

## Research Article

# Three new shrews (Soricidae: Crocidura) from West Sumatra, Indonesia: elevational and morphological divergence in syntopic sister taxa

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## Abstract

We describe 3 new species of shrews (Eulipotyphla, Soricidae, *Crocidura*) from West Sumatra, Indonesia. Two of these taxa were found above 1,800 m on Mt. Singgalang. The third taxon was found above 1,660 m on Mt. Talamau, 65 km northwest of Mt. Singgalang. We also resurrect *Crocidura aequicauda* based on 2 specimens from Mts. Tujuh and Kerinci, which lie near the border between West Sumatra and Jambi provinces. Several methodological approaches support our findings: linear cranial morphometrics, landmark-based 2D geometric morphometrics, and molecular phylogenetics using both mtDNA and 6 nuclear exons. A multilocus species-tree analysis places the 3 new species and *C. aequicauda* in a clade with the Javan endemics *C. monticola* and *C. umbra*. Although the 2 taxa from Mt. Singgalang are recovered as sister species, 1 is nearly twice the size of the other, and they are divergent in several other morphological characters, such as tail length, cranium size, and pelage color and texture. Recently diverged yet morphologically disparate sister taxa living syntopically in an isolated habitat “island,” like the montane forests of Mt. Singgalang, is unusual in mammals but documented in other *Crocidura* on neighboring Java and Borneo; these 2 new taxa represent the first known case of this phenomenon on Sumatra. Our results bring the number of Sumatran *Crocidura* to 10, 9 of which are endemic to the island. All 3 of the new species appear to be endemic to a single mountain and were not detected in similar surveys of nearby mountains. If this local endemism pattern is common, it would indicate that Sumatra’s mammal diversity may be severely underestimated, largely due to the paucity of small-mammal surveys and museum specimens.

**Key words:** biodiversity, *Crocidura*, Indonesia, new species, Sunda.

**Tiga cecurut semut baru (Soricidae: *Crocidura*) dari Sumatra Barat, Indonesia: perbedaan elevasi dan morfologi dalam sintopik, taksa saudara**

## Abstrak

Kami mendeskripsikan tiga species baru cecurut (Eulipotyphla, Soricidae, *Crocidura*) dari Sumatera Barat, Indonesia. Dua dari tiga taksa ini ditemukan pada ketinggian di atas 1,800 meter di Gunung Singgalang. Takson ketiga ditemukan di atas 1,660 m di Gunung Talamau, 65 km di sebelah barat laut Gunung Singgalang. Kami juga membangkitkan kembali *Crocidura aequicauda* berdasarkan dua specimen dari Gunung Tujuh dan Gunung Kerinci, yang terletak didekat perbatasan antara provinsi Sumatera Barat dan provinsi Jambi. Beberapa pendekatan metodologis mendukung temuan kami: morfometrik linear tengkorak, morfometrik geometric 2D berbasis landmark, filogenetika molekuler menggunakan mtDNA dan enam ekson inti. Analisa multilokus kekerabatan antar species menempatkan tiga species baru ini dan *C. aequicauda* dalam satu klad dengan species endemik Jawa, *C. monticola* dan *C. umbra*. Walaupun dua taksa dari Gunung Singgalang ditemukan sebagai species saudara, salah satunya memiliki ukuran dua kali lebih besar dari yang lainnya, dan mereka berbeda dalam beberapa karakter morfologi lainnya, seperti panjang ekor, ukuran tengkorak, dan warna dan tekstur rambut. Taksa bersaudara yang baru saja bercabang tetapi memiliki morfologi berbeda yang hidup terisolasi

di habitat “pulau,” seperti hutan pegunungan di Gunung Singgalang, merupakan hal yang tidak biasa pada mamalia, tetapi juga tercatat pada *Crocidura* lainnya di Jawa dan Kalimantan yang berdekatan; dua species baru ini merepresentasikan kasus pertama yang diketahui tentang fenomena ini di Sumatera. Hasil kami menjadikan jumlah *Crocidura* Sumatera menjadi sepuluh species, sembilan species endemik di pulau tersebut. Ketiga species baru tersebut tampaknya endemik di satu gunung saja dan tidak terdeteksi di survei serupa di gunung-gunung terdekat. Jika pola endemisme lokal ini umum, ini menunjukkan bahwa keanekaragaman mamalia Sumatera mungkin masih jauh dari estimasi sebenarnya, sebagian besar karena kurangnya survei mamalia kecil dan specimen museum dari kawasan tersebut.

**Kata kunci:** biodiversitas, *Crocidura*, Indonesia, species baru, Sunda.

The ongoing effort to document global biodiversity has revealed that the number of living mammal species has been greatly underestimated, particularly in diverse tropical regions (Reeder et al. 2007; Heaney et al. 2016; Esselstyn et al. 2021; Parsons et al. 2022). Intense anthropogenic pressures exerted across the global tropics today add urgency to the need to accurately document biodiversity. Perhaps no group of mammals better exemplifies historic undercounting than the white-toothed shrew genus *Crocidura* (Soricidae), a group of 219 currently described (Mammal Diversity Database 2023), small-bodied (<50 g), nocturnal mammals with a largely conserved morphology. Delimiting species within *Crocidura* using traditional morphometrics has been difficult, as many species look alike, and the paucity of specimens has compounded this predicament. However, recent efforts are revealing the existence of many cryptic species, and 44 new taxa have been described since the end of the 20th century alone (Mammal Diversity Database 2023). Nearly all these discoveries have resulted from combined morphological and molecular approaches. The realization that many evolutionarily distinct populations of shrews—often distantly related—may co-occur in areas previously thought to support only 1 or 2 species has sparked interests in elevational divergence, convergent evolution, character displacement, and community ecospace occupation in *Crocidura* (Esselstyn et al. 2013; Demos et al. 2016a, 2016b; Van de Perre et al. 2020).

Recently improved resolution in vertebrate taxonomy more generally has also enhanced our understanding of the biogeography in Sundaland, Wallacea, and the Philippines. Where island vicariance was once thought to be a key driver of diversification, recent analyses of animal diversity in these areas suggest a complex history of colonization, and a prominent role of in situ diversification of species (Oliveros and Moyle 2010; Esselstyn et al. 2013; Sheldon et al. 2015; Demos et al. 2016a; Rowe et al. 2019; Shaney et al. 2020a, 2020b). Examples in shrews include elevational and morphological divergences of sister species pairs (e.g. *Crocidura monticola* and *C. umbra*; Demos et al. 2016b) and the endemic radiation of 20 *Crocidura* species on Sulawesi, complete with multiple examples of morphological convergence (Esselstyn et al. 2021). Current knowledge contends that nearly all species of Sunda, Wallacean, and Philippine shrews are endemic to a single island.

The island of Sumatra is a biodiversity hotspot, famous for housing some of the remaining mammalian megafauna of the region (e.g. tigers, rhinoceros, orangutans). The Barisan Mountains run nearly the entire length of the island, forming a long chain of wet, tropical lowland forests at their base that quickly rises to montane cloud forests—a habitat gradient that often houses high biodiversity. The shrew fauna of Sumatra has been sparsely sampled, and all but one of the currently recognized species of Sumatran *Crocidura* were described from single specimens (Ruedi 1995). The most recent taxonomic revision of Sumatran *Crocidura* determined there to be 5 species present, along with *C. vosmaeri* from nearby Bangka Island (Ruedi 1995), though recent

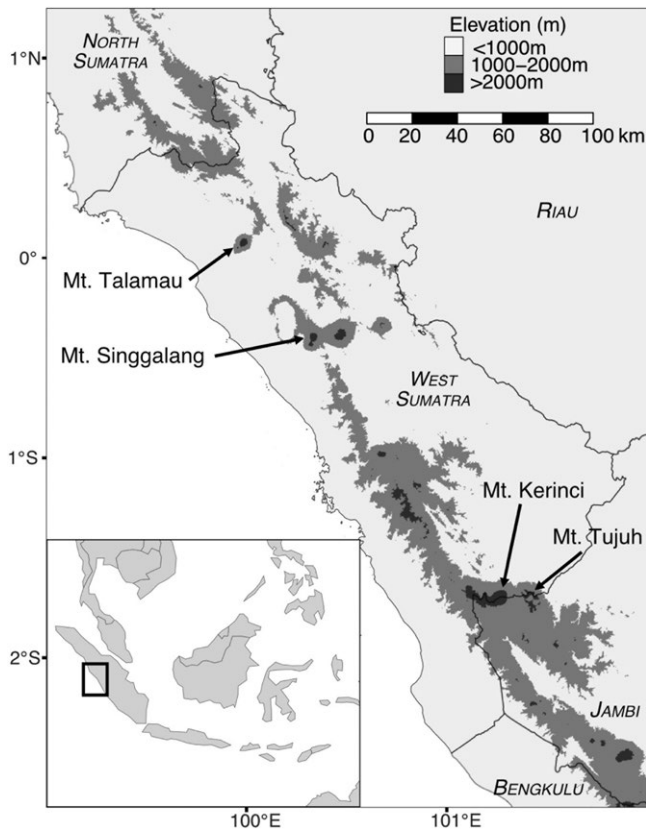
publications suggest the presence of additional taxa. A phylogeographic study of Sundaland shrews points to the presence of an undescribed Sumatran species that is sister to *C. monticola* and *C. umbra* from Java (“*C. sp. nov. 2*”; Demos et al. 2016a). Another Sumatran specimen “previously misidentified as *C. paradoxura*” (Hinckley et al. 2022:493) was recovered as sister to the unnamed taxon “*C. sp. nov. 2*” (Demos et al. 2016a; Hinckley et al. 2022). This discovery has additional taxonomic relevance as the morphology of the misidentified *C. paradoxura* was the basis for synonymizing *C. paradoxura* and *C. aequicauda* (Robinson and Kloss 1918; Ruedi 1995).

In 2011 and 2018, we undertook small-mammal inventories that specifically targeted shrews on 3 mountains in West Sumatra. Here we document 3 new species of *Crocidura* from West Sumatra, Indonesia, and resurrect a fourth species, using cranial morphometrics, external measurements, and multilocus sequence data drawn from these new specimens.

## Materials and methods

### Fieldwork

We surveyed small mammals in 3 locations in West Sumatra, Indonesia: Mount Tujuh (2011), Mount Singgalang (2011 and 2018), and Mount Talamau (2018; Fig. 1). The 2011 trip to Mt. Singgalang surveyed the eastern side of the mountain, while the 2018 trip focused on the northern side. All surveys used a mix of Victor snap traps and pitfall lines, and virtually all shrews were captured in pitfalls. Pitfall lines consisted of 6 to 10 large 20- to 30-l buckets connected by a drift fence made of tarp, though occasionally we used smaller 1- to 3-l buckets with and without a drift fence. On Mount Tujuh, we set pitfall lines at 1,540 m (mix of large and small buckets), 1,600 m (mix of large and small buckets), and 1,950 m (large buckets) for a total of ca. 300 pitfall nights. On Mt. Singgalang in 2011, we set pitfall lines (large buckets) at 1,700 and 2,000 m for a total ca. 120 pitfall nights. In 2018, we added large-bucket pitfall lines at 1,800, 1,880, and 2,100 m for a total of ca. 330 pitfall nights, and a line of 10 small buckets for 1 night at 2,826 m. On Mt. Talamau we set pitfall lines (large buckets) at 1,050, 1,600, 1,660, 1,800, and 2,000 m for a total of ca. 515 pitfall nights. All specimens were deposited at the Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); and Museum Zoologicum Bogoriense (MZB), Bogor. Specimens were measured and weighed, and after tissues harvested, bodies were preserved in formalin, often with the skull removed, or prepared as dried museum skins with dried and cleaned skeletons. Tissues were preserved in liquid nitrogen or 95% ethanol. All collecting methods followed the recommended guidelines of the American Society of Mammalogists (Sikes et al. 2016). We incorporated additional comparative material from University of California Museum of Vertebrate Zoology, Berkeley (MVZ); Rijksmuseum



**Fig. 1.** Map of West Sumatra province showing the sampling locations, Mt. Tujuh, Mt. Talamau, and Mt. Singgalang, from the 2011 and 2018 surveys, as well as Mt. Kerinci where the *Crociodura aequicauda* type was collected. Inset shows the area in the context of SE Asia. Map was generated in the R package tmap (Tennekes 2018).

Natuulijke Historie, Leiden (RMNH); and National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia (USNM).

