unlinked HKY + Γ + I models of sequence evolution and relaxed uncorrelated lognormal clocks. Markov chain Monte Carlo searches consisted of 4 runs of 2×10^8 generations with parameters sampled every 5,000 generations. Evidence of convergence was checked in the same manner as for the mitochondrial gene tree analysis. All runs appeared to converge within the 1st million generations. We again discarded the first 50% of each run as burn-in, leaving 8×10^4 samples in the posterior. Effective sample sizes were $> 1,000$ for nearly all parameters. One parameter (population size for 1 split) had an effective sample size < 500 .

We also calculated locus-specific, uncorrected sequence divergences (p -distances) in Geneious version 5.6 (Drummond et al. 2011) between the new species and the taxa we included in morphological comparisons.

RESULTS

Both morphological and molecular evidence support recognition of the long-tailed shrew inhabiting West Java as a distinct endemic species.

Crocidura absconditus, new species

Holotype.—An adult male (MZB 36998/FMNH 212794) preserved in fluid with the skull removed and cleaned. A liver sample was preserved in home-brewed RNALater in the field and subsequently frozen. The holotype will be permanently curated at the MZB.

Type locality.—Cibodas, Mt. Gede, West Java, Indonesia (6.74818°S, 106.99388°E, 1,611 m elevation).

Referred specimens.—Three additional specimens (FMNH 218724, 218747, and 218756/MZB 36999) are known from a site < 2 km from the type locality: Cipanas, Cianjur, Mt. Gede, West Java (6.7620°S, 106.9840°E, 1,950 m elevation). All 3 paratypes are adults preserved as fluid specimens, with the skull removed and cleaned.

Distribution.—Known only from the Mt. Gede–Pangrango area of West Java. Recent surveys on other mountains of West and Central Java failed to capture any specimens of the new species (Esselstyn et al. 2013).

Etymology.—*Absconditus* is a masculine adjective meaning hidden in Latin. We chose this name in recognition of the hidden diversity of mammals that remains in Southeast Asia, even at the most heavily sampled localities near Jakarta.

Diagnosis.—Relative to other Southeast Asian *Crocidura*, the new species is a gracile, medium-sized, long-tailed shrew, with pale pelage and skin. The fur is medium gray at the base with brown tips on the dorsum and pale gray tips on the venter. The pinnae are large and pale. Palmar surfaces are white. Plantar surfaces are white with some brown scales; darker surfaces are found nearer the posterior and lateral margins of

