



A new genus and species of shrew (Mammalia: Soricidae) from Palawan Island, Philippines

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A 2007 survey of small mammals on Mt. Mantalingahan (2,086 m elevation), southern Palawan Island, Philippines, obtained specimens of a distinctive, previously unknown shrew (Soricidae). We describe these specimens as representing a new, monotypic genus and species, *Palawanosorex muscorum*. The new species was common on Mt. Mantalingahan from 1,550 to 1,950 m (near the peak) but was not detected from 700 to 1,300 m elevation. The previously known native, syntopic shrew, *Crocidura palawanensis*, has a slender body, slender fore and hind feet, and a long, thin tail with a few long bristles. In contrast, the new species has a stout body, broad fore feet, long claws, and a short tail covered by short, dense fur but no bristles. The dental formula traditionally used would result in assignment of the new species to *Suncus*, but several distinctive external and cranial features are present, and phylogenetic analyses of thousands of ultraconserved elements suggest *P. muscorum* is sister to most other Crocidurinae, a clade represented throughout Southeast Asia but numerically dominated by African species. The new species is a distant relative of *Suncus murinus* (the type species of *Suncus*) and all other known Southeast Asian species, including the only other shrew known to occur on Palawan (*Crocidura batakorum*). A time-calibrated phylogenetic analysis estimates divergence between *Palawanosorex* and its closest known relatives at approximately 10 Ma.

Key words: endemism, *Palawanosorex* new genus, *P. muscorum* new species, Philippines, phylogeny, Soricidae, Southeast Asia, taxonomy, ultraconserved elements

Shrews (Soricidae) inhabiting the Philippines have been the subjects of numerous studies of taxonomy, morphology, and biogeography (Miller 1910; Taylor 1934; Rabor 1952; Heaney and Ruedi 1994; Hutterer 2007; Esselstyn and Goodman 2010). Such studies have focused on *Crocidura*, a genus that underwent a rapid and relatively recent radiation in the Philippines (Esselstyn and Brown 2009; Esselstyn et al. 2009, 2011; Esselstyn and Oliveros 2010; Giarla and Esselstyn 2015). Nine endemic species are currently recognized—*C. batakorum* Hutterer, 2007, *C. beatus* Miller, 1910, *C. grandis* Miller, 1910, *C. grayi* Dobson, 1890, *C. mindorus* Miller, 1910, *C. negrina* Rabor, 1952, *C. ninoyi* Esselstyn and Goodman, 2010, *C. palawanensis* Taylor, 1934, and *C. panayensis* Hutterer, 2007—but further species are expected or have already been tentatively identified (Giarla and Esselstyn 2015). In addition, 1 species (*C. tanakae* Kuroda, 1938) that occurs in Taiwan and mainland China also reaches the Batanes Islands, an isolated group between Luzon and Taiwan

(Esselstyn and Oliveros 2010). The diversity of shrews on single islands in the Philippines is low. Most islands with a record of native shrews support only 1 species of *Crocidura*; only Mindoro, Mindanao, Palawan, and perhaps Sibuyan support 2 species each (Esselstyn et al. 2011; Giarla and Esselstyn 2015). The widespread *Suncus murinus* is presumably an introduced species (Hutterer et al. 2008; Heaney et al. 2016). Phylogenetic studies have demonstrated that the extant, endemic shrew fauna of the Philippines is the result of 2 colonization events, both of which probably involved entry to the Philippines via Palawan Island (Esselstyn et al. 2009; Giarla and Esselstyn 2015).

Palawan is a long, narrow island with many associated small islands stretching from northern Borneo northeast toward Mindoro (Fig. 1). Biogeographically, the island group is often treated as part of the Asian continental shelf (Sundaland), as it may have had a mid-Pleistocene connection to Borneo (Everett 1889; Heaney 1986; Esselstyn et al. 2004, 2010; Piper et al. 2011; Brown et al. 2013).

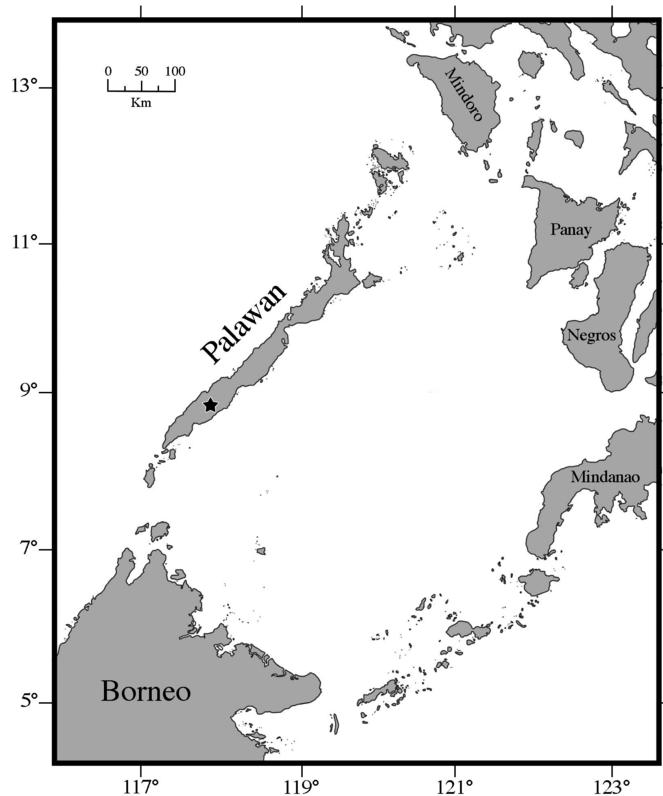


Fig. 1.—Map showing part of Southeast Asia including Palawan and Borneo. The star indicates Mt. Mantalingahan, Palawan.

Palawan is inhabited by house shrews (*S. murinus*) and 2 species of *Crocidura*, the larger, long-tailed *C. palawanensis* and the small, shorter-tailed *C. batakorum* (Esselstyn et al. 2004; Hutterer 2007). However, our 2007 survey of small mammals on Mt. Mantalingahan in southern Palawan Island obtained specimens of a distinctive shrew which could not be identified as any of the species previously known from the region, and whose existence and distinctive morphology challenged previous hypotheses on the biogeography and settlement of the Philippine Islands by shrews. We present the results of our morphological and phylogenetic investigation of this shrew and describe it as a new genus and species.

MATERIALS AND METHODS

Field survey procedures.—Specimens of shrews and other small mammals were collected during a biological survey by the Field Museum's Philippine Mammal Project led by DSB in 2007. From 19 June to 25 July, the team inventoried small terrestrial mammals along an elevational transect on the southern slope of Mt. Mantalingahan in southern Palawan (Fig. 1). Traps were set at 9 localities from 700 to 1,950 m elevation.

Small mammals were collected using a combination of Victor rat snap traps (17.6×8.4 cm), Museum Specials (14×6.8 cm), and small snap traps (9.8×4.6 cm). Specimens were measured and weighed, and either preserved as complete skeletons or in formalin and later transferred to 70% ethanol. Skulls were extracted later and cleaned with dermestid beetles, followed by a wash with a weak ammonia solution. All specimens of shrews and their detailed localities are listed in Appendix I. External

measurements taken in the field include total length, tail length, hind foot length including claw, and ear length. Head and body length was calculated as total length minus tail length. Further measurements, such as hind foot length excluding claws and the degree of pilosity of the tail were taken later from the preserved museum vouchers. Tissues were taken in the field, preserved in 90% ethanol, and subsequently stored at the Field Museum of Natural History, Chicago (FMNH) in liquid nitrogen. We followed all Philippine laws and regulations and all animals were handled consistent with the animal care and use guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Morphological methods.—We analyzed, in detail, 65 specimens from Palawan, 12 from Luzon, and 6 from other regions in Southeast Asia (see Appendix I). Body mass (g) and the following external measurements were obtained: total length, head and body length, tail length, hind foot length including claws, hind foot length excluding claws, and ear length. Pilosity was calculated as the percentage of tail length covered by long bristle hairs. Specimens examined (mainly preserved in ethanol, skulls extracted) were mainly deposited in FMNH, but comparative material (Appendix I) was also studied at the Museum of Comparative Zoology at Harvard University, Boston (MCZ) and at the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK). Half of our specimens from Mt. Mantalingahan (including the holotype) will later be transferred to the National Museum of the Philippines (PNM).