## Morphological analyses

External measurements including total length (TL), head-body length (HB), tail length (Tail), hind-foot length (HF), and ear length (Ear) were taken from field notes. Cranial measurements were taken with digital calipers to the nearest 0.01 mm following Esselstyn et al. (2021): condyloincisive length (CIL), breadth of braincase (BBC), interorbital width (IOW), rostral length (RL), rostral width (RW), postpalatal depth (PPD), postpalatal length (PPL), distance from occipital condyle to glenoid fossa (CGF), upper toothrow length (UTL), distance from alveolar of  $P^4$  to  $M^3$  ( $P^4$ – $M^3$ ), width of the palate from  $M^3$  to  $M^3$  (PW), and labial width at  $M^2$  ( $M^2$ – $M^2$ ). The skull from the type of *C. aequicauda* (cataloged as both Federated Malay States Museum FMSM 448/14 and Natural History Museum BMNH 1919.11.5.28), a junior synonym of *C. paradoxura*, is badly damaged (Robinson and Kloss 1918), and we used the 8 measurements from *C. paradoxura* MZB 16790 reported in Ruedi (1995), as the author concluded that the specimens MZB 16790 and FMSM 448/14 are conspecific (Ruedi 1995). We performed a principal components analysis (PCA) on the correlation matrix of natural log-transformed cranial measurements and visualized the results in R 4.2.0 (R Core Team 2022), and tidyverse 1.3.2 (Wickham et al. 2019). We made a variety of univariate and bivariate plots of external and cranial measurements to visualize

potentially diagnostic features. Measured specimens are listed in [Supplementary Data SD1](#).

Linear cranial measurements are useful in differentiating *Crociodura*, but often overlap among species. Size-corrected cranial measurements identify proportional differences in cranial dimensions (e.g. a wide braincase for a given skull length) that are not easily identified with univariate linear measurements alone. However, the correlation between cranial measurements and skull size may not be consistent among cranial dimensions, and therefore ratios calculated by dividing cranial measurements by skull length may not accurately represent a size-corrected measurement. To exploit the strengths of each approach, we quantified differences in skull proportions between Sumatran *Crociodura* using multiple regression to estimate the mean distribution of 11 cranial measurements, conditioned on the length of the skull (condyloincisive length), or a size-corrected estimate for each cranial dimension. We then constructed 12 linear regression models using each cranial measurement as a response variable, and species as a categorical, group-level predictor variable. Our estimate of CIL simply used CIL as the response and species as the predictor. The remaining 11 models (1 per measurement) used the linear skull measurement as the response, and species + CIL as predictors, generating a measurement estimate for each species, conditioned on the effect of skull length (i.e. a size-corrected estimate). We used Bayesian linear regression modeling in the R package brms 2.18.8 (Bürkner 2018). Before running the models, we mean-centered and scaled each measurement to a standard deviation of 1.0. We used regularizing priors, and ran 4 chains for each model, with each chain set to 2,000 iterations of warm-up and 2,000 iterations of sampling. All data and scripts for these analyses are archived on Zenodo as DOI: [10.5281/zenodo.7916697](https://doi.org/10.5281/zenodo.7916697).

We quantified cranial shape variation in Sumatran *Crociodura* using a 2D geometric morphometric landmarking approach. We photographed the dorsal and ventral sides of the crania of 113 Sumatran shrews housed in the LSUMZ collection using a Fujifilm X-Pro2 Camera with a Fujifilm 90 mm F2 lens and a 16 mm macro extension tube. We placed 16 dorsal landmarks and 23 ventral landmarks on each skull (Supplementary Data SD2) using the digitize2D() function in the R package geomorph 4.0.3 (Baken et al. 2021). In geomorph, we performed a generalized Procrustes analysis (GPA) superimposition using gpa(), and shape coordinates were subjected to a PCA with gm.prcomp(). PC scores are reported in [Supplementary Data SD1](#). We visualized the shape morphospaces using ggplot2.

## Genetic analyses

We extracted genomic DNA from tissue samples (liver, muscle) using Qiagen DNEasy Blood & Tissue kits (Qiagen, Germantown, Maryland) following the manufacturer's instructions. We amplified mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) regions using polymerase chain reaction. We amplified the mitochondrial protein-coding gene cytochrome *b* (Cytb) for 33 specimens of new and previously described *Crociodura* species collected on recent expeditions to Sumatra. Additionally, we sequenced portions of 6 nuclear exons: apolipoprotein B (*Apob*), breast cancer susceptibility 1 (*Brca*), brain-derived neurotrophic factor (*BDNF*), growth hormone receptor exon 10 (*Ghr*), prostaglandin E4 receptor (*Ptger4*), and von Willebrand factor exon 28 (*vWf*) from multiple individuals of the putative species collected on Mount Singgalang and Mount Talamau. We aligned the new mitochondrial and nuclear sequences to previously published sequences, which included specimens from the 2011 surveys of Mts. Tujuh and Singgalang (Demos



et al. 2016a; Hinckley et al. 2022), using MEGA v.11 (Tamura et al. 2021). Specimen catalog numbers and GenBank accessions are available in [Supplementary Data SD3](#), and the Cytb alignment is available in [Supplementary Data SD4](#) and archived on Zenodo as DOI: [10.5281/zenodo.7916697](https://doi.org/10.5281/zenodo.7916697).

We estimated the Cytb mitochondrial gene tree using a suite of tools available in IQTree 1.6.12 (Nguyen et al. 2015). We estimated the optimal substitution model for the mitochondrial data using ModelFinder (Kalyaanamoorthy et al. 2017), which is integrated into the tree topology estimation in IQTree. We used the UFBoot2 method (Hoang et al. 2018) to estimate topological support. We calculated inter- and intraspecific Jukes–Cantor mitochondrial distances in the R package Ape 5.6-2 (Paradis et al. 2004) using a Cytb alignment of all Sumatran and Javan *Crocridura* species.

We concatenated alignments of our 6 nuclear exons and estimated a phylogenetic tree with IQTree 1.6.12 (Nguyen et al. 2015). We estimated the optimal substitution model for each gene using ModelFinder and topological support with UFBoot2. Specimen catalog numbers and GenBank accessions are available in [Supplementary Data SD3](#), and the concatenated nDNA alignment is available in [Supplementary Data SD5](#) and archived on Zenodo as DOI: [10.5281/zenodo.7916697](https://doi.org/10.5281/zenodo.7916697). We also estimated a species tree using StarBEAST in BEAST 2.6.7 (Bouckaert et al. 2019) with the 6 individual nDNA alignments. We unlinked the clock, substitution, and tree models for all genes. We used a relaxed log-normal clock model with a uniform prior, and constant population size. We ran 4 chains of  $10^8$  iterations and stored every 2,000th sample. Convergence was assessed in Tracer 1.7.1 (Rambaut et al. 2018), using estimated sample size (ESS) > 200 as an indication of chain convergence. We removed the first 20% of the trees as burn-in, combined the gene trees and species trees from each chain using LogCombiner (Bouckaert et al. 2019), then estimated maximum clade credibility gene trees and species tree using TreeAnnotator (Bouckaert et al. 2019). Specimen catalog numbers and GenBank accessions are available in [Supplementary Data SD3](#), and the 6 nDNA alignments are archived on Zenodo as DOI: [10.5281/zenodo.7916697](https://doi.org/10.5281/zenodo.7916697).

## Results

### Fieldwork

We collected 8 species of *Crocridura* in total from the 3 Sumatran mountains. On Mt. Tujuh, we collected *C. beccarii*, *C. lepidura*, *C. neglecta*, and *C. paradoxura*. On Mt. Singgalang, we collected *C. beccarii*, *C. hutanis*, *C. neglecta*, and *C. paradoxura* along with 2 undescribed taxa. The first new taxon was documented in 2011 on Mt. Singgalang at 2,000 m elevation (Demos et al. 2016a, 2016b). On the second trip to Mt. Singgalang, the same taxon was collected on the north side of the mountain at 2,100 m, and an additional new taxon was collected at 1,880, 2,100, and 2,826 m. On Mt. Talamau, we collected *C. hutanis*, *C. lepidura*, *C. neglecta*, and *C. paradoxura* as well as an additional species that was not collected on Mt. Tujuh or Mt. Singgalang.

### Morphological evidence

Morphological results support the presence of 3 new species from Sumatra (Fig. 2). PC1 from the linear measurement analyses demonstrates that the 2 smaller new species occupy an intermediate cranial size between the tiny *C. neglecta* and the medium-sized *C. beccarii* (Fig. 2A). A bivariate plot of upper toothrow length and tail length (Fig. 2B) clearly distinguishes the individual species, and the 3 new species all have relatively longer tails than any

previously described species with a similar toothrow length. In addition, MZB 16790 and the *C. aequicauda* type specimen, FMSM 448/14, occupy a distinct region of morphospace (Fig. 2B). The first 2 PCs of the dorsal landmark analysis (Fig. 2C) show substantial overlap between many species; however, the new species from Talamau occupies its own region of morphospace. The first 2 PCs of the ventral landmark analysis (Fig. 2D) however clearly distinguish most Sumatran species, and the 3 new species each occupy their own regions of morphospace and show little overlap with previously described taxa.

Linear regression models of cranial measurement all demonstrated proper convergence. The size-corrected estimates of linear cranial measurements display a distinctive suite of cranial features for each Sumatran *Crocridura* species (Fig. 3). For example, all 3 of the new species have narrow rostra for their skull size (estimates are negative, or below the global mean of zero), but only 2 have a dorsoventrally compressed skull (negative relative postpalate depth values; Fig. 3). Additional comparisons are discussed below.

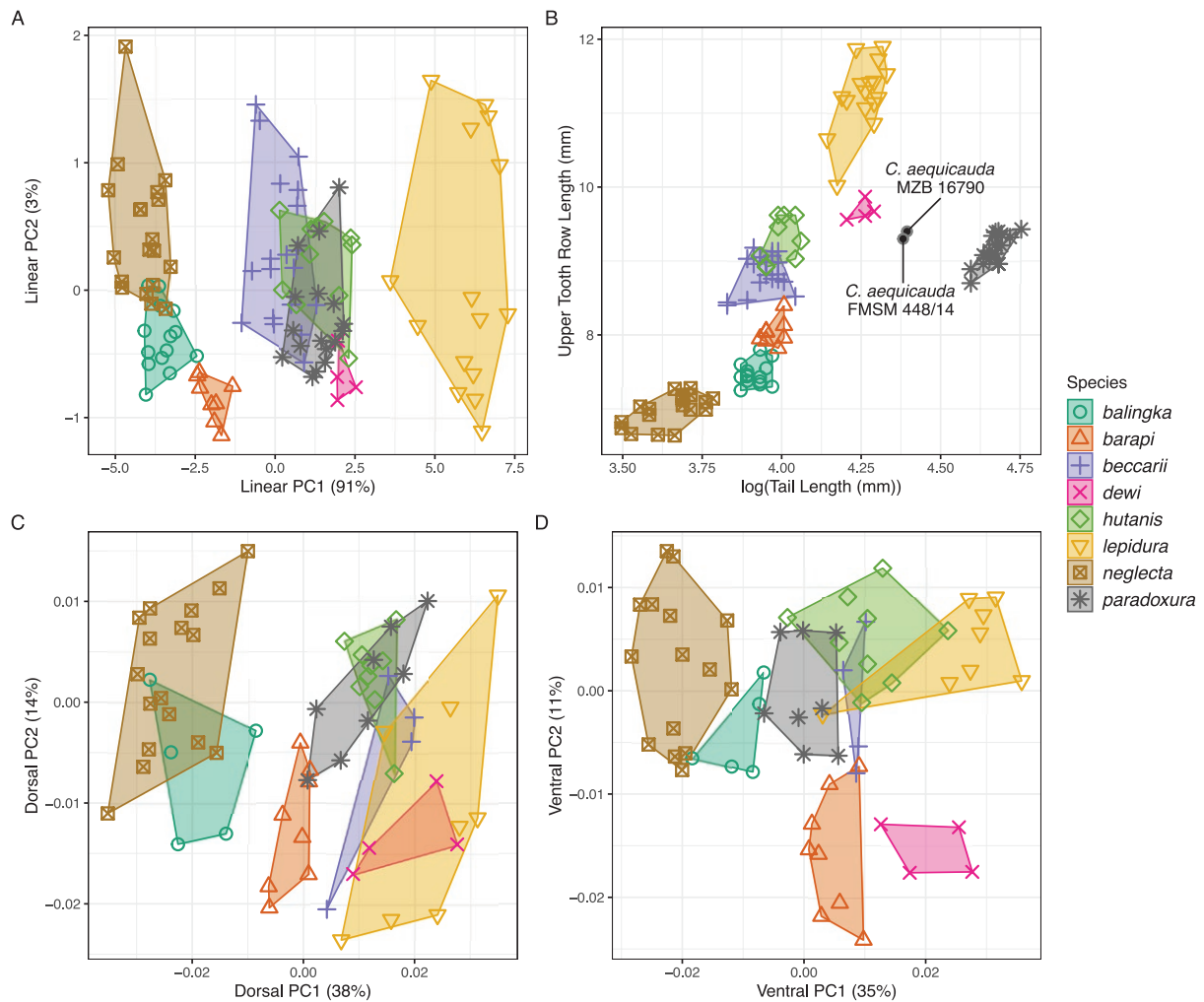
### Genetic evidence

All new sequences were published as GenBank accession numbers OQ944004 to OQ944100 ([Supplementary Data SD3](#)). Our mitochondrial alignment of Southeast Asian shrews contains 760 characters. ModelFinder selected the GTR + I (proportion of invariable sites) +  $\Gamma$  (gamma-distributed rate heterogeneity) model, then used this substitution model to estimate the topology. The resulting mitochondrial gene tree shows 3 monophyletic, unnamed taxa from Sumatra (Fig. 4; [Supplementary Data SD6](#)). These 3 species form a clade with the specimen MZB 16790 as well as *C. monticola* and *C. umbra* from Java, nested within a larger, moderately supported clade that also contains *C. neglecta* from Sumatra and Borneo and several species from mainland Asia and Taiwan. Jukes–Cantor mitochondrial distances among Sumatran species (Table 1) range from 0.04 to 0.15. Each of the 3 new species is at least 0.08 distant from other Sumatran species. Intraspecific mitochondrial divergence means range from 0 to 0.02 (Table 1).