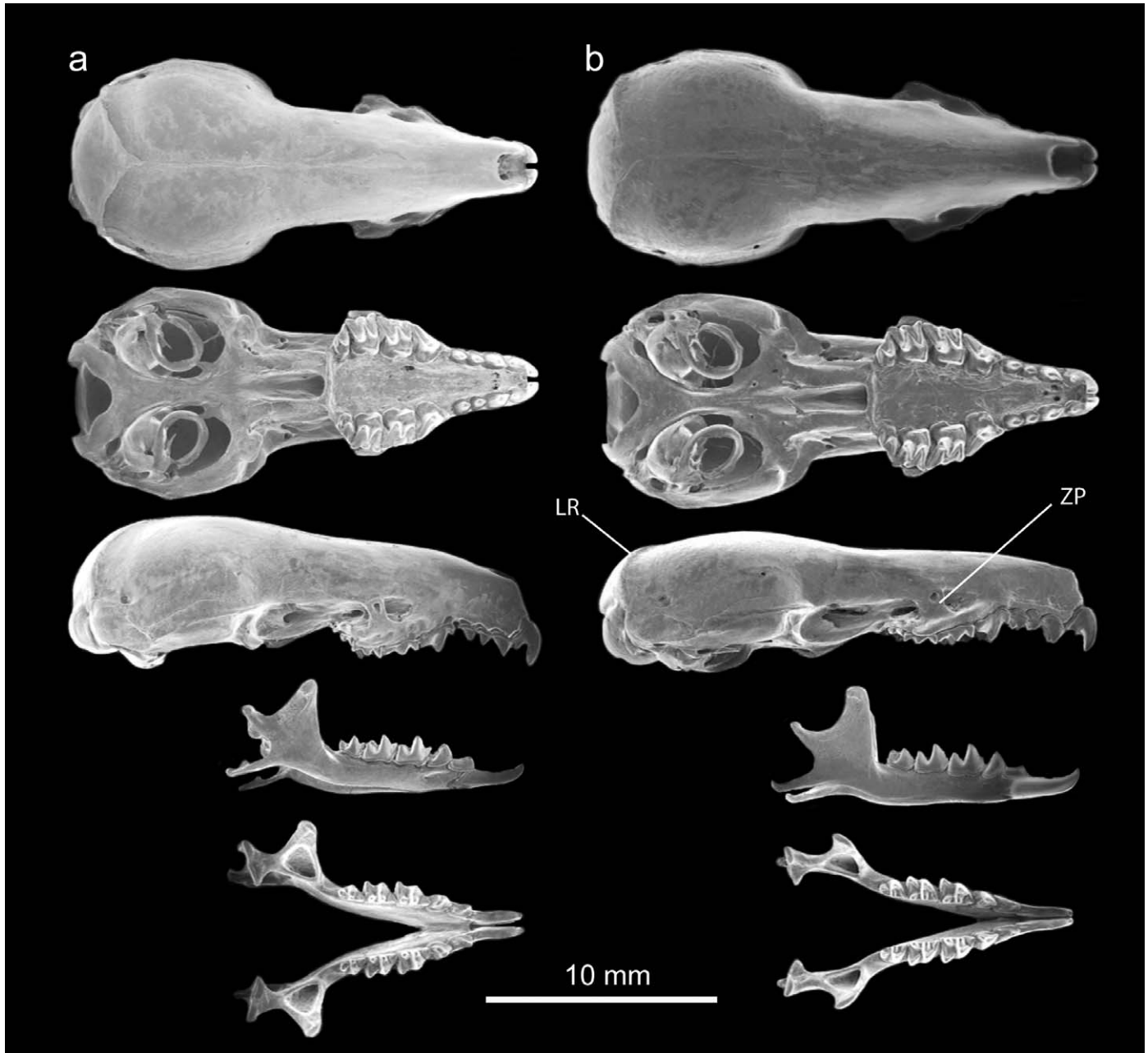


FIG. 2.—Scanning electron micrographs of the cranium and mandible of a) the holotype of *Crocidura absconditus* (MZB 36998/FMNH 212794) and b) a specimen of *C. paradoxura* (FMNH 212959). From top to bottom, views are dorsal, ventral, and lateral views of the cranium and lateral and occlusal views of the mandible. Some morphological features discussed in the text are labeled on *C. paradoxura* (ZP = zygomatic plate; LR = lambdoidal ridge).

the plantar surface. The ventral surfaces of digits III and IV on the hind feet are entirely white, whereas toes I, II, and V have brown scales (increasingly so proximally) surrounded by white integument. The thenar, hypothenar, and 1st and 4th interdigital pads are gray-brown, but the 2nd and 3rd interdigital pads are white. The dorsal surfaces of the hind feet are pale gray, turning to white at the distal portions of the digits. This pattern is the result of black and silver hairs that become progressively thinner and sparser toward the digits. These hairs partially cover a white integument.

The tail is longer than the head and body (Table 1) and holds very sparse bristle hairs along the proximal one-fourth or less of its length. These bristles are brown at the base and white along the terminal two-thirds of their length. Dense, dark brown, applied hairs cover the entire tail, forming a very small pencil at the terminus. The proximal portion of the tail is paler than the more distal parts. The dorsal side of the tail is slightly darker than the ventral side. These color differences are due to the proximal and ventral portions of the integument having a