All cranial measurements (Fig. 2) were taken by RH with electronic digital calipers under a Wild (Heerbrück) binocular microscope (Leica Microsystems, Buffalo Grove, Illinois). Measurements were taken to the nearest 0.01 mm, and the means subsequently rounded. The following measurements were taken: greatest length of skull (GLS), condylo-incisive length (CIL), hard palatine length (PL), maxillary breadth (MB), rostrum width (RW), width of antorbital bridge (WAB), least interorbital width (IO), greatest width of skull (GW), height of cranial capsule (HCC), postglenoid width (PGL), upper toothrow length (UTR), length of anterior tip of P4 to posterior border of M3 (P4–M3), length of 3rd upper molar (M3L), width of 3rd upper molar (M3W), length of 1st upper incisor (in lateral view) from tip to upper margin of cingulum (LI1), length of mandible from tip of incisor to posterior edge of condyle (ML), height of coronoid process (COR), width of condyle (CONW), height of condyle (CONH), length of lower toothrow including incisor (LTR), length of lower molar series (m1–m3), length of 1st lower incisor from tip to posterior margin of cingulum (Li1). All adults (young adults to old adults with little worn to heavily worn teeth, and with fused basioccipital and basisphenoid bones) were included. Sexes were pooled, as no sexual dimorphism in cranial measurements was found, except for a slight dimorphism in the *S. murinus* population from Luzon. The maximum length measurement was taken from some postcranial bones.

Our terminology for external characters follows Brown (1971) and Brown and Yalden (1973). Cranial and dental nomenclature follows Meester (1963), Repenning (1967), and Jenkins (1984). Terminology of the upper (3 in *Crocidura*, 4 in *Suncus*) and lower (1 each) unicuspisid teeth is still not settled (Hutterer 2005b). Herein, we simply call them U1–U4 and u1.

We photographed gross morphological features with a Lumix Panasonic DMC-LF1 camera (Panasonic Corp., Osaka, Japan). To obtain images of the microstructure of hairs, we cleaned them ultrasonically, and mounted, gold-coated, and processed them with a Zeiss Sigma 300VP scanning electron microscope (SEM; Carl Zeiss Corp., Oberkochen, Germany). Images of skulls were taken (without coating) with an Amray 1810 scanning electron microscope (Adams Microfabrication Facility, Lawrence, Kansas). Drawings were made with a Wild (Heerbrugg) binocular microscope with an attached *camera lucida* and further processed with Photoshop.

Morphometrics.—We performed a principal component analysis (PCA) using SYSTAT 10 for Windows (SPSS Inc. 2000), employing the correlation matrix of log₁₀-transformed cranial and dental measurements. Measurements were from complete data sets from 11 of the new Palawan shrews, 22 *Crocidura palawanensis*, and 10 *Suncus murinus luzoniensis*.

DNA sequencing and phylogenetics.—We amplified and sequenced a portion of the mitochondrial protein-coding gene cytochrome *b* (*Cytb*) from DNA samples from 10 individuals (Table 1) following the protocol described in Esselstyn et al. (2009). *Cytb* sequences from additional species were downloaded from GenBank and aligned to our new sequences using MAFFT (Katoh and Standley 2013) in Geneious R9 (BioMatters Inc., Auckland, New Zealand). We divided the *Cytb* alignment into 3 data subsets partitioned by codon position. We then used PartitionFinder 2 (Lanfear et al. 2017) to estimate the best-fitting partitioning scheme and corresponding set of best-fitting nucleotide substitution models. We inferred a phylogeny in MrBayes 3.2.6 (Ronquist et al. 2012) on the CIPRES Science Gateway (Miller et al. 2010) using the best-fitting models. Model parameters were unlinked across the different data subsets. We initialized 2 MrBayes runs simultaneously, each comprising 4 Markov chain Monte Carlo chains of 5×10^6 generations. The average SD of split frequencies across the 2 runs was monitored to assess stationarity.

Using high-throughput technologies and a custom probe set, 5,060 ultraconserved elements (UCEs—Faircloth et al. 2012) and exon segments of 2 protein-coding nuclear genes (recombination-activating gene 1 [*Rag1*] and brain-derived neurotrophic factor [*Bdnf*]) were enriched and sequenced by RAPiD Genomics (Gainesville, Florida). Twenty-four species were included across a range of soricid species, with all crocidurine genera except *Feroculus* and *Solisorex* represented (Table 1). A gymnure, *Hylomys suillus*, was used as an outgroup. UCE sequences from 2 of our samples were included in another study (Esselstyn et al. 2017) and are already publicly available (NCBI BioProject PRJNA390442). Prior to probe hybridization, genomic libraries were constructed using standard single-index Illumina TruSeq adapters with unique 8 bp barcodes for each individual. Pooled and target-enriched DNA samples were sequenced on an Illumina HiSeq 2500, and we received demultiplexed raw reads directly from RAPiD Genomics (available for download from NCBI BioProject PRJNA433997). We trimmed reads of low-quality bases and adapter sequences using the Illumiprocessor pipeline (<https://github.com/faircloth-lab/illumiprocessor>), which relies on the software package

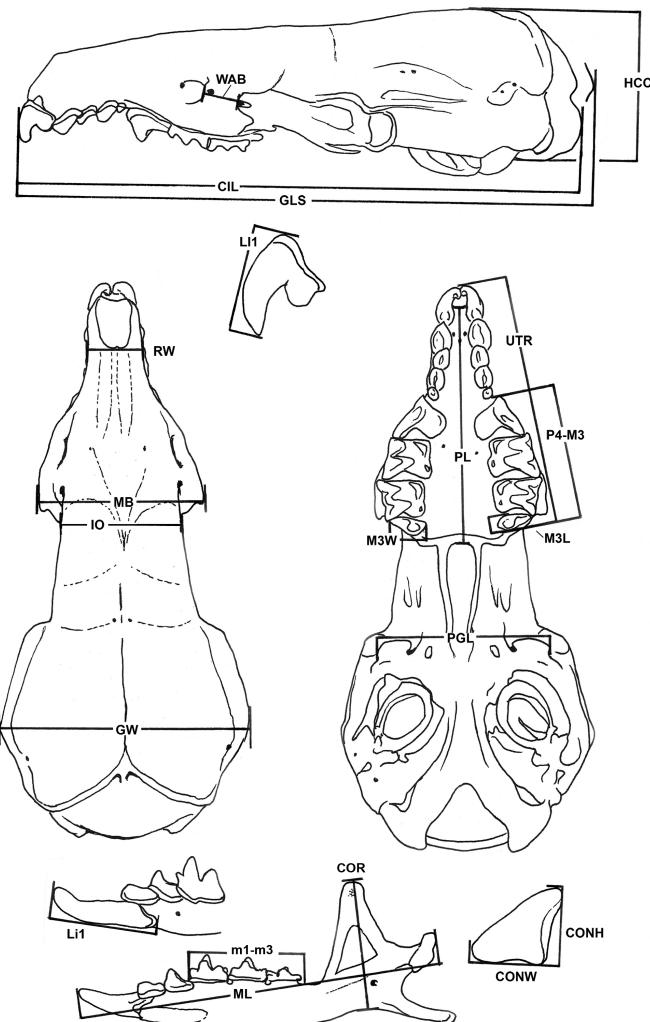


Fig. 2.—Sketch of a skull and mandible of *Palawanosorex muscorum* (FMNH 195240) with the measurements taken for this study indicated.