For our concatenated alignment of 3,243 characters from 6 nuclear exons, ModelFinder selected the HKY + I model for *BDNF* and *Ptger4*, HKY + R (FreeRate model; Yang 1995) for *Apob* and *Brca*, GTR+G for *Ghr*, and GTR + I + G for *vWf*. The resulting nuclear tree recovers each of the 3 unnamed taxa from Sumatra as monophyletic (Fig. 5; [Supplementary Data SD7](#)). Two species from Singgalang form a clade with MZB 16790 that is sister to *C. monticola* and *C. umbra* from Java. The third new taxon is sister to this clade of 5 species.

All parameters in the StarBEAST analysis demonstrated evidence of convergence (ESS > 200). The resulting species-tree topology from 6 exons places the 2 new species from Mt. Singgalang as sister to *C. umbra* and *C. monticola* from Java, and the new species from Mt. Talamau as sister to these 4 taxa, all with moderate to high nodal support (Fig. 6). These results are concordant with the concatenated nuclear tree and previous species-tree analyses using nuclear DNA (Demos et al. 2016a). Individual gene trees are presented as [Supplementary Data SD9](#).

The results of our mitochondrial gene tree estimation, concatenated nuclear tree estimation, and morphometric analyses support the presence of 3 previously undocumented *Crocridura* species on Sumatra. We describe these species below. Comparisons between the new and previously described taxa focus on similarly sized species, as these are the most difficult to distinguish. When



**Fig. 2.** Inter- and intraspecific morphological variation in Sumatran *Crocidura* support the existence of 3 new species. (A) First 2 axes of a PCA from 11 linear cranium dimensions. The first axis, representing 91% of the variation, separates most species by size. (B) Bivariate plot of the natural log of tail length and condyloincisive length for the 8 Sumatran *Crocidura*. Lower plots show the first 2 PCs of an analysis of 16 dorsal landmarks (C) and 23 ventral landmarks (D). All linear measurements and PC scores are reported in [Supplementary Data SD1](#).

describing dentition, we use the dental homology of [Hutterer \(2005\)](#): I3 C1 P1 M3/i2 c1 p0 m3 = 28. All measurements referenced in the descriptions are available in [Table 2](#).

## Systematics

*Crocidura balingka*, new species  
Balingka Shrew

*Crocidura* sp. nov. 2: [Demos et al. 2016a](#):5164

*Crocidura* sp. 1: [Demos et al. 2016b](#):8

## Holotype

LSUMZ 40239, an adult male collected 23 November 2018 by Ahmad Mursyid and prepared as a cleaned skull and skeleton, study skin, and frozen liver and lung tissues. External measurements are total length = 108 mm, tail length = 48 mm, hind-foot length = 12 mm, ear length = 8 mm, and mass = 5.6 g. The voucher specimen and a tissue sample will be permanently curated at MZB with the catalog number MZB 43651; duplicate tissue samples will be retained at LSUMZ.

## Type locality

Indonesia, Sumatera Barat, Agam, Kecamatan IV Koto, Kenagarian Balingka, Jorong Pahambatan, northern slope of Mt. Singgalang, 0.37389°S, 100.32799°E, 2,100 m elevation.

## Paratypes

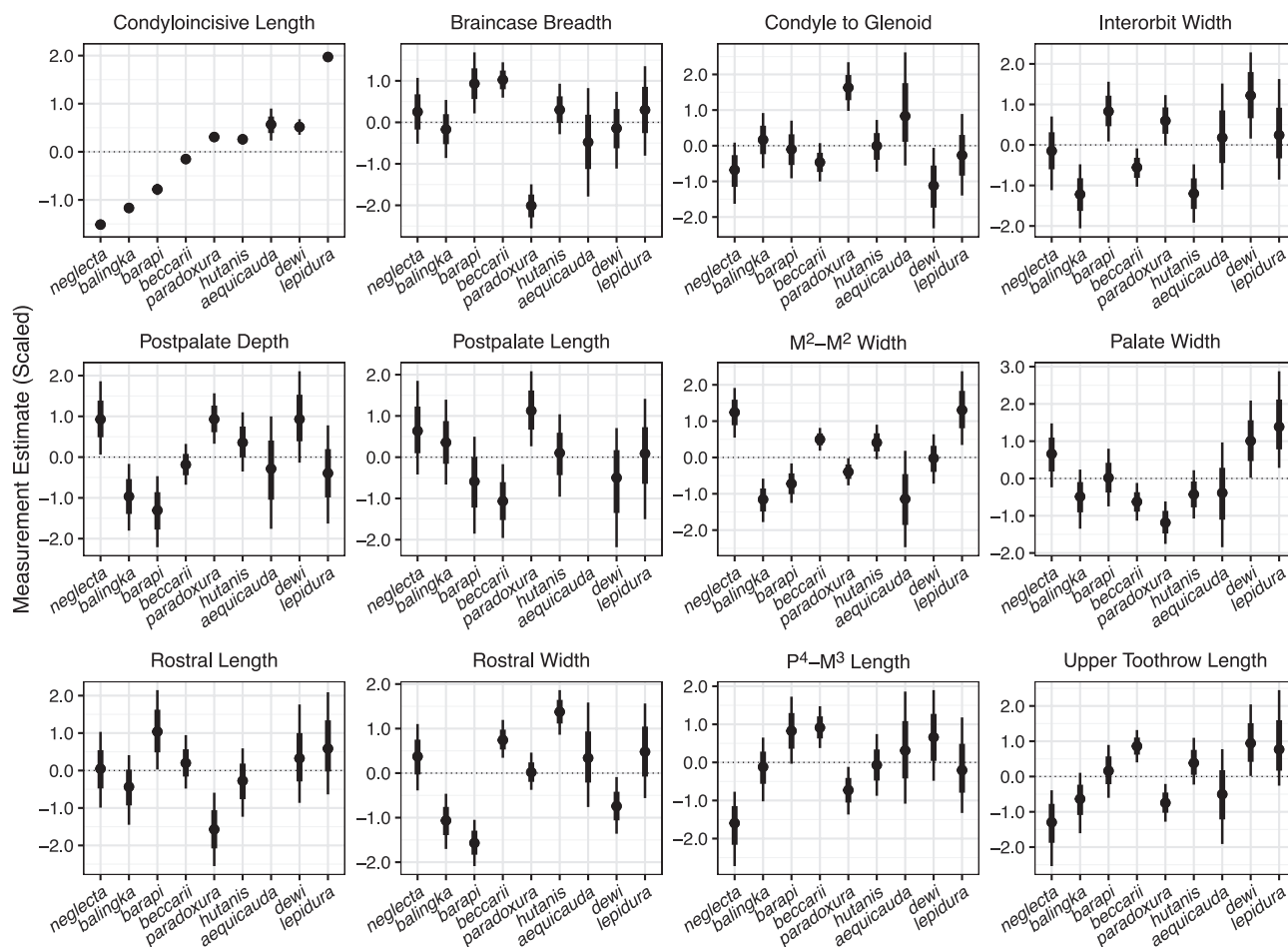
LSUMZ 40214, 40234, 40235, 40236, 40237, 40238, 40240, 40241, 40242.

## Other examined material

FMNH 212952, 212964, 212965, 212967, 212971, 212972, 212973, 212974, 212976.

## Etymology

Named in honor of the people of Balingka, a village in IV Koto, Agam, West Sumatra, who, through their generosity and knowledge, have provided critical support to Indonesian and foreign mammalogists interested in the biodiversity of Mt. Singgalang. We recommend the English common name “Balingka Shrew.”



**Fig. 3.** Size-corrected cranial measurement variation in Sumatran *Crocidura*. Mean-centered and scaled measurement estimates are on the y-axis, and species are on the x-axis. The point represents the median measurement probability, the wider vertical line indicates the 60% probability interval, and the thin vertical line represents the 89% probability interval. All measurement estimates (apart from condylolincisive length) are conditioned on the condylolincisive length, reflecting an estimate of each cranial character free from the influence of skull length. The mean value for each measurement is 0, shown with a dotted line. The greater uncertainty around *C. aequicauda* estimates stems from the small sample size ( $n = 1$  to  $2$ ).

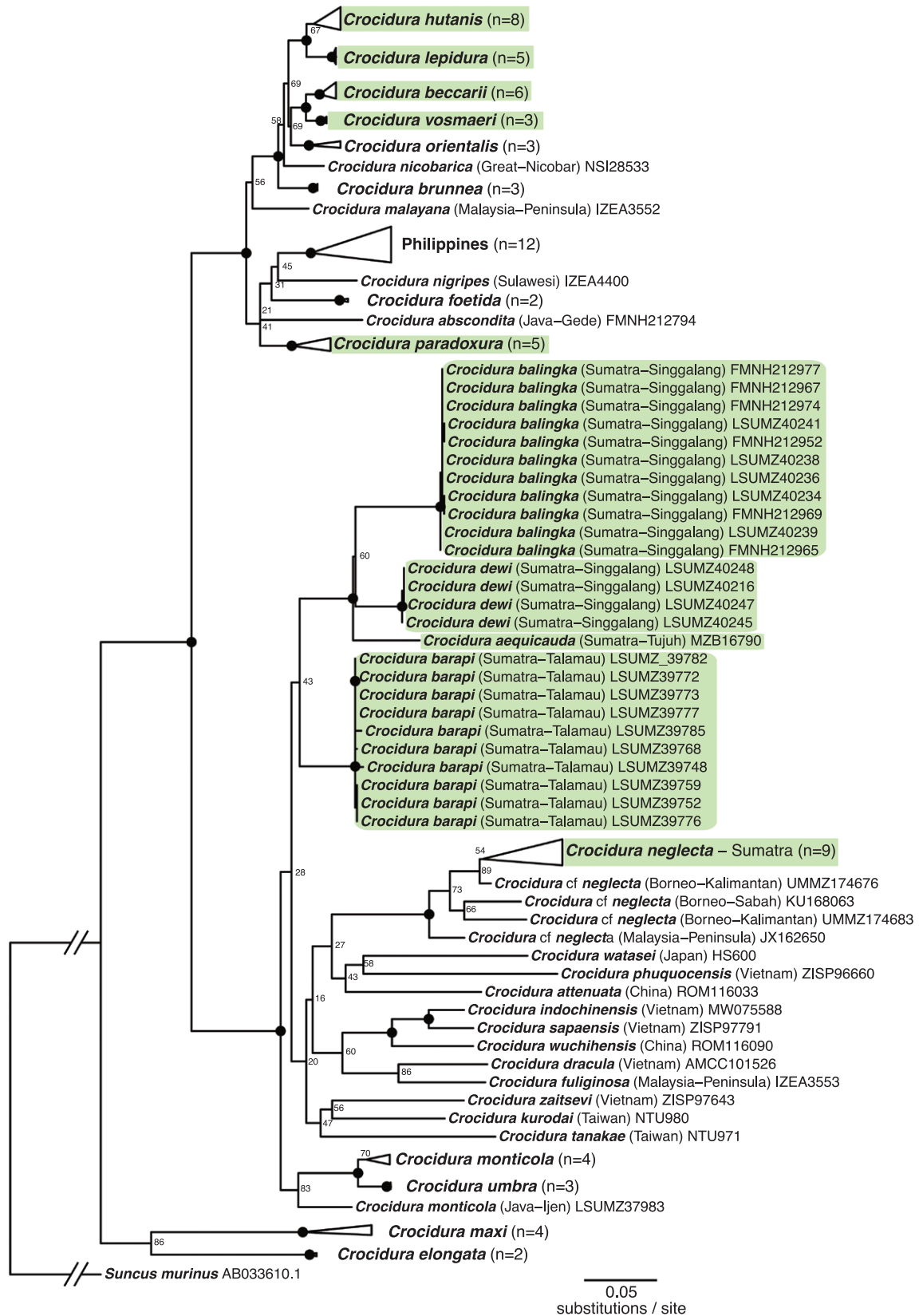
## Diagnosis

*Crocidura balingka* is a small- to medium-sized shrew (4.1 to 6.5 g), dark gray-brown in color, with a thin, medium-length tail roughly 80% of head-body length (Supplementary Data SD9). Individual hairs of the dorsum are paler brown at the base and darker brown toward the tips. The ventral pelage is slightly paler (gray-brown) than the dorsal pelage; however, there is no clear demarcation between dorsal and ventral coloration. The tail is relatively long for similar-sized Sumatran *Crocidura*, with very short, sparse applied hairs along the entire length of the tail, giving a hairless impression when viewed with the naked eye. However, a small tuft of 1-mm-length hairs is visible at the tail tip. The proximal portion of the tail is lightly bristled with 3-mm hairs extending to approximately 1/2 of the total tail length. The skull is small (16.9 to 17.9 mm CIL; Table 2) and has a poorly developed lambdoidal crest. The junction of the lambdoidal suture and the sagittal suture is anteriorly positioned on the skull. The edges of the braincase are not rounded but taper both anteriorly and posteriorly from the widest point, which juts out laterally. The braincase is relatively narrow for a skull of this size. The rostrum tapers strongly, but anterior to the  $I^3$  the taper wanes, resulting in a narrow rostrum (Fig. 3) with lateral surfaces that run parallel to the midline of the skull. The palate is relatively small in both length and breadth and the upper tooth row is relatively short, resulting

in a longer postpalatal length relative to the skull size (Fig. 3). The coronoid processes are strongly tapered dorsally, and angular processes are very long and thin.