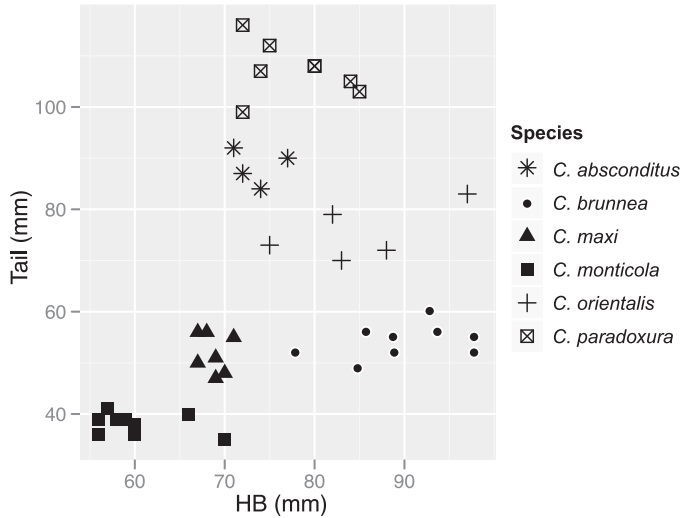


FIG. 3.—Bivariate plot of head and body length (HB) versus tail length (Tail) in all species of *Crocidura* known from Java and from *C. paradoxura*, a species endemic to Sumatra.

paler color, and to the greater density of applied hairs near the tip of the tail.

The lips are unpigmented, whereas the anterior facing surface of the rhinarium is gray-brown. The mystacial vibrissae are dense and extend beyond the pinnae, the longest approaching 20 mm in length. Shorter vibrissae (4–7 mm) emanate from the chin.

The skull is long and slender relative to those of most other Southeast Asian *Crocidura* species. The braincase is rounded, with weak lambdoidal ridges (Fig. 2a). The rostrum is gracile and the teeth are somewhat small relative to the skull. When viewed from a lateral aspect, the rostrum appears angled downward and a slight valley is visible in the dorsal profile above the orbital region (Fig. 2a).

Description and comparisons.—The new species is readily distinguished from all other Javan shrews by its body size and tail length (Fig. 3; Table 1). It has a more gracile body than any other Javan shrew, but is similar in this regard to *C. paradoxura*. It is considerably smaller, in terms of both head and body length and mass, than *C. brunnea* and *C. orientalis*, slightly smaller than *C. paradoxura*, and substantially larger than *C. maxi* and *C. monticola* (Table 1).

Tail length, relative to head and body length, is greater in the new species than in any other Javan shrew species (Fig. 3; Table 1). Among the known Javan *Crocidura*, only *C. orientalis* has a tail length approaching head and body length (Fig. 3; Table 1). *C. paradoxura* from Sumatra also has tail length greater than head and body length, but its tail is absolutely and relatively longer than that of the new species (Fig. 3; Table 1). In most individuals of *C. paradoxura* that we examined, the terminal ~20 mm of the tail is white; in the new species, pigmentation does not change dramatically anywhere along the length of the tail, but distal portions are slightly darker than proximal portions, as noted above. The new species possesses sparse bristle hairs along the proximal one-fourth of

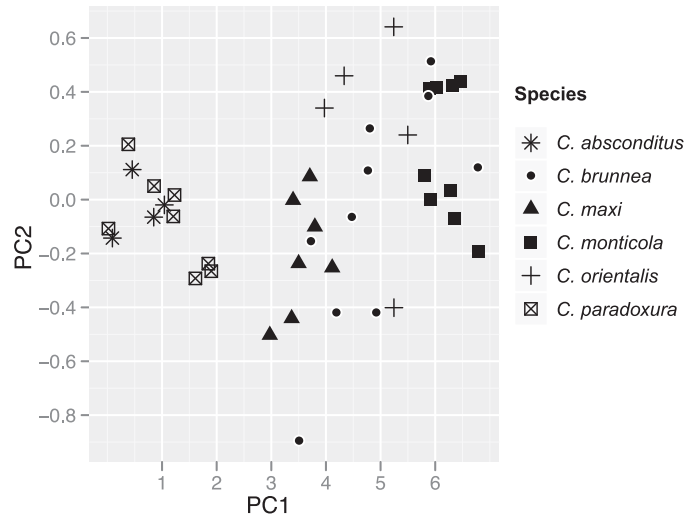


FIG. 4.—Bivariate plot of the 1st and 2nd principal components derived from analysis of 11 cranial dimensions taken from all known species of *Crocidura* from Java and *C. paradoxura*, a species endemic to Sumatra. Loadings are presented in Table 2.