Trimmomatic (Bolger et al. 2014). We used the PHYLUCE 1.5 pipeline (Faircloth 2016) to automate the remaining data processing steps. We assembled reads de novo using Trinity 2.0.6 (Grabherr et al. 2011) and identified all resulting contigs that matched our UCE or protein-coding gene probes. For each locus, we aligned the contigs using MAFFT. For the UCE data set, any locus alignment shorter than 300 bp or with 3 or fewer taxa was excluded. We analyzed 2 UCE data sets to examine the effects of missing loci and taxa: 1) a comprehensive data set tolerating up to 84% missing taxa per locus, and 2) a restricted data set tolerating only 20% missing taxa per locus.

For the UCE data sets, we conducted both a concatenated maximum likelihood analysis and a coalescent species tree analysis. For the maximum likelihood analyses, we concatenated the UCE loci in Geneious and inferred a maximum likelihood phylogeny with 100 bootstrap replicates using the GTRCAT model in RAxML 8 (Stamatakis 2014). We conducted these analyses on the CIPRES Science Gateway, with all other RAxML settings at their default values. For the coalescent analyses, we first inferred gene trees for each locus in RAxML under the GTRGAMMA

model. We then used ASTRAL-III 5.5.6 (Mirarab et al. 2014; Zhang et al. 2017) to estimate a species tree from those gene trees. Internal branch support was measured via local posterior probabilities (Sayyari and Mirarab 2016).

For the 2 protein-coding genes, alignments were examined by eye to check for frameshifts and premature stop codons. We expanded taxon sampling with additional *Bdnf* and *Rag1* sequences from GenBank (Table 1) and aligned them to our sequences using MAFFT. We concatenated these nuclear sequences with the *Cytb* sequences and inferred a time-calibrated phylogeny in BEAST 2.4.7 (Bouckaert et al. 2014). Each gene was assigned to its own subset, and we unlinked nucleotide substitution and clock model parameters across the partitions. We used the bModelTest package (Bouckaert and Drummond 2017) in BEAST to simultaneously estimate the tree and nucleotide substitution models, averaging over the uncertainty in model selection. Each gene was assigned a relaxed clock model with lognormal rate distribution. To time-calibrate the tree, we applied lognormal most recent common ancestor (MRCA) priors (mean = 1, SD = 1.25) on the minimum age of 3 clades for which fossil information is available (offset by 5 Ma for the minimum age of *Crocidura*—Mein and Pickford 2006; 12 Ma for the minimum age of Crocidurinae—Robinson and Black 1974; and 20 Ma for the minimum age of Soricidae—Reumer 1989). Lognormal priors offset by the age of the oldest known fossil are

appropriate representations of the probability of clade age (Ho and Phillips 2009). A calibrated Yule model was used as the tree prior. The BEAST analysis was run for 2×10^8 generations, with effective sample size (ESS) values assessed in Tracer.

RESULTS

Based on morphological and molecular phylogenetic characters described in the following sections, we recognize the population of dark, short-tailed, long-clawed shrews from the higher elevations of Mt. Mantalingahan as representing a new genus and species. We compare this newly recognized taxon in detail to specimens of the syntopic *C. palawanensis*, and with *Crocidura batakorum*, which was not collected during this survey but has been recorded near Mt. Mantalingahan. We also compare the new species with *S. murinus*, an invasive species known from throughout much of the Philippines, and with other genera of crocidurines.

Family Soricidae G. Fischer, 1814
Subfamily Crocidurinae Milne-Edwards, 1872
Palawanosorex, new genus

Type species.—*Palawanosorex muscorum*, new species.

Diagnosis.—The new genus is defined by the following combination of characters. Tail 65% of head and body length,

Table 1.—Specimens with GenBank and NCBI Targeted Locus Study (TLS) accession records. Asterisks (*) denote new sequences generated as part of this study. Blank cells indicate loci where DNA sequencing was not attempted or was unsuccessful. Ultraconserved element loci are deposited as a TLS in NCBI BioProject PRJNA433997.

Species	Museum code	<i>Cytb</i>	<i>Bdnf</i>	<i>Rag1</i>	Ultraconserved elements TLS
<i>Blarinella griselda</i>	AMNH 274263	AB175144	*MG973435	*MG973450	*KBVF00000000
<i>Congosorex phillipsorum</i>	FMNH 177682	*MG973425		*MG973452	*KBVG00000000
<i>Crocidura batakorum</i>	KU 165320	FJ813968	*MG973436	*MG973455	*KBVH00000000
<i>Crocidura batesi</i>	FMNH 167706	*MG973432	*MG973437	*MG973456	*KBVI00000000
<i>Crocidura goliath</i>	MVZ 196210				*KBVJ00000000
<i>Crocidura horsfieldii</i>	MSB 231668	FJ814028	*MG973438	*MG973463	*KBVK00000000
<i>Crocidura leucodon</i>	IZEA 6040	DQ065609			
<i>Crocidura palawanensis</i>	FMNH 195224	FJ813912	*MG973440	*MG973458	*KBVL00000000
<i>Crocidura russula</i>	ZFMK 2013.383	NC006893	*MG973441	*MG973460	*KBVM00000000
<i>Crocidura sibirica</i>	TTU 111201	AB077085	*MG973439	*MG973461	*KBVN00000000
<i>Crocidura tansaniana</i>	FMNH 149973	KP062072	*MG973442	*MG973457	KBVO00000000
<i>Diplomesodon pulchellum</i>	MVZ 179157	*MG973433	*MG973443	*MG973459	*KBVP00000000
<i>Episoriculus caudatus</i>	CAS 29115	AB175115	*MG973448	*MG973451	*KBVQ00000000
<i>Feroculus feroculus</i>	WHY 6827	JQ433898	JQ433908	JQ433892	
<i>Hylomys suillus</i>	FMNH168652				*KBVR00000000
<i>Myosorex geata</i>	FMNH 158299	JQ433901		*MG973453	*KBVS00000000
<i>Myosorex kihalei</i>	FMNH 205242	JQ433902		*MG973454	*KBVT00000000
<i>Palawanosorex muscorum</i>	FMNH 195234	*MG973426			*KBVU00000000
<i>Palawanosorex muscorum</i>	FMNH 195240	*MG973430			*KBVV00000000
<i>Palawanosorex muscorum</i>	FMNH 195241	*MG973427	*MG973449	*MG973467	*KBVW00000000
<i>Palawanosorex muscorum</i>	FMNH 195243	*MG973428			
<i>Palawanosorex muscorum</i>	FMNH 195997	*MG973429			
<i>Paracrocidura schoutedeni</i>	FMNH 167721	*MG973434	*MG973445	*MG973462	*KBVX00000000
<i>Ruwenzorisorex suncoides</i>	FMNH 148939	*MG973431	*MG973444	*MG973464	*KBVY00000000
<i>Scutisorex thori</i>	FMNH 219669	KF110765	*MG973446	*MG973465	*KBVZ00000000
<i>Solisorex pearsoni</i>	WHT 6810	JQ433899	JQ433909	JQ433893	
<i>Solisorex pearsoni</i>	WHTM 184	JQ433900	JQ433910	JQ433894	
<i>Suncus cf. etruscus</i>	AMNH 275574	JN556043			*KBWA00000000
<i>Suncus murinus</i>	KU 164724	AB175075	*MG973447	*MG973466	*KBWB00000000
<i>Surdisorex norae</i>	FMNH 190259				*KBWC00000000
<i>Sylvisorex morio</i>	ZFMK 2016.0355				*KBWU00000000

densely covered by very short black hairs, but lacking long bristles (pilosity 0%; Figs. 3A and 4A). Front and hind feet broad and armed with long claws (Figs. 4A and 5A). Interdigital ventral surface of fore and hind feet smooth, only crossed by a few wrinkles (Fig. 6A). Skull slender and pointed; dorsal suture open or covered by a very thin bone layer in 65% of examined specimens, often accompanied by a pair of (closed) dorsal foramina (Figs. 7 and 8). First upper incisor small with pronounced posterior cusp (Fig. 9A). Four upper unicuspids are present. Upper P4 narrow (Fig. 7A). A small 3rd cusp between protocone and hypocone on M1 (Fig. 10) is present at a low frequency. Genetic analyses of DNA sequence data show that the new genus is monotypic, branching off near or at the base of crocidurine shrews (Figs. 11 and 12).