## Description

Dorsal pelage dark gray-brown (Supplementary Data SD9). Hairs are medium gray near the base and darken to charcoal brown toward the tips. The dorsal pelage is short, measuring 3 mm in length at mid-dorsum. The ventral pelage is slightly lighter in color, but there is no clear demarcation between dorsal and ventral coloration. The dorsal portions of the hind feet are brown, with sparse, short, medium-brown hairs, similar in color to the dorsum, covering the entire surface. There are faint tufts of light brown hairs at the distal ends of the digits. The digits are slightly paler than the proximal regions of the foot. The forefeet show a similar color and pilosity to the hind feet and have very faint tufts of light brown hairs at the distal phalanges (1 to 4 hairs per digit). The rhinarium is brown and the lips are unpigmented. Most mystacial vibrissae are 12 to 13 mm in length, with the longest extending 16 to 18 mm from the face. The chin vibrissae are 4 mm long and very sparse. Hairs on the dorsal portion of the hind feet are dark, similar in color to the hairs of the dorsum, with detectable tufts near the distal ends of the digits. The hind feet are narrow. The sole and palm are pale. The thenar pads are



**Fig. 4.** Maximum likelihood Cytb gene tree inferred in IQTree. Black circles at nodes indicate a UFBoot2 bootstrap value of  $\geq 95\%$ . The remaining UFBoot2 values are reported at the nodes. Sumatran species are highlighted. The locality of each specimen is noted in parentheses in the form of island locality for insular species. Nodes are collapsed apart from the 3 newly described species, and the outgroup branch length to *Suncus murinus* is truncated for a clearer presentation of results. The figure without the collapsed nodes is available as [Supplementary Data SD6](#).



**Table 1.** Inter- and intraspecific Cytb distances between Sumatran *Crociodura* species. The means are reported, with the minimum and maximum distances in parentheses. The diagonal shows intraspecific distances.

	<i>aequicauda</i>	<i>balingka</i>	<i>barapi</i>	<i>beccarii</i>	<i>dewi</i>	<i>hutanis</i>	<i>lepidura</i>	<i>neglecta</i>	<i>paradoxura</i>
<i>aequicauda</i>	-								
<i>balingka</i>	0.09 (0.09, 0.09)	0 (0, 0)							
<i>barapi</i>	0.10 (0.10, 0.11)	0.11 (0.10, 0.12)	0 (0.0, 0.01)						
<i>beccarii</i>	0.14 (0.14, 0.15)	0.14 (0.13, 0.15)	0.13 (0.12, 0.14)	0.02 (0, 0.03)					
<i>dewi</i>	0.08 (0.08, 0.08)	0.08 (0.08, 0.08)	0.09 (0.08, 0.09)	0.13 (0.13, 0.14)	0 (0,0)				
<i>hutanis</i>	0.17 (0.15, 0.17)	0.15 (0.14, 0.16)	0.14 (0.13, 0.15)	0.06 (0.04, 0.07)	0.14 (0.13, 0.15)	0.02 (0, 0.04)			
<i>lepidura</i>	0.15 (0.15, 0.16)	0.15 (0.14, 0.15)	0.13 (0.13, 0.14)	0.05 (0.05, 0.06)	0.14 (0.14, 0.14)	0.04 (0.03, 0.05)	0 (0,0)		
<i>neglecta</i>	0.11 (0.09, 0.12)	0.15 (0.14, 0.16)	0.12 (0.12, 0.13)	0.13 (0.13, 0.14)	0.14 (0.13, 0.15)	0.14 (0.14, 0.15)	0.13 (0.13, 0.14)	0.02 (0, 0.04)	
<i>paradoxura</i>	0.15 (0.12, 0.15)	0.14 (0.13, 0.16)	0.13 (0.13, 0.14)	0.08 (0.07, 0.09)	0.15 (0.15, 0.16)	0.08 (0.07, 0.10)	0.09 (0.09, 0.09)	0.14 (0.13, 0.15)	0.02 (0, 0.04)

medium brown, and the hypothenar and digital pads are pale brown. Claws on the fore and hind feet are medium in length, with an intermediate curvature. The tail is medium length and slender, with sparse 3-mm bristles on the proximal half of the tail. Applied hairs are short, giving the tail a hairless impression when viewed with the naked eye. They are dark dorsally, gradually becoming a lighter gray-brown ventrally. The tip of the tail has a tuft of 1-mm hairs that are slightly paler than the applied hairs. The skull is small and narrow for a shrew of this size. The lambdoidal crest is weakly formed. The interorbital constriction is narrow for a Sumatran *Crociodura* of this size (Table 2; Fig. 3). The upper tooththrow is short and the palate is narrow for the skull length, resulting in a long postpalatal region (Fig. 3). The rostrum narrows sharply toward the distal portion of the maxilla (Fig. 7). I<sup>1</sup> is falciform and rounded and extends beyond the premaxilla. It is larger than I<sup>2</sup>, and I<sup>2</sup> is larger than I<sup>3</sup>. The upper canine is distinctly larger than I<sup>3</sup>. The P<sup>4</sup> talonid is dorsoventrally compressed with a strong convex posterior margin. M<sup>1</sup> is slightly larger in occlusal area and height than M<sup>2</sup>, and M<sup>3</sup> is considerably smaller than both.

### Comparisons

*Crociodura balingka* is easily distinguished from the larger Sumatran *Crociodura* (*C. lepidura*, and *C. hutanis*) based on the size of all external and cranial measurements (Table 2). The new species is similar in size to *C. beccarii*, *C. paradoxura*, and *C. neglecta*. Though similar in body length and mass, *C. paradoxura* has a long tail (Table 2), elongate skull (as evidenced by a long condyloincisive length and narrow braincase; Fig. 3; Table 2), pale feet with lightly pigmented skin, and distinct light gray coloration, none of which are shared by *C. balingka*. Therefore, *C. balingka* will be compared to *C. beccarii* and *C. neglecta* in turn.

*Crociodura balingka* overlaps with *C. beccarii* in all external measurements (head-body length, tail length, hind-foot length, ear length, and mass); however, *C. balingka* is less robust than *C. beccarii* and has a lower mean head-body length, hind-foot length, and mass measurements (Table 2). The new species has a higher mean relative tail length than *C. beccarii* (Table 2). Dorsally, the feet are darker in *C. balingka* than in *C. beccarii*. The claws of *C.*

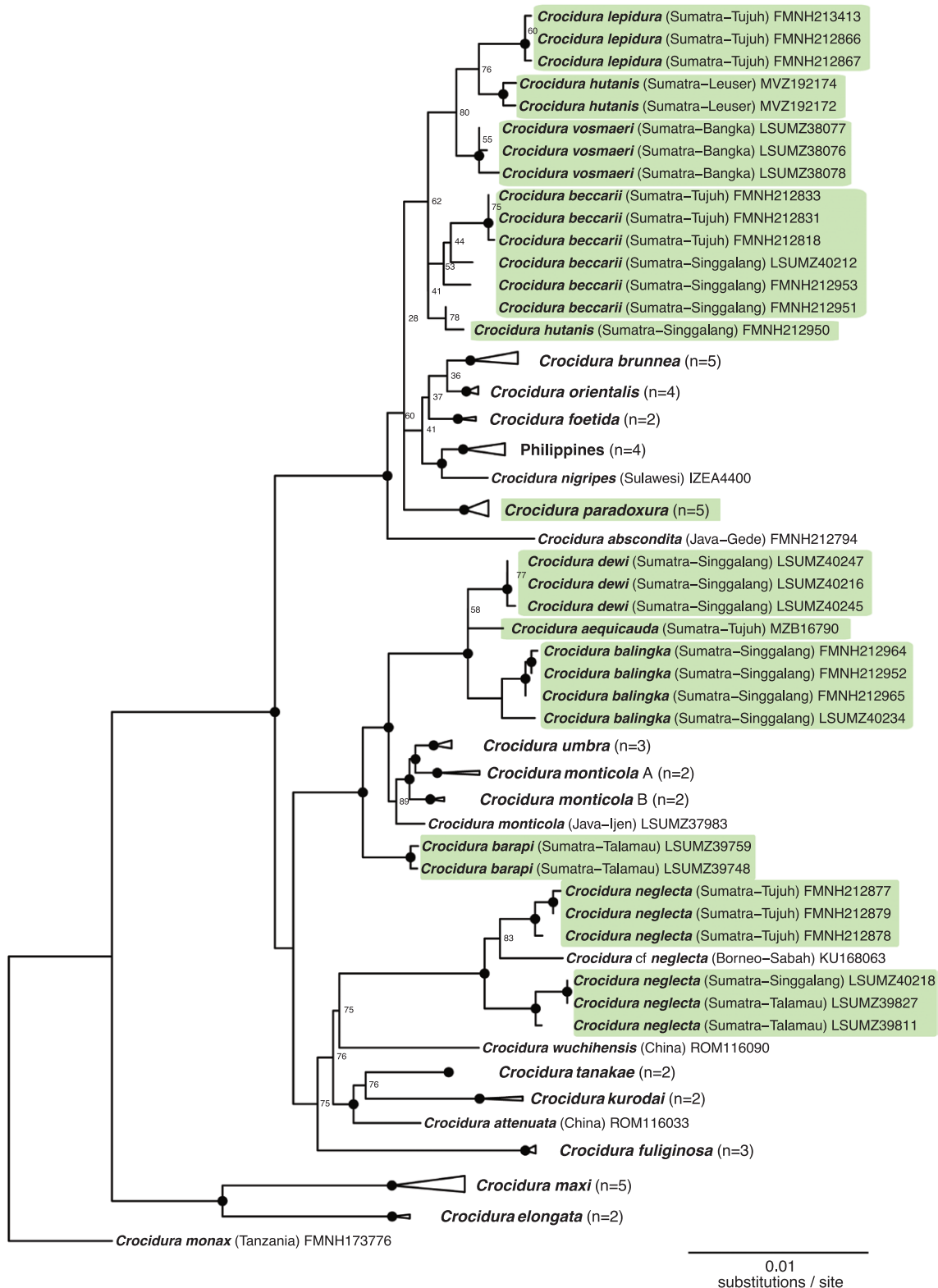
*balingka* are slightly shorter and more sharply curved than those of *C. beccarii*. Consistent with external measurements being smaller, the skull of *C. balingka* is more diminutive than that of *C. beccarii*, as evidenced by smaller condyloincisive length, postpalatal depth, brain breadth, interorbital width, rostral length, and rostral width (Table 2). The foramen magnum is proportionally larger in *C. balingka* than in *C. beccarii*. *Crociodura balingka* also has a similar palatal width but narrower M<sup>2</sup>–M<sup>2</sup> width, indicating less robust dentition than in *C. beccarii* (Table 2; Fig. 3). These cranial differences manifest on the first axis of the linear measurement PCA, and the dorsal- and ventral-landmark PCAs (Fig. 2).

The smallest *Crociodura* found on Sumatra is *C. neglecta*. This species is found on both Sumatra and Borneo, but our comparisons are limited to specimens from Sumatra. Though they overlap in some external and cranial measurements, *C. balingka* has higher average measurement values for all external and cranial characters (Table 2). *Crociodura balingka* also has a distinctly longer tail than *C. neglecta*, both in absolute and relative measures. The palate of *C. balingka* is narrower and longer than of *C. neglecta*, as evidenced by a longer tooththrow, longer P<sup>4</sup>–M<sup>3</sup>, and narrower M<sup>2</sup>–M<sup>2</sup> width relative to skull length (Fig. 3). The feet of *C. balingka* are slightly darker than the pale brown feet of *C. neglecta*. The base of the tail of *C. balingka* is slender, unlike the proximally thick tail base in *C. neglecta* that strongly tapers distally. The ventral portion of the tail is also much darker in *C. balingka* than in *C. neglecta*. The pinnae of *C. balingka* are much darker than the pale pinnae of *C. neglecta*.