the tail; *C. orientalis* and *C. paradoxura* have tails that are either free, or nearly free, of these hairs. *C. maxi* has a relatively thick tail with moderately dense bristles along the proximal one-third of its length, whereas *C. monticola* has a relatively slender tail with sparser bristles along the proximal one-fourth of the length. We caution that the extent of bristles on the tail may vary with elevation in some species (Ruedi 1995); the idiosyncratic elevational distribution of our samples may therefore affect these descriptions. Many, but not all, specimens of *C. orientalis* have a white ring around the base of the tail formed by hairless skin (Ruedi 1995). The base of the tail also is thinner than the immediately more distal section of the tail in *C. orientalis*. In the new species and other Javan *Crocidura*, the white ring and constricted base are absent.

The pelage and feet of the new species are similar in color (gray-brown to white) to those of *C. paradoxura*, but paler than those of other Javan *Crocidura*. Both *C. maxi* and *C. monticola*

TABLE 2.—Variable loadings and variance explained in a principal component analysis of 11 cranial measurements of all known species of *Crocidura* from Java and *C. paradoxura* from Sumatra. Variable acronyms are defined in the “Materials and Methods.”

Variable	Component 1	Component 2
CIL	0.702	0.165
BB	0.237	−0.355
IOW	0.117	−0.350
RL	0.326	0.375
PPD	0.108	−0.254
RW	0.0	−0.534
PPL	0.293	0.108
CGF	0.208	−0.193
UTR	0.338	0.101
P4–M3	0.179	0.0
M2–M2	0.197	−0.415
Variance explained	0.984	0.005

TABLE 3.—Uncorrected genetic distances (p -distances) between the holotype of *Crocidura absconditus* sp. nov. and sympatric species of *Crocidura* from Java and *C. paradoxura* from Sumatra. Loci acronyms are defined in the “Materials and Methods.”

Species	<i>Cytb</i>	<i>ApoB</i>	<i>BDNF</i>	<i>BRCA</i>	<i>GHR</i>	<i>MCGF</i>	<i>PTGER4</i>	<i>RAG1</i>	<i>vWF</i>
<i>C. brunnea</i>	0.17	0.009	0.006	0.063	0.013	0.000	0.000	0.007	0.036
<i>C. maxi</i>	0.20	0.011	0.003	0.067	0.017	0.024	0.008	0.012	0.040
<i>C. monticola</i>	0.20	0.015	0.007	0.066	0.022	0.024	0.010	0.014	0.040
<i>C. orientalis</i>	0.18	0.009	0.005	0.057	0.013	0.009	0.002	0.005	0.026
<i>C. paradoxura</i>	0.17	0.010	0.003	0.043	0.009	0.024	0.003	0.005	0.025

have dark brown to black feet, tails, and pelage. The pelage and feet are dark brown in *C. brunnea* and dark brown to charcoal in *C. orientalis*.

The skull of *C. absconditus* is more gracile, with a relatively narrow interorbital region and rostrum, than that of any other Javan species. The new species was readily distinguished from all other Javan shrews along the 1st principal component of cranial variables (Fig. 4; Table 2). The skulls of *C. absconditus* and *C. paradoxura* are similar in overall proportions (Figs. 2 and 4), but the former is slightly smaller (Fig. 2). The braincase of *C. absconditus* is slightly less inflated than that of *C. paradoxura*. This gives the appearance that the transition from the interorbital region to the braincase is relatively continuous in *C. absconditus*, but more discrete in *C. paradoxura* (Fig. 2). When the dorsal margin of the skull is viewed laterally, a low point is visible above the interorbital region in *C. absconditus*, but it is far more prominent in *C. paradoxura* (Fig. 2). The rostrum and interorbital region also are slightly broader in *C. absconditus*, relative to braincase breadth. The zygomatic plate is much narrower in *C. absconditus* than in *C. paradoxura* (Fig. 2).