Comparisons.—The new species is clearly distinguished from all other Philippine shrews by its long blackish pelage, tail densely covered by short black hairs and lacking long bristles, long claws on the front and hind feet, and by its almost smooth interdigital surface of palm and sole. Among soricids, only the myosoricine *Congosorex phillipsorum* also has a fissure in the dorsal cranial suture (Stanley et al. 2005:figure 6). *Crocidura* have 3 upper unicuspids (28 teeth), some bristles near the base of the tail, and palms and soles of the feet usually with many small granules. The tooth formula of the new species (30 teeth) is shared with crocidurines from Asia (*Suncus* and *Feroculus*) and Africa (*Ruwenzorisorex*, *Suncus*, *Surdisorex*, and *Sylvisorex*); however, the details of the unicuspids teeth differ between these genera (Hutterer 2005b). In *Suncus*, the tail has many bristles (Figs. 3C and 4C), the fore and hind feet are proportionately longer and narrower with palms and soles covered by many creases and raised areas (Figs. 4C and 6C), the skull lacks traces of dorsal foramina (Fig. 8), and the front teeth and condyles are more robust (Fig. 9C). Figures 9C and 9D depict details of *S. murinus* and *S. montanus*, a smaller and darker species from Sri Lanka in which characters of the incisors and the condyle are similar to *S. murinus*. *Feroculus* (endemic to Sri Lanka and India) is dark gray, the tail length is 60–70% of head of body length but covered with long bristle hairs over almost its entire length (as in *Suncus*); in addition, the fore feet bear very long claws (up to 5.5 mm long in FMNH 99454). Compared to *Palawanosorex*, the rostrum is longer and more slender, the antorbital bridge is very narrow, the upper molars are greatly reduced and in contact only at the lingual side of the toothrow; in lateral view, U1–U3 are almost equal in size, while U4 is smaller. In addition, the anterior palate bears only 1 pair of foramina, and the 1st lower incisor has 3 deep indentations. Genetically *Feroculus* is placed within the *Suncus* clade (Meegaskumbura et al. 2014), which demonstrates a need for taxonomic revision. *Solisorex* has a different tooth formula, a massive skull and dentition, extremely long front claws (6 mm in FMNH 108990), ears concealed in the fur, grayish pelage, and a very short tail with no bristles. Taken together, Meegaskumbura et al. (2014), our mitochondrial gene tree analysis (Supplementary Data SD1), and our fossil-calibrated analysis of concatenated protein-coding genes (Fig. 12), suggest *Solisorex* is sister to all other Crocidurinae, including *Palawanosorex*.

Description.—Because the new genus is monotypic, the description is the same as in the species description, presented below.

Etymology.—Named for the island of Palawan in combination with Latin *sorex*, shrew. Gender of genus is masculine.

Species included.—The new species described herein.

Palawanosorex muscorum, new species

Holotype.—FMNH 195241, young adult male, field number DSB 4855, collected 27 June 2007 by DSB; body preserved in 70% ethanol, tail broken at base, a slight slipping of hair on belly, otherwise in good condition. Skull extracted and in excellent condition (Fig. 7). The skull has the dentition of a young adult, with slightly worn teeth and a fully fused basisphenoid–basioccipital suture. External measurements made in the field include: total length, 159 mm; tail length, 60 mm; hind foot length including claws, 19 mm; ear length, 10 mm; mass, 22 g. The specimen was captured in a Victor rat trap baited with fried coconut coated with peanut butter. The holotype will eventually be transferred to the National Museum of the Philippines, Manila. Muscle tissue was taken from the specimen in the field and preserved in 90% ethanol prior to cryogenic storage at FMNH. The holotype was used in all morphological, morphometric, and molecular analyses.

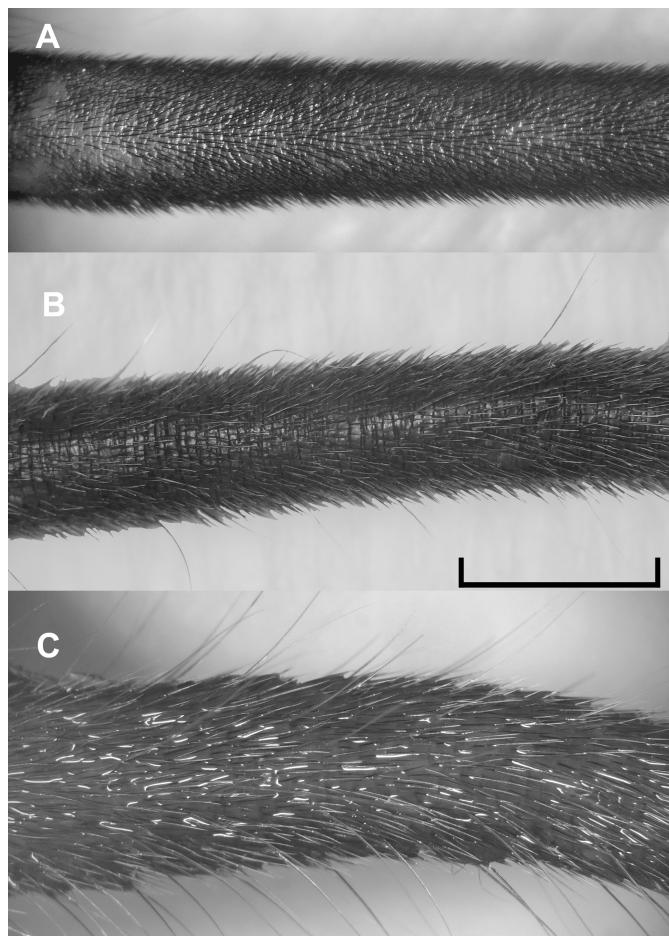


Fig. 3.—Detail of a proximal portion of the tail of (A) *Palawanosorex muscorum* (FMNH 195238), (B) *Crocidura palawanensis* (FMNH 195222), and (C) *Suncus murinus luzoniensis* (FMNH 183286). Scale bar equals 1 mm.