### Distribution and ecology

*Crociodura balingka* appears to be a microendemic, montane specialist restricted to elevations above 2,000 m on Mt. Singgalang. During 2 surveys of Mount Singgalang, *C. balingka* was frequently caught in pitfall traps above 2,000 m. A brief survey (only 10 pitfall trap-nights) at 2,826 m near the summit of Mt. Singgalang did not obtain any *C. balingka* specimens, though given this limited effort, we contend that its upper elevational limit remains unclear. Substantial pitfall effort (around 300 pitfall nights total) at 1,700, 1,800, and 1,880 m did not capture any *C. balingka*, suggesting that there is a lower limit to its elevational distribution.

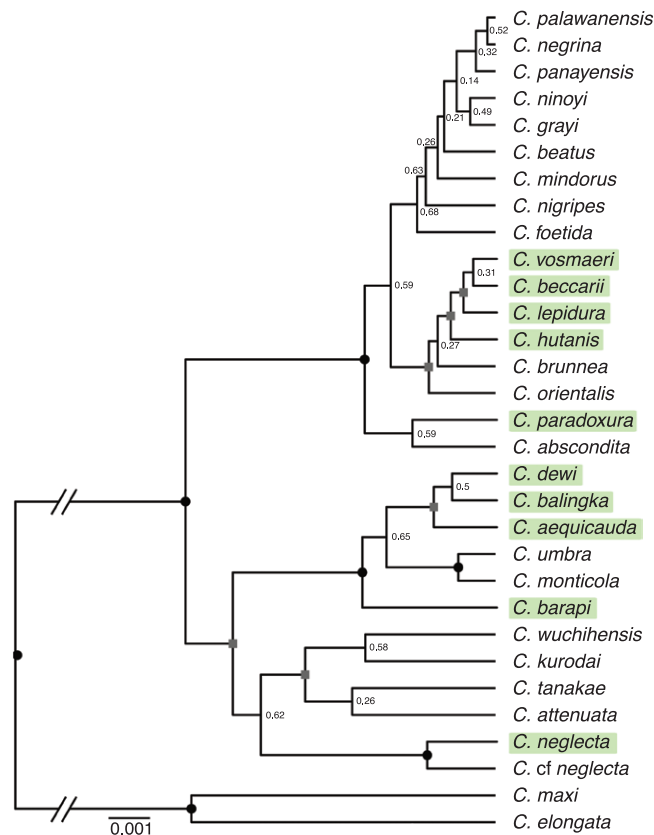




**Fig. 5.** Maximum likelihood phylogeny inferred in IQTree from a concatenated alignment of 6 nuclear genes detailing the phylogenetic placement of *Crocidura balingka* sp. nov., *C. dewi* sp. nov., and *C. barapi* sp. nov. Black circles at nodes indicate a UFBoot2 bootstrap value of >0.95. Sumatran species are highlighted. Nodes of non-Sumatran taxa are collapsed. The figure without the collapsed nodes is available in [Supplementary Data SD7](#).

Anthropogenic forest disturbance extends to roughly 1,600 m on Mt. Singgalang, which may affect the distribution of *C. balingka*; however, our pitfall lines at 1,800 and 1,880 m were in forest with minimal human impact, and captured several other *Crocidura*,

further suggesting a restricted, montane distribution for this species. *Crocidura beccarii*, *C. paradoxura*, and the *Crocidura* from Singgalang described below were captured in the same pitfall lines as *C. balingka*, suggesting syntopy among at least these 4



**Fig. 6.** Species tree estimated using StarBEAST detailing the phylogenetic placement of *Crocidura balingka* sp. nov., *C. dewi* sp. nov., and *C. barapi* sp. nov. Black circles at nodes indicate a posterior probability (pp) > 0.9, and gray squares indicate a pp < 0.9 and > 0.7. Nodes with a pp < 0.7 have values shown. Sumatran species are highlighted. Outgroup branches are truncated. The scale bar is in coalescent units.

species. *Crocidura balingka* was not detected in similar habitats at similar elevations on recent surveys of Mt. Tujuh (185 km SE of Mt. Singgalang) or Mt. Talamau (65 km NW of Singgalang).

*Crocidura dewi*, new species  
Dewi Shrew

### Holotype

LSUMZ 40245, an adult female, collected 4 December 2018 by Jonathan Nations and prepared as a cleaned skull and skeleton, study skin, frozen liver and lung tissue samples, and a gastrointestinal tract preserved in ethanol. External measurements: total length = 163 mm, tail length = 73 mm, hind-foot length = 17 mm, ear length = 12 mm, and mass = 10.7 g. The voucher specimen and a tissue sample will be permanently curated at MZB with the catalog number MZB 43652, with additional tissues retained at LSUMZ.

### Type locality

Indonesia, Sumatera Barat, Agam, Kecamatan IV Koto, Kenagarian Balingka, Jorong Pahambatan, Mt. Singgalang, Talago Dewi crater lake; 0.39489°S, 100.33360°E, 2,826 m elevation.

### Paratypes

LSUMZ 40216, 40217, 40246, 40247, 40248.

### Etymology

Noun of the Indonesian word for “goddess.” Named for the picturesque crater lagoon Talago Dewi, near the summit of Mt. Singgalang where 4 of the 6 specimens were captured. We recommend the English common name “Dewi Shrew.”

### Diagnosis

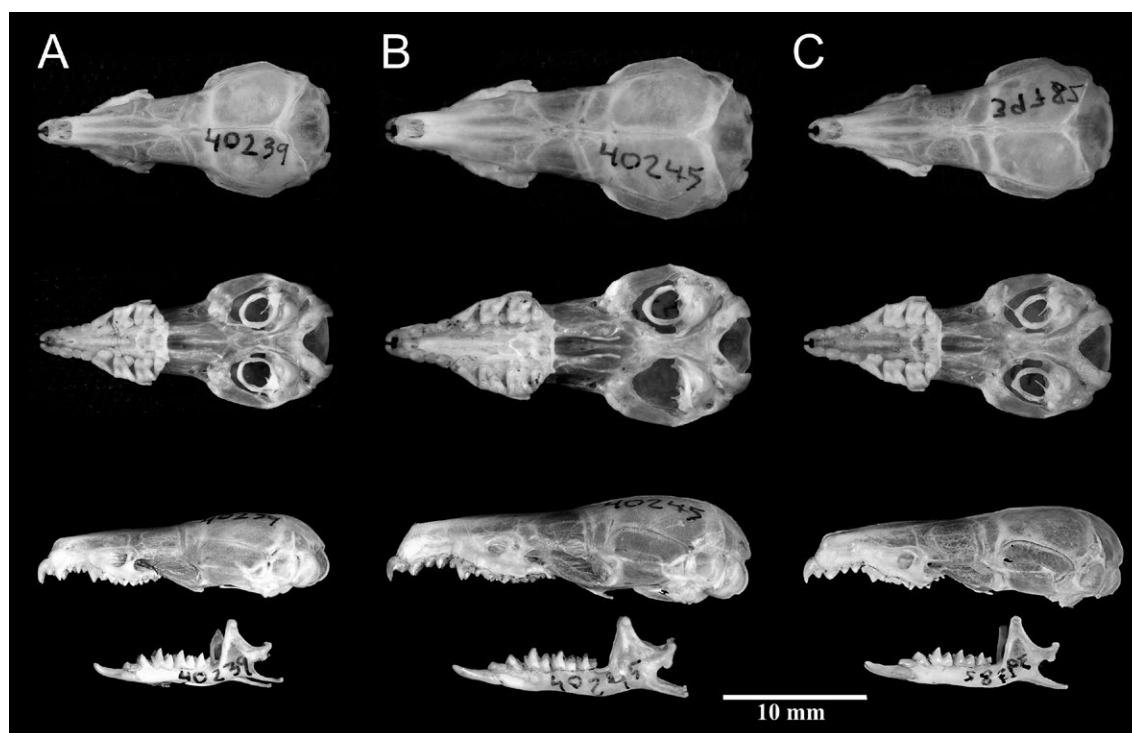
*Crocidura dewi* is a medium-sized shrew (8.2 to 10.7 g), gray-brown in color, with thick, wooly fur that is 7 mm long at mid-dorsum (Supplementary Data SD9). Individual hairs are dark gray at the base, paler and browner at the distal tips, and overall, the pelage is iridescent. The dorsal pelage is only slightly darker than the ventral pelage, and there is no clear demarcation between the two. The tail is relatively long, roughly 85% of the head-body length, with very short applied hairs that are uniform in color dorsoventrally. The tail is lightly bristled with 4-mm hairs on the proximal 1/3 of the tail. The dorsal portion of the hind feet are chocolate brown proximally, and paler distally, with distinct 1 to 2 mm pale gray hair tufts on the tips of digits II and III. The claws are deeply curved. The braincase is tall and compressed anteroposteriorly, with a short condyle-glenoid and postpalatal length relative to skull length (Fig. 3), giving the braincase a circular shape from the dorsal view. A lambdoidal crest is present. The rostrum has a strong taper that wanes anterior to the I<sup>3</sup>, resulting in a narrow, straight rostrum with edges parallel to the skull midline (Fig. 7). Dentition is small for a shrew of this size, evidenced by a wide palate but a narrow M<sup>2</sup>–M<sup>2</sup> distance relative to skull length (Fig. 3).

### Description

Gray-brown in color, with thick and wooly fur that measures 7 mm at mid-dorsum (Supplementary Data SD9). The pelage is dark gray at the base, becoming lighter and browner at the distal tips, the opposite pattern of other Sumatran *Crocidura*. The fur has a shiny, iridescent quality. The ventral pelage is very slightly paler than the dorsal pelage. Pinnae hairs are short, brown, and lighter at the tip. The rhinarium is brown and the lips are unpigmented. Mystacial vibrissae are long, up to 19 mm. The mental vibrissae are short and sparse. Dorsal portions of the hind feet are chocolate brown, transitioning to paler brown near the digits. There are distinct tufts of pale brown and gray hairs at the tips of the hind digits, especially on digits II and III. The forefeet are similar in color and pilosity to the hind feet. The thenar and hypothenar pads of the fore and hind feet are dark brown, and the digital pads are medium brown. The claws on the fore and hind feet are well-developed and deeply curved. The tail is medium length to long (Table 2), with sparse, short 4-mm bristles on the proximal third of the tail. Applied hairs on the tail are uniformly brown and short, giving the tail a hairless impression. The skull is medium in size. The interorbital constriction is wide for a Sumatran *Crocidura* of this size (Fig. 3). The posterior edge of the occipital bone curves gently outward then inward at the midline, then outward again over the foramen magnum. The lambdoid crest is present but not well-developed. The braincase is short anteroposteriorly, with a width just below average for a skull of this size, resulting in a rounded braincase (Figs. 3 and 7). The widest portion of the zygomatic process of the maxilla is posteriorly angled, giving the impression that the zygomatic process is pointing toward the posterior of the skull rather than laterally. This point extends to the posterior edge of M<sup>2</sup>. Anterior to the infraorbital foramen, the angle of the rostrum moves sharply toward the midline of the skull, and the rostrum becomes very narrow anteriorly. I<sup>1</sup> is falciform and rounded and extends beyond the premaxilla. I<sup>2</sup>

**Table 2.** Cranial and external measurements from 8 species of Sumatran *Crocidura*. All measurements are in millimeters except Mass (g). Columns represent species, with the number of specimens sampled in parentheses. Cells report mean value  $\pm$  standard deviation, with the range of measurements in parentheses. Total = total length; HB = head and body length; Tail = tail length; HF = hind-foot length with claw; Mass = body mass; CIL = condyloincisive length; BBC = breadth of braincase; IOW = interorbital width; RL = rostral length; RW = rostral width; PPD = postpalatal depth; PPL = postpalatal length; CGF = distance from occipital condyle to glenoid fossa; UTL = upper toothrow length; P<sup>4</sup>-M<sup>3</sup> = distance from alveolar P<sup>4</sup> to M<sup>3</sup>; M<sup>2</sup>-M<sup>2</sup> = labial width at M<sup>2</sup>. For *C. aequicauda* specimens, cells with single values from MZB 16790, and empty cells are missing measurements.