The dentition of the new species is moderately small relative to skull size (Fig. 2a). More-robust teeth are present in *C. paradoxura* (Fig. 2b), *C. orientalis*, and especially *C. brunnea*. M3 is substantially smaller in the new species than in *C. paradoxura*. A prominent gap is present between P3 and P4 in *C. absconditus* (Fig. 2a), but not in any of the other species we examined. The parastyle on P4 is small in the new species and not projecting as far anteriorly as in the other species. *C. maxi*, *C. monticola*, and *C. paradoxura* each have relatively prominent parastyles that fill the gap between the roots of P3 and P4, whereas *C. brunnea* and *C. orientalis* have small parastyles, but nevertheless, no gap is visible. The horizontal plane formed by the teeth anterior to P4 forms an obtuse angle with the plane of the palate from P4 to M3. This angle is narrower in the new species than in *C. paradoxura* or any of the other Javan species, reflecting the downward angle of the rostrum in the new species (Fig. 2a). The upper molars of *C. absconditus* have relatively modest hypocones. Hypocones are slightly more prominent in *C. orientalis*, *C. paradoxura*, *C. maxi*, and *C. monticola*, especially on M1, and vary from slightly less prominent to more prominent in *C. brunnea*.

Molecular analyses.—Uncorrected genetic distances from the new species to sympatric *Crocidura* and *C. paradoxura* were 0.17–0.20 for mitochondrial DNA and 0.0–0.043 for nuclear loci (Table 3). These genetic distances indicate a long, independent evolutionary history. The 0.17 uncorrected p -

distance between *C. absconditus* and *C. paradoxura*, for example, translates to a Jukes–Cantor corrected distance of 0.19, which, assuming a crude substitution rate of 0.01 substitutions site⁻¹ million years⁻¹, yields a coarse divergence estimate of 9.5 million years ago. Although these calculations are simplistic and should not be used to infer particular biogeographic or evolutionary processes, their magnitude clearly indicates isolated evolutionary lineages.

In our species tree analysis of nuclear DNA, we infer a sister relationship, albeit with limited support, between *C. absconditus* and *C. paradoxura* (Fig. 5b). Given the similarity in overall body proportions between *C. paradoxura* and the new species, a sister relationship between them is logical. The clade formed by these 2 species rests in a well-supported sister relationship with species from the Sunda Shelf, Sulawesi, and the Philippines (Fig. 5b).

DISCUSSION

Morphological and molecular evidence clearly support the distinction of *C. absconditus* from all other species. This new species is genetically unique at most of the loci we sampled, and it is easily distinguished by its external morphology from all other species known from Java. Only *C. paradoxura* has a similar gross morphology, but the new species differs in body size, tail length and color, and orientation of the rostrum (Figs. 2 and 3; Table 1). The new species also is genetically distinct from *C. paradoxura* (Fig. 5; Table 3). The only other Southeast Asian *Crocidura* with a similarly proportioned tail (relative to head and body length) is *C. elongata*, which is endemic to Sulawesi and a member of a distantly related clade (Ruedi et al. 1998; Esselstyn et al. 2009).

The type locality of *C. absconditus*, Mt. Gede, is only 60 km from central Jakarta, one of the world’s most populous cities. Moreover, Mt. Gede is the probable type locality for many mammals described during previous centuries (many older type localities are simply “Java”), suggesting it is the most heavily studied area in Indonesia. The discovery of a new species of mammal on what almost certainly represents the most intensively surveyed mountain in all of Indonesia highlights the need for additional biodiversity surveys in the country. Moreover, it illuminates the limitations of current knowledge regarding species-level diversity, species’ geographic distributions, and hence current impressions of conservation status and capacity to test evolutionary and biogeographic hypotheses (Heaney et al. 2011; Esselstyn et al. 2013). Although we suggest Java’s mammal fauna may not