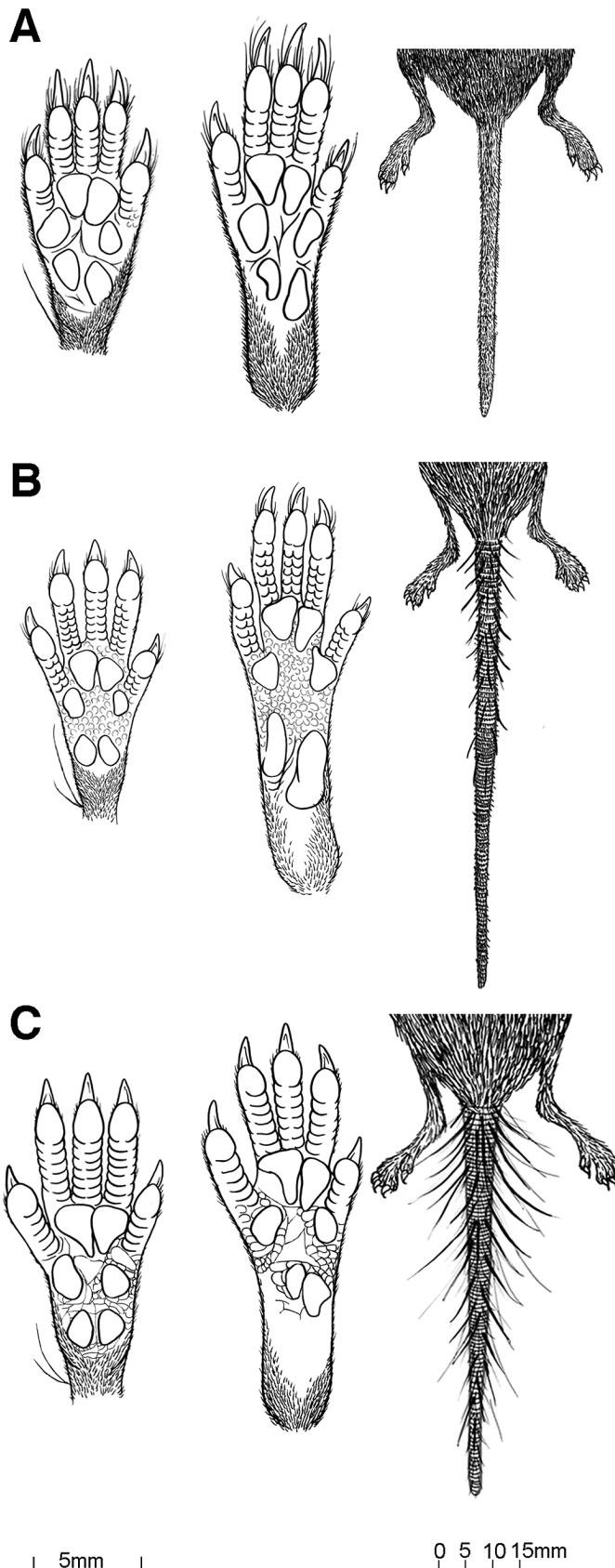


Fig. 4.—Comparative summary of morphological characters of fore and hind limb and tail in (A) *Palawanosorex muscorum*, (B) *Crocidura palawanensis*, and (C) *Suncus murinus luzoniensis*. Sketches by Kayleigh Kueffner and Leia Uí Dhalaígh.

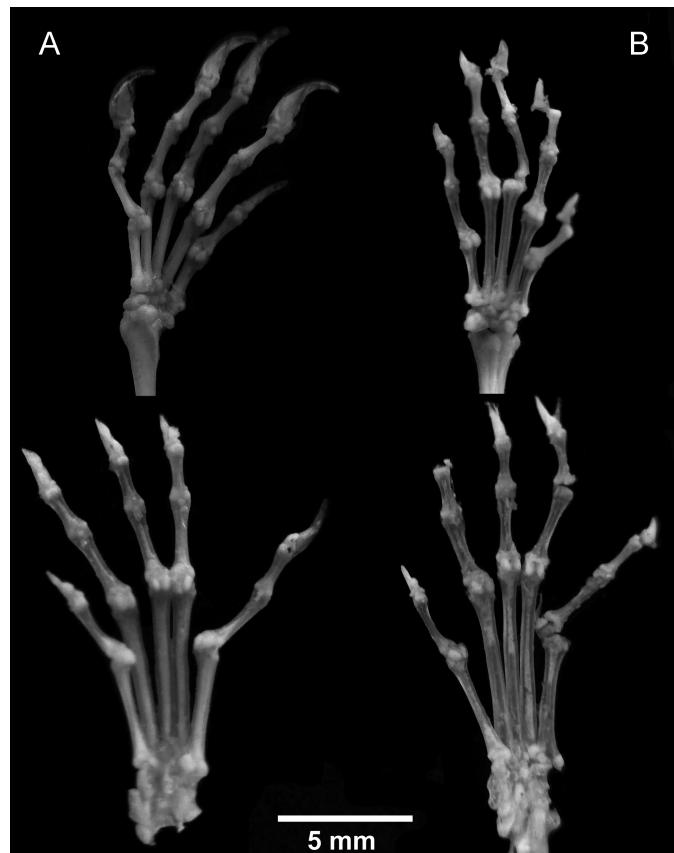


Fig. 5.—Photographs of skeletal elements of the fore and hind feet of *Palawanosorex muscorum* (A) and *Crocidura palawanensis* (B).

Type locality.—Philippine Islands, Palawan Island, Palawan Province, Rizal Municipality, 2 km W, 0.7 km S Mt. Mantalingahan peak, 1,750 m, 8.81301°N, 117.66313°E.

Paratypes.—Eight males (FMNH 195236, 195239, 195243–195244, 195997–196000), and 12 females (195234–195235, 195237–195238, 195240, 195242, 195245–195246, 196001–196004), all collected between 21 June and 1 July 2007 in the environs of Mt. Mantalingahan at elevations between 1,550 and 1,950 m.

Diagnosis.—As for genus (see above).

Description.—*Palawanosorex muscorum* is a middle-sized shrew with the following mean body measurements: mass 20 g, head and body length 90.6 mm, tail length 59 mm (17 tail vertebrae), and hind foot length, including claws, 18.4 mm (Table 2). The overall color of the shrew is slate gray to black (Fig. 13), with dorsal hairs 8 mm and ventral hairs 3.2 mm long. The fur on the dorsum, venter, tail, and limbs are of the same dark color. The microstructure of dorsal shield curly overhairs (also awn hairs; terminology follows Ducommun et al. 1994) is of type c, groove with irregular notches. The scales of these hairs are more widely spaced in *P. muscorum* than in *C. palawanensis* (Fig. 14). Tail length averages 65% of head and body length; the tail is densely covered by very short black hairs, but has no long bristles (Fig. 3A). Front and hind feet are broad and armed with long claws (Figs. 4A and 5A). Claws on the fore feet are 3.0 mm and on the hind feet 2.5 mm long on average and are accompanied by long curved bristle hairs (Figs. 4A and 5A).