Measurement	<i>C. aequicauda</i> (n = 2)	<i>C. balingka</i> (n = 13)	<i>C. barapi</i> (n = 9)	<i>C. beccarii</i> (n = 9)	<i>C. dewi</i> (n = 4)	<i>C. hutani</i> (n = 9)	<i>C. lepidura</i> (n = 14)	<i>C. neglect</i> (n = 17)	<i>C. paradoxura</i> (n = 16)
Total	154 $\pm$ 4.24 (151 to 157)	111.23 $\pm$ 5.21 (102 to 122)	115.22 $\pm$ 3.99 (110 to 121)	124.88 $\pm$ 5.77 (114 to 132)	155.25 $\pm$ 5.8 (149 to 163)	134.44 $\pm$ 7.6 (121 to 148)	166.57 $\pm$ 11.12 (147 to 192)	100.82 $\pm$ 5.23 (93 to 112)	183.94 $\pm$ 6.69 (171 to 193)
HB	73.5 $\pm$ 4.5 (70 to 77)	61 $\pm$ 4.51 (53 to 69)	62.22 $\pm$ 2.82 (59 to 66)	73.35 $\pm$ 4.17 (65 to 80)	84.75 $\pm$ 3.59 (82 to 90)	80 $\pm$ 6.46 (70 to 91)	95.79 $\pm$ 9.21 (80 to 117)	61.88 $\pm$ 3.53 (56 to 70)	77.19 $\pm$ 5.72 (65 to 85)
Tail	80.5 $\pm$ 0.71 (80 to 81)	50.23 $\pm$ 1.83 (48 to 53)	53 $\pm$ 1.73 (51 to 55)	51.53 $\pm$ 2.74 (46 to 55)	70.5 $\pm$ 2.52 (67 to 73)	54.44 $\pm$ 2.51 (51 to 58)	70.79 $\pm$ 4.08 (63 to 76)	38.94 $\pm$ 3.38 (33 to 44)	106.75 $\pm$ 4.23 (99 to 116)
HF	15.5 $\pm$ 0 (15.5)	11.46 $\pm$ 0.78 (10 to 13)	12.67 $\pm$ 0.5 (12 to 13)	13.12 $\pm$ 0.49 (12 to 14)	16.75 $\pm$ 0.5 (16 to 17)	14 $\pm$ 0.87 (13 to 16)	18.14 $\pm$ 1.41 (15 to 20)	10.88 $\pm$ 1.11 (7 to 12)	17 $\pm$ 0.89 (15 to 18)
Mass		5.22 $\pm$ 0.58 (4.1 to 6.5)	6.23 $\pm$ 0.54 (5.4 to 7)	7.1 $\pm$ 1.31 (5.2 to 10.2)	10.05 $\pm$ 1.23 (8.2 to 10.7)	9.3 $\pm$ 1.66 (7.6 to 11.4)	19.16 $\pm$ 3.99 (13.4 to 27.5)	4.48 $\pm$ 0.72 (3.5 to 6.2)	8.55 $\pm$ 1.08 (6.2 to 10)
CIL	21.7	17.33 $\pm$ 0.32 (16.92 to 17.96)	18.39 $\pm$ 0.46 (17.8 to 19.39)	19.86 $\pm$ 0.52 (18.93 to 20.67)	21.48 $\pm$ 0.26 (21.22 to 21.83)	20.74 $\pm$ 0.67 (20.05 to 21.82)	24.96 $\pm$ 0.82 (23.2 to 26.29)	16.54 $\pm$ 0.42 (15.7 to 17.09)	20.99 $\pm$ 0.44 (20.22 to 21.65)
BBC	9.4	7.92 $\pm$ 0.17 (7.65 to 8.27)	8.48 $\pm$ 0.23 (8.06 to 8.78)	9.02 $\pm$ 0.23 (8.54 to 9.37)	9.38 $\pm$ 0.27 (9 to 9.61)	9.29 $\pm$ 0.4 (8.81 to 10.08)	10.72 $\pm$ 0.37 (10.04 to 11.41)	7.73 $\pm$ 0.22 (7.31 to 8.06)	8.9 $\pm$ 0.35 (7.79 to 9.22)
IOW	4.7	3.8 $\pm$ 0.08 (3.67 to 4.01)	4.21 $\pm$ 0.13 (4.02 to 4.46)	4.28 $\pm$ 0.15 (3.98 to 4.59)	4.78 $\pm$ 0.08 (4.67 to 4.83)	4.37 $\pm$ 0.16 (4.14 to 4.61)	5.3 $\pm$ 0.34 (4.79 to 6.05)	3.84 $\pm$ 0.22 (3.62 to 4.51)	4.65 $\pm$ 0.23 (4.34 to 5.28)
RL		6.75 $\pm$ 0.17 (6.45 to 7.04)	7.47 $\pm$ 0.27 (7.24 to 8.13)	7.99 $\pm$ 0.31 (7.5 to 8.71)	8.84 $\pm$ 0.25 (8.52 to 9.13)	8.49 $\pm$ 0.45 (7.99 to 9.24)	10.45 $\pm$ 0.57 (9.18 to 11.27)	6.47 $\pm$ 0.22 (5.9 to 6.74)	8.31 $\pm$ 0.22 (7.9 to 8.72)
RW	2.3	1.78 $\pm$ 0.09 (1.62 to 1.92)	1.81 $\pm$ 0.14 (1.7 to 2.16)	2.32 $\pm$ 0.22 (1.99 to 2.72)	2.12 $\pm$ 0.05 (2.05 to 2.17)	2.39 $\pm$ 0.14 (2.18 to 2.58)	2.9 $\pm$ 0.5 (2.39 to 3.63)	1.94 $\pm$ 0.11 (1.76 to 2.16)	2.28 $\pm$ 0.19 (2.05 to 2.77)
PPD	3.9	3.17 $\pm$ 0.13 (2.95 to 3.36)	3.33 $\pm$ 0.18 (3.16 to 3.73)	3.66 $\pm$ 0.11 (3.49 to 3.82)	4.04 $\pm$ 0.19 (3.8 to 4.24)	3.84 $\pm$ 0.19 (3.49 to 4.04)	4.47 $\pm$ 0.16 (4.18 to 4.7)	3.22 $\pm$ 0.11 (3.06 to 3.39)	3.95 $\pm$ 0.17 (3.66 to 4.23)
PPL	11.8	8.07 $\pm$ 0.21 (7.67 to 8.4)	8.45 $\pm$ 0.43 (7.97 to 9.46)	8.93 $\pm$ 0.34 (8.24 to 9.55)	9.55 $\pm$ 0.34 (9.23 to 10)	9.44 $\pm$ 0.43 (8.93 to 9.95)	11.1 $\pm$ 0.39 (10.34 to 11.71)	7.78 $\pm$ 0.27 (7.32 to 8.31)	9.65 $\pm$ 0.23 (9.17 to 10.08)
CGF	8.5	6.96 $\pm$ 0.19 (6.71 to 7.33)	7.22 $\pm$ 0.3 (6.8 to 7.77)	7.5 $\pm$ 0.24 (6.97 to 7.78)	7.82 $\pm$ 0.23 (7.52 to 8.06)	7.84 $\pm$ 0.36 (7.43 to 8.35)	9.01 $\pm$ 0.27 (8.5 to 9.47)	6.57 $\pm$ 0.25 (6.16 to 6.93)	8.2 $\pm$ 0.26 (7.75 to 8.69)
UTL	9.35 $\pm$ 0.07 (9.3 to 9.4)	7.47 $\pm$ 0.16 (7.25 to 7.8)	8.15 $\pm$ 0.39 (7.82 to 9.08)	8.84 $\pm$ 0.24 (8.4 to 9.13)	9.68 $\pm$ 0.14 (9.56 to 9.87)	9.28 $\pm$ 0.3 (8.92 to 9.62)	11.23 $\pm$ 0.5 (10.02 to 11.9)	7.03 $\pm$ 0.18 (6.65 to 7.28)	9.15 $\pm$ 0.22 (8.7 to 9.43)
P <sup>4</sup> -M <sup>3</sup>	5.6	4.32 $\pm$ 0.17 (4.04 to 4.61)	4.75 $\pm$ 0.26 (4.49 to 5.18)	5.06 $\pm$ 0.19 (4.54 to 5.27)	5.44 $\pm$ 0.3 (4.99 to 5.64)	5.24 $\pm$ 0.16 (5.05 to 5.53)	6.19 $\pm$ 0.37 (5.39 to 6.68)	3.91 $\pm$ 0.14 (3.62 to 4.12)	5.12 $\pm$ 0.21 (4.62 to 5.38)
M <sup>2</sup> -M <sup>2</sup>	6.15 $\pm$ 0.49 (5.8 to 6.5)	4.75 $\pm$ 0.12 (4.55 to 4.93)	5.16 $\pm$ 0.19 (5 to 5.66)	5.79 $\pm$ 0.18 (5.36 to 6.06)	6.12 $\pm$ 0.1 (6 to 6.23)	6.02 $\pm$ 0.25 (5.59 to 6.39)	7.33 $\pm$ 0.36 (6.48 to 7.93)	4.99 $\pm$ 0.13 (4.77 to 5.21)	5.92 $\pm$ 0.17 (5.54 to 6.14)



**Fig. 7.** Images showing dorsal, and ventral views of the skull and lateral views of the dentary of the holotypes of 3 new shrew species from Sumatra: (A) *Crocidura balingka*, LSUMZ 40239; (B) *Crocidura dewi*, LSUMZ 40245; (C) *Crocidura barapi*, LSUMZ 39782 (image reversed horizontally).

is much larger than  $I^3$ . The upper canine is larger than  $I^3$ .  $M^1$  is slightly larger than  $M^2$ , and  $M^3$  is smaller in comparison to the other upper molars but large and well-developed for a Southeast Asian *Crocidura* (Fig. 7). The mandible is gracile for a shrew of this body size. The coronoid process is short and strongly tapers dorsally. The angular processes are long and thin.  $i^1$  is dorsoventrally compressed.

### Comparisons

Overall body size distinguishes *C. dewi* from the smaller Sumatran *Crocidura* (*C. balingka*, *C. beccarii*, and *C. neglecta*; Table 2) and shorter tail length, browner pelage, and darker feet easily distinguish *C. dewi* from *C. paradoxura* (Table 2; Supplementary Data SD9). Detailed comparisons of *C. dewi* are focused on the larger Sumatran species, *C. hutanis* and *C. lepidura*.

*Crocidura dewi* has a similar head-body length and tail length as *C. lepidura*; however, *C. lepidura* has a greater mass (Table 2) and is a much darker chocolate brown in color with shorter, 5 mm dorsal pelage. The feet of *C. dewi* are paler than those of *C. lepidura*, and also have more hair and pale-colored tufts at the distal end of the rear digits II and III that are absent in *C. lepidura*. The claws of *C. dewi* are distinctly more curved than those of *C. lepidura*, which has only weakly curved claws that extend outward from the digits. *Crocidura dewi* is smaller in nearly every cranial measurement than *C. lepidura* (Table 2). The  $i^1$  of *C. dewi* is narrow and gracile while the  $i^1$  of *C. lepidura* is robust.

*Crocidura dewi* can be distinguished from *C. hutanis* by its lighter gray-brown coloration, longer dorsal pelage (7 mm vs. 4 mm in *C. hutanis*), and much longer tail, both absolute and relative values. The hind foot of *C. dewi* is longer on average than the hind foot of *C. hutanis*. The claws of *C. dewi* are much more curved than the lightly curved claws of *C. hutanis*. The overall appearance of the

cranium of *C. dewi* is less robust than the cranium of *C. hutanis*, with smaller dentition, a weak lambdoidal crest, and a dorsoventrally narrower rostrum. *Crocidura dewi* has a much wider palate but narrower  $M^2$ – $M^2$  width than *C. hutanis*, relative to skull length (Fig. 3), indicating smaller cheek teeth. The dentaries of *C. dewi* are less robust than *C. hutanis*.

### Distribution and ecology

As with the sister taxon *C. balingka*, *C. dewi* appears to be a microendemic, montane specialist, most abundant at high elevations on Mt. Singgalang. *Crocidura dewi* was captured at 1,880 m (1 specimen), 2,100 m (1 specimen), and 2,826 m (4 specimens) on Mt. Singgalang. *Crocidura neglecta*, *C. beccarii*, *C. balingka*, *C. hutanis*, and *C. paradoxura* were all caught in pitfall lines with *C. dewi*. The number and elevational distribution of the captures, considered in conjunction with the limited nature of our sampling at 2,826 m (only 10 pitfall nights), suggest that *C. dewi* is less abundant at the lower levels of its elevational range (1,800 to 2,000 m) than at the highest elevations. The long, wooly fur of *C. dewi* is reminiscent of the fur of other shrews and rodents in tropical montane habitats. The apparent lower elevational limit of *C. dewi* (1,880 m) is below that of *C. balingka* and at the upper limit of *C. hutanis* and *C. neglecta* captures on Mt. Singgalang. Claw curvature has been used to describe locomotor or microhabitat affinities in small mammals, with highly curved claws associated with climbing (Tulli et al. 2016). The deeply curved claws of *C. dewi*, vastly different from the long, slightly curved claws of the similarly sized *C. lepidura* and *C. hutanis*, suggest climbing or scrambling behavior rather than burrowing, but currently nothing is known of its habits.