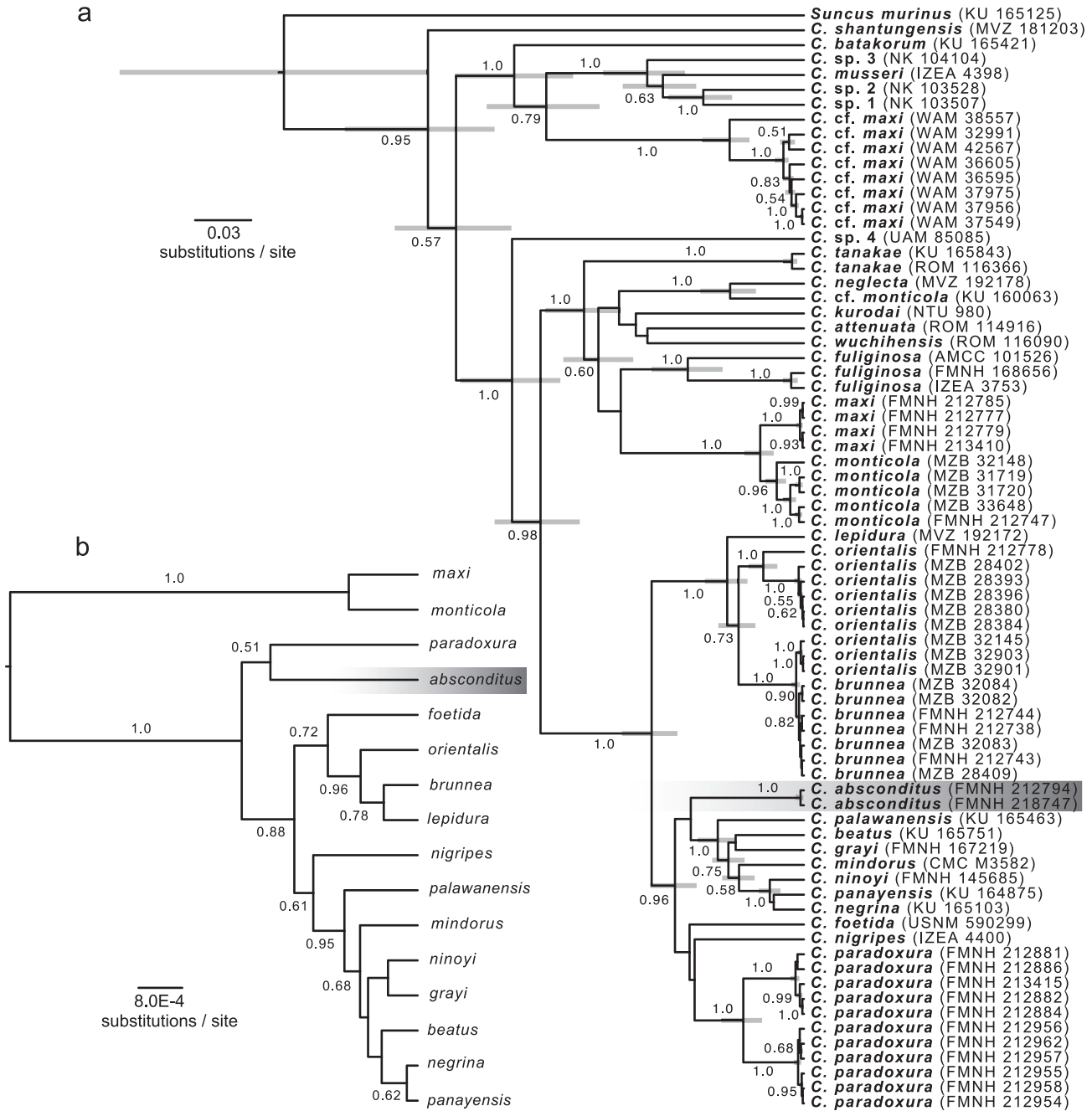


FIG. 5.—Bayesian estimates of phylogenetic relationships showing a) the mitochondrial gene tree of Southeast Asian *Crocidura* and b) species tree relationships for *C. absconditus* and its closest mitochondrial relatives. Numbers at nodes indicate posterior probabilities and horizontal gray bars indicate 95% highest posterior densities of node ages (on an arbitrary timescale) in the mitochondrial gene tree. Terminals are labeled with species names and museum catalog numbers are given on the mitochondrial gene tree terminals.