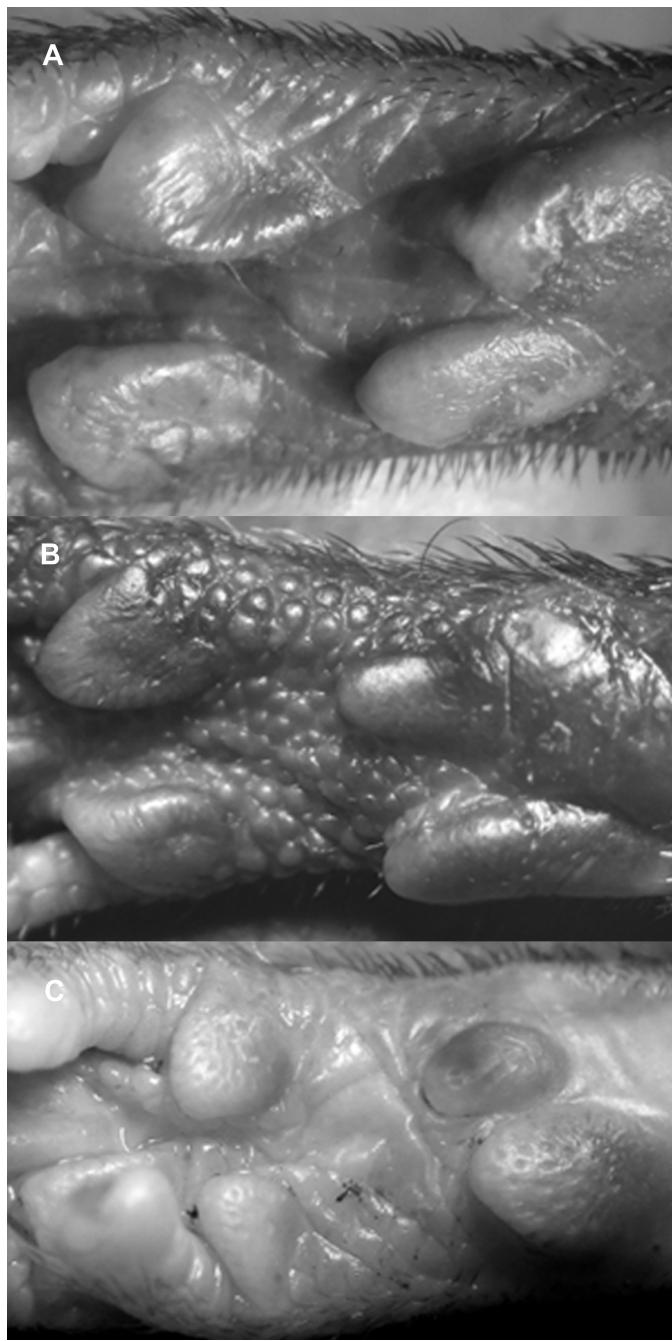


Fig. 6.—Detail of the plantar surface of the hind foot in (A) *Palawanosorex muscorum* (FMNH 195238), (B) *Crocidura palawensis* (FMNH 195222), and (C) *Suncus murinus luzoniensis* (FMNH 183286).

The plantar and interdigital pads are large and cover most of the plantar surface; the hypothenar of the hind foot is smaller than the thenar. The remaining interdigital surfaces of hands and feet are smooth but crossed by a few wrinkles (Figs. 4A and 6A). Dorsal surfaces of fore and hind feet and part of wrist and ankle are covered by very short dark hairs. Each fore foot has one long stiff sensory hair inserting laterally at the wrist. The ear pinna (external ear) is rounded, on average 9.2 mm long from the notch, and covered by very short dark hairs (Supplementary

Data SD2). Eyes are open and surrounded by slightly paler skin; the eye opening is about 1 mm wide. The rhinarium is smooth, without any sculpturing, deeply divided into 2 parts by a groove following the philtrum; the infranarial portion and the ala nasi form a slightly undulated lobe, serving as the posterior part of the nostril. The muzzle is pale-colored, swollen on both sides, and bears numerous whiskers, the longest of which reach 28 mm. Females have 3 pairs of nipples, which are equally spaced in the inguinal area.

The skull is slender and pointed, with a flat dorsal profile and a slightly elevated braincase (Fig. 7). In dorsal view the braincase is semihexagonal; the interorbital region is long with straight, slightly tapering edges; the maxillary is narrow and the rostrum long. Sagittal and lambdoid crests, superior articular facets, occipital condyle and paroccipital process are minimally developed. The antorbital bridge is wide (1.10–1.55 mm; Table 3), the lacrymal foramen is small and placed in an upper anterior position on the bridge (Fig. 7). In 16 out of 17 skulls examined, a fissure in the dorsal suture is either open (Figs. 8A and 8B) or covered by a very thin bone layer but discernible (Fig. 8C); in 1 specimen (FMNH 195997) no trace of an opening is present. In 13 of 17 skulls, faint paired dorsal foramina, lying posterior to the fissure along the suture opening, are visible but closed (Fig. 8). The anterior palate has a pair of incisive foramina at the level of U1, followed by a narrow, slit-like central foramen.

The mandible is slender, with a low mandibular ramus, a moderately high coronoid process (average 5.78 mm in height), and a weak and small condyle (Fig. 7G). The angular process projects far beyond the posterior margin of the condyle. The position of the mental foramen is below the contact between p4 and m1.

The dentition is generally weak (Figs. 7 and 9A). The species has 30 teeth. The tooth formula could be: I1 I2 I3 C P1 P4 M1 M2 M3/i1 i2 p4 m1 m2 m3 (following Hutterer 2005b), or as: I1 U1 U2 U3 U4 P4 M1 M2 M3/i1 u1 u4 m1 m2 m3 (applied here), if the homology of the unicuspids teeth is questioned. LI1 is small and short (9.2% of greatest length of skull; see Table 3), the anterior hook pointed and the posterior cusp round and set apart; its cingulum is narrow (Fig. 9A). The 4 upper unicuspids teeth (U1–U4) all differ in size. Their size sequence from largest to smallest is U1, U3, U2, and U4; the last is about 1/3rd of the length of U1, but still visible in side view. All unicuspids are in contact with adjacent unicuspids. Cingula are thin but pronounced. In 13 of 17 specimens (76%), U4 has no contact with the following P4. P4 is slender and low; its parastyle is reduced, visible in ventral but invisible in lateral view, the talonid is narrow and branching off in a rectangle; the protocone is small and shifted labially (Figs. 7B, 7D, and 7F). P4 and upper molars are in contact at the labial side but widely spaced on the lingual side (Fig. 7D). M1 and M2 are large and semi-rectangular in occlusal view; both have a large protocone and a small rounded hypocone. Two specimens (FMNH 196002, 196003) display a small additional 3rd cusp between protocone and hypocone on M1 (Fig. 10), which seems to be previously unknown for shrews. The M3 is short and narrow (Table 3).

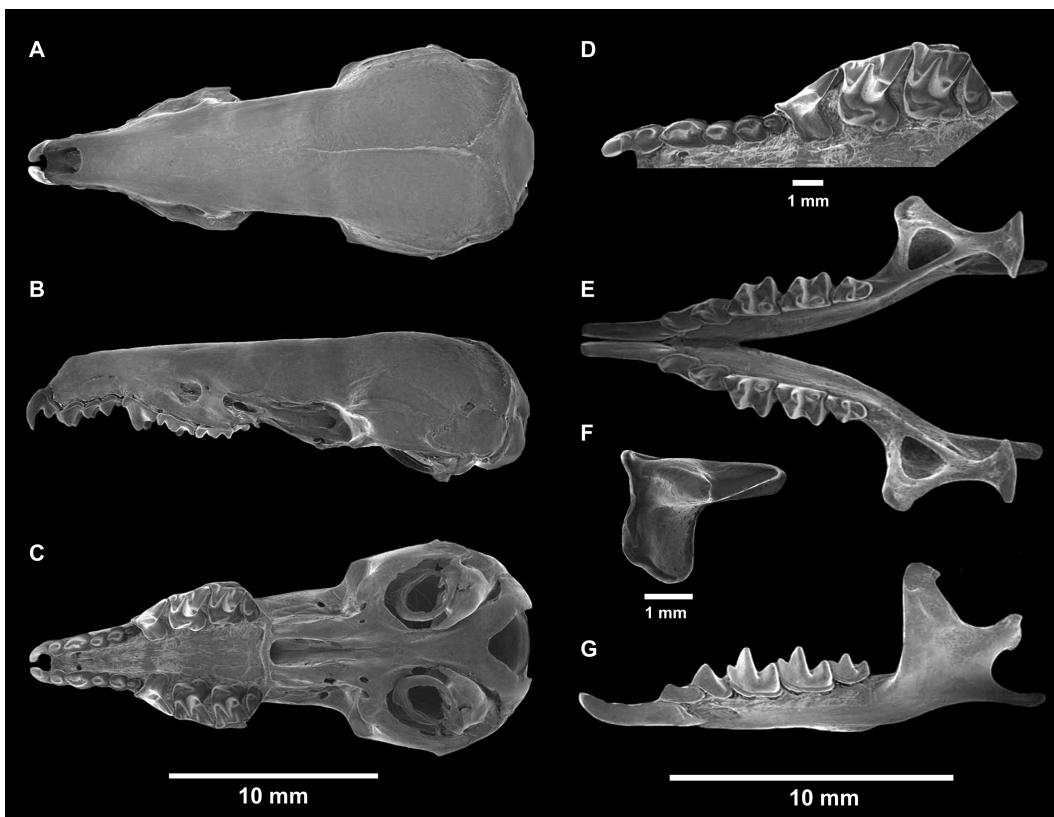


Fig. 7.—Scanning electron micrographs of the holotype skull (FMNH 195241) of *Palawanosorex muscorum* in dorsal (A), lateral (B), and ventral (C) view, enlarged left upper toothrow (D) in ventral view, pair of mandibles (E) in dorsal view, left upper P4 (F) in occlusal view, and (G) left mandible in labial view.