*Crocidura barapi*, new species  
Barapi Shrew



## Holotype

LSUMZ 39782, an adult male, collected 21 April 2018 by Heru Handika and prepared as a cleaned skull and fluid-preserved specimen and frozen liver samples. External measurements: total length = 113 mm, tail length = 51 mm, hind-foot length = 13 mm, ear length = 9 mm, and mass = 6.4 g. The voucher specimen and a tissue sample will be permanently curated at MZB with the catalog number MZB 43653, with a duplicate tissue retained at LSUMZ.

## Type locality

Indonesia, Sumatera Barat, Pasaman Barat, Kecamatan Pasaman, Nagari Aur Kuning, Jorong Lubuak Landua, Mt. Talamau, 0.08660°N, 99.96884°E, 2,004 m elevation.

## Paratypes

LSUMZ 39748, 39752, 39759, 39768, 39772, 39773, 39776, 39777, 39785, 39792.

## Etymology

Noun for “volcano” in the Minangkabau language of West Sumatra, a reference to the Talamau volcano where the discovery took place and an homage to the Minangkabau people of the region who facilitated this research. We recommend the English common name “Barapi Shrew.”

## Diagnosis

*Crociodura barapi* is a small to medium shrew (5.4 to 7 g), dark gray-brown in color, with slightly woolly fur that measures 5 mm at mid-dorsum (Supplementary Data SD9). The pelage is light gray at the base, becoming chocolate brown at the distal tips. The ventral pelage is slightly paler than the dorsal pelage, but it is not discretely bicolored. The tail is relatively long for similar-sized Southeast Asian *Crociodura*, roughly 85% of the head-body length, with very short, sparse applied hairs. The proximal portion of the tail is lightly bristled with 6-mm hairs extending to approximately 1/3 of the total tail length. The skull is small for its body size, and flat in lateral view (postpalatal depth; Table 2; Fig. 3). The braincase is wide and the interorbital region is average for a skull of this size (Fig. 3). There is no lambdoidal crest. The palate is narrow. The rostrum is narrow and long, and strongly tapers toward the anterior portion of the skull; however, the taper wanes anterior to I<sup>3</sup> (Fig. 7). The dentition is weak. Toothrow length and palatal width are average for the skull size, but the M<sup>2</sup>–M<sup>2</sup> width is small, indicating weak molars.

## Description

Dorsal pelage is a dark gray-brown, with hairs being grayer toward the base and darkening to chocolate brown at the tips (Supplementary Data SD9). The dorsal pelage measures 5 mm in length at the mid-dorsum. The ventral pelage is lighter in color, but there is no discrete boundary between the dorsal and ventral pelage. The dorsal portion of the hind feet is uniformly pale brown, with sparse, short, medium-brown hairs, similar in color to the dorsum, covering most of the feet, but with greater density on medial portions. There are no distal tufts of hair on the digits, and the digits are similar in color to the proximal regions of the foot. The soles of the hind feet are pale brown, and the thenar, hypothenar, and interdigital pads are paler than the plantar surface. The forefeet share a similar pale brown color and uniform, sparse pilosity with the hind feet. The claws on the fore and hind feet are long and slightly curved. The pinnae hairs are short, sparse, and uniformly brown. The rhinarium is brown and the

lips are unpigmented. The mystacial vibrissae are 12 to 13 mm in length, with the longest extending 15 mm from the face. The mental vibrissae are short and sparse. Hairs on the dorsal portion of the hind feet are chocolate brown. The tail is relatively long, with sparse 6-mm hairs on the proximal third of the tail. Applied hairs are short, giving the tail a hairless impression, and are dark on the dorsal portion of the tail, gradually becoming a paler gray-brown ventrally. The skull is relatively small and narrow for a shrew of this size, and short dorsoventrally. There is no lambdoidal crest. The braincase is wide, but the postpalatal and condyle–glenoid lengths are average for the skull length, resulting in a somewhat rounded braincase (Figs. 3 and 7). The interorbital constriction is slightly wide for a Sumatran *Crociodura* of this size (Fig. 3). The rostrum is long and very narrow, and tapers sharply toward the distal portion of the maxilla (Fig. 3). The palate is average in width. The dentition is weak for a shrew of this size; incisors and canines are relatively small, and premolars and molars are not robust (Fig. 7). I<sup>1</sup> is falciform and rounded and extends beyond the premaxilla. I<sup>1</sup> is larger than I<sup>2</sup>, and I<sup>2</sup> is larger than I<sup>3</sup>. The upper canine is only slightly larger than I<sup>3</sup>. M<sup>1</sup> is slightly larger than M<sup>2</sup>, and M<sup>3</sup> is small in comparison.

## Comparisons

Overall body size easily distinguished *C. barapi* from the larger Sumatran *Crociodura* (*C. lepidura*, *C. dewi*, and *C. hutani*), and shorter tail length and darker pelage and feet easily distinguishes *C. barapi* from *C. paradoxura*. We will therefore limit the *C. barapi* comparisons to similarly sized Sumatran shrews, *C. beccarii*, *C. balingka*, and *C. neglecta*.

The only similar size shrew to *C. barapi* detected on Mt. Talamau is *C. neglecta*. Though largely overlapping in head-body length, *C. barapi* is a more robust shrew than *C. neglecta* with, on average, a higher mass and hind-foot length, and longer, woollier pelage (5 mm vs. 2.5 mm). *Crociodura barapi* can easily be distinguished from *C. neglecta* by its much longer tail (Table 2). The pinnae, forefeet, and hind feet of *C. barapi* are much darker than *C. neglecta*. The skull of *C. barapi* is also longer and wider than the skull of *C. neglecta* in raw values (Table 2), and the dentition of *C. barapi* is larger with nonoverlapping values of upper toothrow and molar toothrow lengths (Table 2). However, relative to skull length, *C. barapi* has a narrow M<sup>2</sup>–M<sup>2</sup> width while *C. neglecta* has a wide palate, short molar row, and short toothrow (Fig. 3). These differences in cranial morphology result in a separation of *C. barapi* and *C. neglecta* in all measures of cranial morphospace (Fig. 2).

*Crociodura barapi* is generally smaller than the allopatric *C. beccarii* with, on average, smaller head-body length, mass, and hind-foot length values, though *C. barapi* has a longer average tail length than *C. beccarii* (Table 2). The skull of *C. barapi* is more diminutive than *C. beccarii* as evidenced by a smaller condyloincisive length, narrower rostrum, shorter upper toothrow (Table 2), and relatively narrower braincase (Fig. 3). The incisors take up a proportionally smaller portion of the toothrow in *C. barapi* than *C. beccarii* (Fig. 3). The occipital bone of *C. barapi* is relatively flat along the posterior edge of the cranium, while *C. beccarii* has a more rounded posterior edge of the skull. These cranial differences lead to a clear separation of *C. barapi*, *C. beccarii*, and *C. neglecta* on the first 2 components of the linear and geometric PCAs (Fig. 2).

*Crociodura barapi* is larger in most external and cranial measurements than the allopatric *C. balingka*. It has a longer dorsal pelage than *C. balingka*, and the stiff bristles on its tail do not extend as far on the tail in *C. barapi* as in *C. balingka*. The skull of *C. barapi* is on average larger than the skull of *C. balingka* in

all measurements, and interorbital width, rostral length, upper toothrow length, and  $M^2$ – $M^2$  width are nonoverlapping (Table 2). The dentition of *C. barapi* is more robust than the dentition of *C. balingka* (Fig. 7), evidenced by a longer molar length and upper toothrow length relative to skull size (Fig. 3). *C. barapi* has a wider interorbit than *C. balingka* relative to skull size (Fig. 3). The hind feet of *C. barapi* are darker and wider than those of *C. balingka*. Currently *C. barapi* is known from only Mount Talamau; it was not detected on Mount Singgalang where *C. balingka* is abundant.

### Distribution and ecology

*Crociodura barapi* was relatively abundant above 1,662 m on Mount Talamau. As of now, this species has only been detected on this mountain. Pitfall traps were not placed above 2,004 m on Mount Talamau. Given the overall montane distribution of *C. barapi*, we suspect that it occurs above the 2,000 m sampling limit we achieved on this nearly 3,000 m volcano. *Crociodura barapi* and *C. neglecta* appear to be parapatrically distributed along the elevational gradient. In our survey, *C. neglecta* was detected from 1,050 to 1,662 m, while *C. barapi* was found from 1,600 to 2,004 m, or the upper limits of our pitfall efforts. *Crociodura barapi* was found on the same pitfall lines as *C. paradoxura* and *C. lepidura*, and found to overlap with *C. hutanis* and *C. neglecta* only at the lower elevations of its known range (~1,650 to 1,700 m). Surveys on Mount Singgalang, 65 km southeast of Talamau, did not detect *C. barapi*.

### Long-tailed shrew from Mt. Tujuh

In 1991, a single shrew with a relatively long tail was collected at 2,200 m on the slopes of Mt. Tujuh in Jambi Province (Fig. 1), assigned to the species *C. paradoxura*, and cataloged as MZB 16790/IZEA 4503 (Supplementary Data SD9). In a subsequent revision of Malay Archipelago *Crociodura*, MZB 16790 was compared to the type of *C. aequicauda*, collected on nearby Mt. Kerinci (Fig. 1; Robinson and Kloss 1918; Ruedi 1995). Based on the tail length relative to head–body length, 104% in the *C. aequicauda* type, 116% in MZB 16790, and 159% in the *C. paradoxura* type (Dobson 1886), along with the relatively pale feet and gray-brown fur color, Ruedi (1995) referred these 2 specimens to *C. paradoxura*. The taxon *C. aequicauda* has therefore been considered to be a junior synonym of *C. paradoxura* (Ruedi 1995). However, Ruedi (1995) did not examine the holotype of *C. paradoxura* when making this decision and there were few, if any, additional *C. paradoxura* specimens available at the time of his revision.

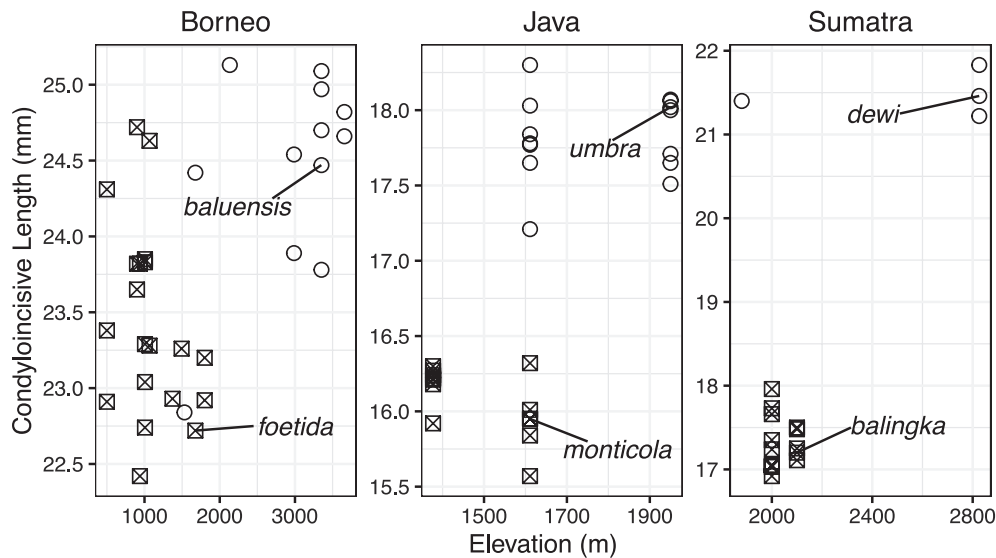
Recent molecular phylogenetics work, leveraging both mitochondrial and nuclear DNA sequences, revealed that the Mt. Tujuh specimen MZB 16790 is not nested within *C. paradoxura*. Instead, this specimen, referred to as “*Crociodura cf. paradoxura* MZB16790,” “*Crociodura* sp 1 aH 2020,” and “*Crociodura* sp 1” (see Supplementary Data SD1: Fig. S1, Supplementary Data SD2: Fig. S2, and Table S1 in Hinckley et al. 2022), is sister to *C. balingka* (“*Crociodura* sp. 2 TCD 2016” in Hinckley et al. 2022: Fig. S1). Our phylogenetic analyses suggest that MZB 16790 is sister to the clade that contains *C. balingka* and *C. dewi* (Figs. 4 and 6) or nested within the clade (Fig. 5). Since 1995, numerous *C. paradoxura* specimens, including topotypes, have been collected and archived, and our examination of MZB 16790 reveals that it is not representative of the distinctive *C. paradoxura* (Supplementary Data SD9). The morphological (Figs. 2 and 3; Supplementary Data SD9) and genetic differences ( $\geq 0.08$  Jukes–Cantor Cytb distance from other Sumatran shrews; Table 1) between MZB 16790 and the 3 newly described taxa warrant its recognition as a species, supporting the conclusions of Hinckley et al. (2022). Previous morphological analyses determined that MZB 16790 and the *C. aequicauda* type represent the same species

(Ruedi 1995), a conclusion supported by the proximity of their collecting localities (Fig. 1). Therefore, we recognize *C. aequicauda* as a species. *Crociodura aequicauda* is currently represented by 2 specimens: the type (Federated Malay States Museum 448/14, also cataloged as British Museum of Natural History 19.11.5.28) and MZB 16790. Based on our examination of MZB 16790, *C. aequicauda* is a medium-sized shrew that can be distinguished from other Sumatran shrews using fur color and body proportions. The long (7 to 8 mm) slate-gray fur is lighter than all Sumatran shrews other than *C. paradoxura* (Supplementary Data SD9). It is larger in head–body length than *C. neglecta*, *C. balingka*, and *C. barapi*, and smaller in head–body length than *C. dewi* and *C. lepidura* (Table 2). The tail of *C. aequicauda* is perhaps the most distinguishing feature, as it is longer in both absolute (Table 2) and relative length (110% of head–body length) than all other Sumatran shrews apart from *C. paradoxura*, which has a much longer tail, often with a white tip (Supplementary Data SD9).