be well documented (for another example, see Sargis et al. 2013), we recognize that it is far better surveyed than many other parts of Indonesia (e.g., Sulawesi and Papua). The need for additional biodiversity surveys and continued investigations of diversity in shrews and other mammals is, of course, not unique to Indonesia. New species are being documented regularly as biologists adopt a combination of new surveys and examinations of morphological and molecular characters

to delimit species and test taxonomic hypotheses (e.g., Abramov et al. 2012; Hope et al. 2012).

Our results, and those of previous investigations (Ruedi 1995; Esselstyn et al. 2013; Omar et al. 2013), demonstrate that at least 5 species of *Crocidura* live on Java, and all are endemic to the island. The presence of multiple endemic species on the island raises questions regarding why the island has endemic species, given that it was connected to neighboring islands and

the mainland a mere 10,000 years ago (Rohling et al. 1998; Voris 2000). Such continental islands are expected to harbor mere subsets of the regional fauna (Patterson and Atmar 1986), not endemic species. During the Pleistocene, savanna habitats on the exposed Sunda Shelf (Heaney 1991; Bird et al. 2005) or large rivers (Voris 2000), or both, may have contributed to the isolation of forest-dependent species (Meijaard 2003), providing plausible mechanisms of speciation. To date, however, most evidence for this scenario consists of simple observations of older-than-expected divergences between Sunda Shelf populations (e.g., Gorog et al. 2004; den Tex et al. 2010), but they have not led to statistical tests among plausible mechanisms of speciation on the Sundaic islands. Nevertheless, modern Java, with its strong east–west climate gradient (Whitten et al. 1996), may offer a powerful system for testing the effects of dry habitat barriers on forest-dependent species, potentially providing clues as to whether Pleistocene savannas represented formidable barriers to gene flow. Unfortunately, most natural habitats on Java are now restricted to a few montane areas (Smiet 1990, 1992), possibly limiting opportunities for understanding the effect of geographic variation in climate on the diversification processes of Sundaic lineages.

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APPENDIX I

Specimens examined

Specimens examined in this study. Museum acronyms are given in the “Materials and Methods.”

Crocidura absconditus ($n = 4$).—**West Java, Mt. Gede:** MZB 36998/FMNH 212794, 218724, 218747, MZB 36999/FMNH 218756.

Crocidura brunnea ($n = 18$).—**West Java, Mt. Gede:** FMNH 212738–212746, 213404, MZB 33649, ROM 101935, USNM 481299, 481305; **West Java, Bogor, Cibuni:** USNM 257641, AMNH 106645, 106647; **West Java, Mt. Ciremai:** MZB 28409.

Crocidura maxi ($n = 20$).—**West Java, Mt. Gede:** FMNH 212763, 212779–212793, 213408–213410, USNM 481306.

Crocidura monticola ($n = 37$).—**West Java, Mt. Gede:** FMNH 212747–212762, 212764–212776, 213405–213407, MZB 33644–33648.

Crocidura orientalis ($n = 34$).—**West Java, Mt. Gede:** FMNH 212778, 218709–218720, 218723, 218979, 218980, ROM 101934, USNM 481303, 481304; **West Java, Mt. Ciremai:** MZB 28380–28383, 28391–28394, 28399–28405.

Crocidura paradoxura ($n = 17$).—**West Sumatra, Mt. Singgalang:** FMNH 212954–212963; **Jambi, Mt. Tujuh:** FMNH 212880–212886, 213415.