The lower incisor (i1) is relatively short and simple (Fig. 9A); its cingulum is narrow and runs only along the upper anterolinguinal ridge of the tooth; the incisor is slightly curved upwards and forming a tip (not rounded); the posterior ridge of the incisor is a little wrinkled, not smooth. The following tooth (u1) is elongated and has a single cusp; posteriorly it slopes down in a narrow groove that flows around the tip of p4 and continues into the bilateral cingulum. The p4 is about the same size, has a broad cingulum and a triangular tip, which may become V-shaped with age. There is no trace of a metaconid or protostyloid. Molars m1 and m2 are unspecific, low in height, and with a pronounced labial and a weak lingual cingulum. The m3 is small, reduced, with a small hypoconid and a small talonid basin (Fig. 7E).

The bones of the postcranial skeleton are robust (in comparison to *C. palawanensis*). The distal phalanx of all 5 digits of the fore foot holds a large claw, and less so but still elongated in the hind foot (Fig. 5A). Length measurements (mm; mean \pm SD, range; $n = 8$) for limb bones and pelvis are: humerus 11.4 ± 0.2 , $10.9\text{--}11.5$; femur 12.3 ± 0.3 , $11.7\text{--}12.7$; tibia 19.4 ± 0.4 , $18.5\text{--}20.0$; and pelvis 15.5 ± 0.6 , $14.5\text{--}16.4$ mm. The tail has only 17 vertebrae (21 in *C. palawanensis*).

Comparisons.—*Palawanosorex muscorum* is easily distinguished from the syntopic *C. palawanensis* and the allopatric *C. batakorum* and *S. murinus* in skull characters and external measurements, particularly in body mass, total length, and tail length (Table 2). The long pelage and its dark, almost black coloration separates *P. muscorum* from the gray, shorter-haired

C. palawanensis (Fig. 13), the dark brown dorsally, medium gray ventrally, shorter-haired *C. batakorum*, and the yellowish to brownish gray *S. murinus*. Length, thickness, and pilosity of the tails (Fig. 3) are also discriminating characters. *Crocidura batakorum*, a Palawan endemic, is a very small shrew (H&B 63.5 mm; CIL 18.74 mm) with a short tail (43 mm) possessing sparse bristles along the proximal half (Hutterer 2007). We found clear-cut differences in the anatomy of the limbs of the 3 genera (Figs. 4–6). *Palawanosorex* has broad fore and hind feet with long claws, large thenar and hypothenar pads, and plain, slightly wrinkled palms and soles. By contrast, *C. palawanensis* has a very long tail with more than 30% supporting long bristles; the species has also slender, elongated feet with small pads, and the surfaces of palms and soles are covered by numerous small granules (Figs. 4 and 6), as is typical for *Crocidura* spp., including *C. batakorum*. *Suncus murinus* is distinguished by a thick tail with long bristles over its entire length, and its fore and hind feet are large and wide (Fig. 4C). The surface of the palms and soles is covered partly by larger scales (Figs. 4C and 6C).

In their cranial dimensions (Table 3) and proportions (Fig. 15), *P. muscorum*, *C. palawanensis*, and *S. murinus* are distinct. Skulls of *Palawanosorex* have the highest values in width of antorbital bridge (WAB) and interorbital width (IO), but have the lowest values for length and width of upper 3rd molar (M3L and M3W), and for height and width of the condyle (CONW and CONH). The very small upper incisor (Fig. 9),

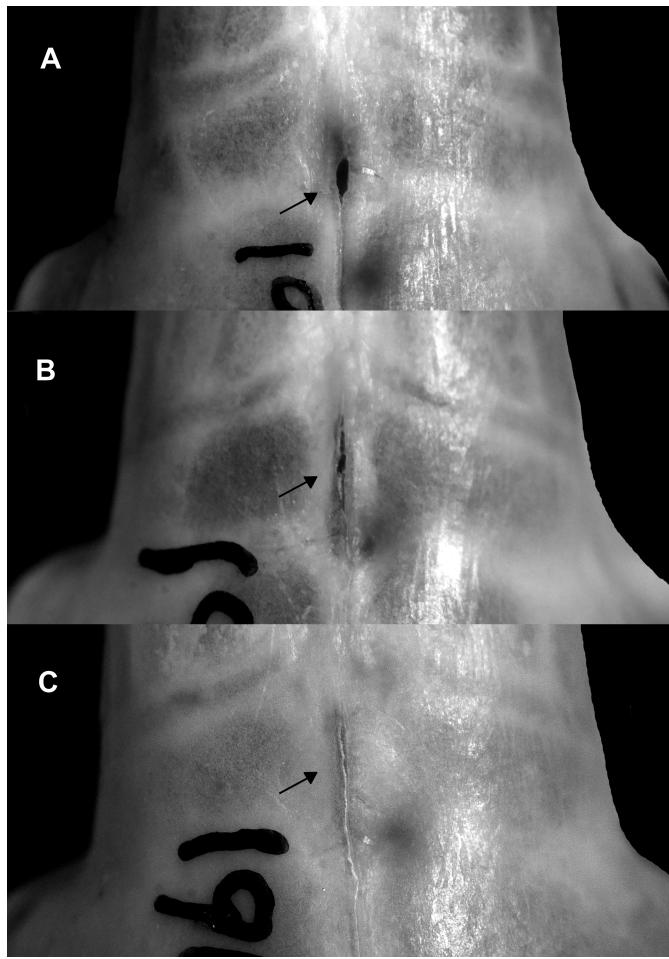


Fig. 8.—Three examples of the condition of the dorsal foramen (arrows) in *Palawanosorex muscorum*. (A) FMNH 195240, (B) FMNH 195235, (C) FMNH 196003.

the reduced upper premolar and molar series (Fig. 7D), and the wedge-shaped cranium (Fig. 7A) are also diagnostic. The presence or trace of a dorsal cranial fissure in 16 out of 17 *P. muscorum* is also remarkable (Fig. 8); a trace of such a fissure was observed in 1 of 25 skulls of *C. palawanensis*, but not in a single *S. murinus*. Comparisons with other genera in the subfamily Crocidurinae are given in the genus Comparisons, above.