### Discussion

Recent collecting efforts and subsequent morphological and molecular analyses are revealing the degree to which small-mammal diversity in Southeast Asia has been underestimated. Here we present morphological and molecular evidence of the presence of 3 new species of *Crociodura* on Sumatra. These discoveries bring the total number of Sumatran *Crociodura* to 9, including the Bangka Island endemic, *C. vosmaeri*. Apart from *C. neglecta*, all Sumatran shrew species are endemic to the island, though molecular evidence suggests that there is substantial inter-island evolutionary divergence within *C. neglecta* (Demos et al. 2016a; Hinckley et al. 2022; this study). Results from surveys of 3 mountains in West Sumatra suggest that each of these new taxa has a very limited distribution and may be endemic to a single mountain. The 2 new species from Mt. Singgalang, *C. dewi* and *C. balingka*, were not detected on Mt. Talamau despite similar elevational sampling, which lies only 65 km to the northwest (Fig. 1). Similarly, *C. barapi* was only detected on Mt. Talamau. None of these 3 species were detected on Mt. Tujuh, 190 km southeast of Mt. Singgalang and 250 km southeast of Mt. Talamau (Fig. 1). Similar patterns of localized, montane endemism have been noted in other Sumatran mammals (e.g. squirrels; Hinckley et al. 2020) and in *Crociodura* on the neighboring islands of Borneo (Hinckley et al. 2022), Java (Esselstyn et al. 2013; Demos et al. 2016a), and Sulawesi (Esselstyn et al. 2021).

The newly described *C. balingka* and *C. dewi* are recovered as recently diverged, reciprocally monophyletic sister taxa in the mitochondrial gene tree (Fig. 4), the coalescent-based species tree (Fig. 6), and in 5 of the 6 individual exon gene trees (Supplementary Data SD8). Additionally, they strongly differ in every quantitative and qualitative morphological metric used in this study. This pattern is not unique to this species pair, but rather represents the first Sumatran example of a phenomenon known from other Malay Archipelago *Crociodura* (Fig. 8). On Mt. Gede in Java, *C. monticola*, a smaller shrew that is widespread across Java, is abundant at mid-elevations while its larger-bodied closest relative, *C. umbra*, is more abundant at higher elevations (Fig. 8). On Mt. Kinabalu and neighboring Mt. Tambuyukon in Borneo, as elevation increases, *C. foetida sensu lato* (Hinckley et al. 2022) gradually decreases in abundance, and its larger-bodied sister taxon *C. baluensis* (Fig. 8) increases in abundance (Hinckley et al. 2022). Each of the 3 larger, high-elevation shrews are thought to be endemic to a single massif. Notably, phenotypic and genetic differences between *C. dewi* and *C. balingka* are much greater than



**Fig. 8.** Three examples of a low to mid-elevation, medium-sized shrew overlapping with a higher elevation, larger-bodied sister taxon. Elevation is on the x-axis, and condylolincisive length is on the y-axis. On Mt. Kinabalu in Borneo, *Crocidura foetida* sensu lato is present at lower elevations and *Crocidura baluensis* is found at higher elevations. On Mt. Gede in Java, *C. monticola* is found at lower elevations and *C. umbra* is found at higher elevations. In Sumatra, we hypothesize the same pattern between *C. balingka* (lower elevation) and *C. dewi* (higher elevation), despite the elevational overlap. Elevation and condylolincisive lengths for *C. foetida* sensu lato and *C. baluensis* were taken from the supporting information of [Hinckley et al. \(2022\)](#).

differences between the other sister pairs ([Tables 1 and 2](#); [Fig. 8](#); [Demos et al. 2016b](#); [Hinckley et al. 2022](#)), and the elevational overlap between these 2 species may be greater than in the other examples, though sampling is limited. The causal mechanisms leading to this pattern of elevational, morphological, and molecular divergences are unknown. [Demos et al. \(2016a, 2016b\)](#) considered ecological speciation along an elevational gradient followed by subsequent niche separation as a possible mechanism for the distribution of *C. monticola* and *C. umbra* on Mt. Gede—however, testing this hypothesis or alternatives such as vicariance via high-elevation refugia during the Pleistocene requires a better understanding of the historical biogeography, demography, and ecology of these Sunda shrews.

Though it is the sixth largest island in the world and has a human population near 60 million, Sumatran small mammals and Sumatran vertebrates in general ([Arifin et al. 2022](#)) are underrepresented in museum collections and, as a result, understudied. The last taxonomic revision of Sumatran *Crocidura*, using all available material, was based on 42 specimens, 30 of which the author collected a few years prior to the publication ([Ruedi 1995](#)). Since this time, 4 surveys of 3 mountains in West Sumatra have uncovered 3 new species of *Crocidura*, suggesting that the shrew diversity of Sumatra may be much greater than previously thought. Recent Sumatran phylogeographic studies suggest that reptile, amphibian, and teleost populations are structured along a north-south gradient, following the Barisan mountains, and that northern, central, and southern portions of the mountain chain house their own endemic species ([Lumbangtobing 2010](#); [Harvey et al. 2017](#); [Sarker et al. 2019](#); [Shaney et al. 2020a](#); [Arifin et al. 2022](#)). The northernmost region of the island is especially rugged and mountainous, a geography that often houses high levels of biodiversity and endemism ([Lumbangtobing 2010](#); [Harvey et al. 2017](#); [Sarker et al. 2019](#); [Shaney et al. 2020b](#)), yet lacks comprehensive small mammal surveys. Equally, many isolated mountains in the south of the island remain unsurveyed

for small mammals. Recent work on lizards in the subfamily Draconinae suggests a pattern of 4 biogeographic regions across Sumatra ([Shaney et al. 2020b](#))—however, within these biogeographic regions, individual mountains house, or are anticipated to house, their own endemic species ([Shaney et al. 2020a](#)). Though only separated by a total of 250 km, we found that just 2 of the 8 described Sumatran *Crocidura* species—*C. neglecta* and *C. paradoxura*—were found in all 3 montane sites discussed here, and all 3 of the newly described species appear to be endemic to 1 mountain, supporting the pattern suggested by [Shaney et al. \(2020a\)](#). Additionally, the *C. paradoxura* samples from Singgalang and Tujuh form distinct clades ([Supplementary Data SD6](#)) and have a 4% *Cytb* divergence ([Table 1](#)), suggesting little maternal gene flow between these 2 mountain populations. While limited in geographic scale, our results support the hypothesis of substantial endemism along a north-south gradient in Sumatra. This finding points to the need of revisiting other taxonomic issues, such as the status of *C. weberi*, known from 1 specimen from Lake Singkarak in West Sumatra ([Jentink 1890](#)), as a junior synonym of *C. beccarii* ([Ruedi 1995](#)). Much of the lowland forests, often up to 1,500 m, has and continues to undergo extreme anthropogenic modification from logging and conversion to oil palm plantations. Additional field surveys and collection of vouchered specimens are urgently needed to fully document the mammal diversity on this large, tropical island.

## Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**— .csv table containing all the specimens, museums, catalog numbers, external measurements (in mm, except mass in g), linear cranial measurements (in mm), linear principal components scores, dorsal geometric morphometric principal components scores, and ventral geometric morphometric principal components scores.



**Supplementary Data SD2.**—Figure containing the 16 dorsal and 23 ventral 2D geometric morphometric landmarks.

**Supplementary Data SD3.**—csv table containing the GenBank accession numbers for each sequence used in the molecular analyses; 1 mitochondrial gene and 6 nuclear exons.

**Supplementary Data SD4.**—Alignment of mitochondrial Cytb sequence data used in IQTree analysis, in nexus format.

**Supplementary Data SD5.**—Alignment of concatenated nuclear DNA sequence data used in concatenated IQTree analysis, in nexus format. Concatenated genes are APO, BDNF, BRCA, GHR, PTGER, and vWF. Partitions are listed in the “sets” block at the end of the nexus file.

**Supplementary Data SD6.**—Figure of Cytb phylogenetic tree generated in IQTree. The same tree is presented in Fig. 4 but without the collapsed nodes. Node labels represent UFBoot2 values.

**Supplementary Data SD7.**—Figure of concatenated nDNA phylogenetic tree generated in IQTree. The same tree is presented in Fig. 5 but without the collapsed nodes. Node labels represent UFBoot2 values.

**Supplementary Data SD8.**—Figure of APO, BDNF, BRCA, GHR, PTGER, and vWF phylogenetic trees generated in the StarBEAST species-tree analysis. Node labels represent posterior probabilities.

**Supplementary Data SD9.**—Figure of the dorsal photograph of representatives of the newly described Sumatran taxa, *Crociodura aequicauda*, and *C. paradoxura*. (A) *C. balingka* LSUMZ 40239, (B) *C. barapi* LSUMZ 39748, (C) *C. dewi* LSUMZ 40248, (D) *C. aequicauda* MZB 16790, (E) *C. paradoxura* MZB 41100.

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## Author contributions

JAN and JAE conceived the study. ASA, Apandi, AM, HH, and RDB organized fieldwork and collection permits. JAN and JAE collected skull measurements from museum specimens. HH took photographs. JAN performed analyses and wrote the first draft. All authors contributed to fieldwork, specimen collection, data acquisition, and edited and approved the final version of the manuscript.

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## Conflict of interest

None declared.

## Data availability

All data and code used in this study are available in a GitHub repository available at [https://github.com/jonnations/Sumatra\\_Shrew\\_1](https://github.com/jonnations/Sumatra_Shrew_1), and are archived on Zenodo as DOI: [10.5281/zenodo.7916697](https://doi.org/10.5281/zenodo.7916697).

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## Appendix I

### Specimens examined

*Crocidura aequicauda*: **Mt. Tujuh**: MZB 16970.

*Crocidura balingka*: **Mt. Singgalang**: FMNH 212964, 212965, 212967, 212971 to 212974, 212976, LSUMZ 40214, 40234 to 40242.

*Crocidura barapi*: **Mt. Talamau**: LSUMZ 39748, 39752, 39759, 39768, 39772, 39773, 39776, 39777, 39782, 39785, 39792.

*Crocidura beccarii*: **Mt. Singgalang**: FMNH 212953, LSUMZ 40203, 40207, 40208, 40211 to 40213, 40215, 40243, 40244; **Mt. Talamau**:

LSUMZ 39749; **Mt. Tujuh**: FMNH 212819, 212821, 212823, 212828, 212830, 212831, 212841, 212843, 212850, 212851, 212887, 213411, 213412, RMNH 38350, 38351.

*Crocidura dewi*: **Mt. Singgalang**: LSUMZ 40216, 40217, 40245 to 40248.

*Crocidura hutani*: **Mt. Leuser**: RMNH 38410; **Mt. Singgalang**: FMNH 212950, LSUMZ 40204 to 40206, 40209, 40210, 39786 to 39791, 39794, 39795.

*Crocidura lepidura*: **Kateman River, East Sumatra**: USNM 123140; **Sindingin**: LSUMZ 39332; **Mt. Talamau**: LSUMZ 39796 to 39798, 39800, 39842, 39843, 39845; **Mt. Tujuh**: FMNH 212856, 212861, 212866, 212868, 212873 to 212875, 213413, 213414.

*Crocidura neglecta*: **Bukit Lawang**: MVZ 192177, 192178; **Mt. Singgalang**: 40218 to 40222; **Mt. Talamau**: LSUMZ 39801, 39804 to 39828, 39802, 39803; **Mt. Tujuh**: FMNH 212877, 212878.

*Crocidura paradoxura*: **Mt. Singgalang**: FMNH 212954 to 212956, 212959, 212960, LSUMZ 40223 to 40233; **Mt. Talamau**: LSUMZ 39830, 39833, 39835, 39836, 39840; **Mt. Tujuh**: FMNH 212882, 212884, 213415.