Note on *Suncus ater*.—Medway (1965) described this black species on the basis of a skin and skull collected at 5,500 feet at Gunung Kinabalu, Borneo (now Sabah, Malaysia) in 1937. The species is only known by the holotype (MCZ 36574). The description and skull figures of the species presented by the author raised the question whether it might be related to the Palawan shrew. We therefore examined the holotype carefully and found that it does not meet the diagnostic criteria of *P. muscorum*, i.e., the tail without bristles (28% pilosity in *S. ater*), the broad and long-clawed feet (normal condition in *S. ater*), the bare surface of the interdigital space (scaled in *S. ater*), the wide antorbital bridge (narrow in *S. ater*), presence of a dorsal fissure and dorsal foramina (absent in *S. ater*), and the labially reduced P4 and molars (larger in *S. ater*). Rather, *S. ater* resembles the blackish forest shrews of Sri Lanka and India,

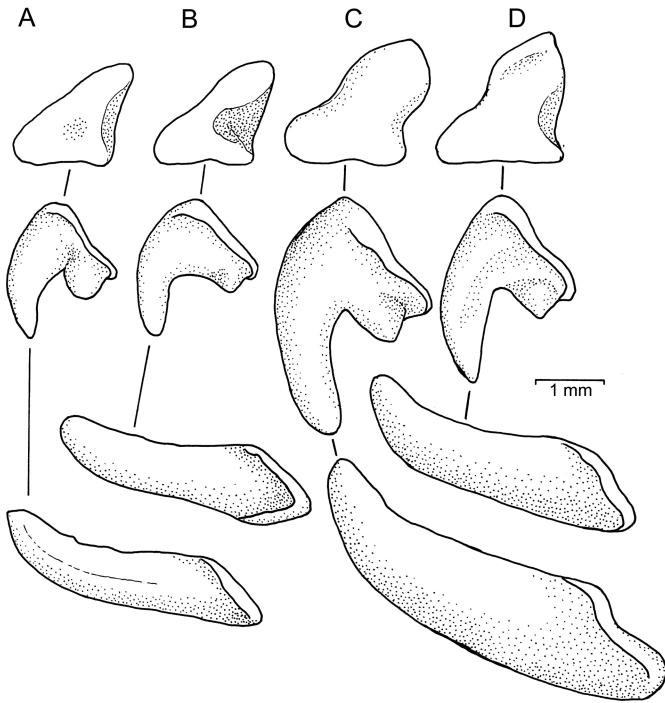


Fig. 9.—Details of the articular facets of the condyle (upper, posterior view), 1st upper incisor (middle, lateral view), and 1st lower incisor (lower, lateral views) of (A) *Palawanosorex muscorum* (FMNH 195241, holotype), (B) *Crocidura palawanensis* (FMNH 195216), (C) *Suncus murinus* (FMNH 230754), and (D) *Suncus montanus* (FMNH 99441). Drawings by R. Hutterer.

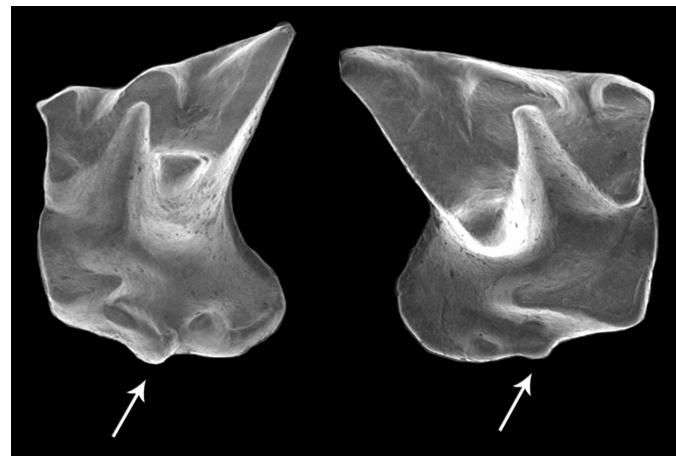


Fig. 10.—Scanning electron micrograph of M1 showing small 3rd cusp between protocone and hypocone (FMNH 196003, left, and 196002, right).

S. montanus, *S. niger*, and potentially *S. nemorivagus* (Ruedi et al. 1996; Meegaskumbura and Schneider 2008). We therefore conclude that *S. ater* is part of the radiation of *Suncus* species inhabiting the montane forests of South and Southeast Asia.

Nomenclatural statement.—LSID numbers were obtained for the new genus, *Palawanosorex* (urn:lsid:zoobank.org:act:89CD0139-DA6C-4E84-9D4C-0DF9BEDA83CD); and the new species, *P. muscorum* (urn:lsid:zoobank.org:pub:8DC17179-1D3E-4190-B6B3-25AB9C48433A).

Table 2.—External measurements of *Palawanosorex muscorum*, *Crocidura palawanensis*, and *Suncus murinus luzoniensis*. Mean \pm SD (top), range (middle), and sample size (bottom).

Measurement	<i>Palawanosorex muscorum</i>	<i>Crocidura palawanensis</i>	<i>Suncus murinus</i>
Weight (g)	20.02 \pm 2.20 16–24 21	13.70 \pm 2.29 8–19.5 30	24.71 \pm 4.56 16–34 11
Total length (mm)	149.8 \pm 9.30 130–165 21	175.24 \pm 6.50 157–186 29	164.91 \pm 10.13 148–181 10
Head and body length	90.62 \pm 5.09 84–99 21	80.10 \pm 3.91 70–86 19	108.30 \pm 8.72 90–119 10
Tail length	59.06 \pm 5.11 53–68 21	88.00 \pm 5.00 76–96 29	57.30 \pm 3.61 52–62 10
Pilosity (%)	0.0 0.0–0.0 13	36.01 \pm 7.58 25.4–54.4 19	89.90 \pm 3.99 83.3–96.4 8
Hind foot including claw	18.36 \pm 1.03 17–20 21	18.20 \pm 0.66 17–20 30	17.73 \pm 0.79 16–19 11
Hind foot without claw	16.27 \pm 0.67 15.2–17.5 13	16.61 \pm 0.71 14.9–17.5 20	15.92 \pm 0.72 15.3–17.1 9
Ear	9.20 \pm 0.86 8–11 20	9.50 \pm 0.78 8–11 30	11.27 \pm 1.49 8–12 11

Etymology.—The species name was derived from *muscorum*, genitive of Latin *musci*, mosses, meaning “of the mosses,” referring to the mossy habitat of the shrew. As an English vernacular name, we propose “Palawan moss shrew.”

Morphometrics.—We performed a PCA on 22 log-transformed craniodontal variables for specimens of *P. muscorum*, *C. palawanensis*, and *S. murinus* (Luzon population). Variable loadings on components 1–3 (only these are interpretable, with eigenvalues > 1.2) account for $> 80\%$ of the total variance (Table 4). Loadings for most variables on component 1 are high, with CIL and GSL highest, indicating that this axis is a general indicator of overall size. However, interorbital width (IO) and upper 3rd molar length (M3L) have low loadings, and upper 3rd molar width (M3W) and coronoid process height (CONH) have moderate loadings, indicating that these variables do not vary directly with overall size. Loadings on component 2 principally show the converse of component 1: interorbital width (IO) loads heavily and positively; height of cranial capsule (HCC) loads moderately and positively, and length of the upper and lower 1st incisors (LI1 and Li1), and coronoid process height (COH) load moderately but negatively, while all others have low loadings. In combination, these 2 components (with 62% and 13% of the total variation, respectively) show a complete separation of the 3 groups, with *S. murinus* and *C. palawanensis* differing by size along component 1, and *P. muscorum* differing from *S. murinus* by smaller size and from both by high scores on component 2 (with a broad interorbital region, high cranial capsule, short upper and lower 1st incisors, and low coronoid process; Fig. 15). Component 3 was not discriminative.

Molecular phylogenetic analyses.—Our comprehensive UCE data set included 3,630 loci that had 4 or more individuals and

an average alignment length of 518 bp per locus. When concatenated, it was 1,968,816 bp long. The restricted data set, in which all loci included at least 20 of the 25 total taxa, comprised 716 loci (average length 582 bp) and, when concatenated, was 419,183 bp long. For the *Cytb* phylogenetic analysis, PartitionFinder identified a best-fit partition scheme in which all codon positions were separated into different data subsets, each with their own model (position 1: SYM+I+Γ; position 2: HKY+I+Γ; position 3: HKY+Γ). Analysis of *Cytb* sequences shows all 5 *P. muscorum* individuals clustering at the end of a long branch (Supplementary Data SD1). However, *Palawanosorex*'s relationships to other taxa were not well resolved in the mitochondrial gene tree. Rather, the new species was part of a poorly supported clade that includes *Ruwenzorisorex* and *Scutisorex*. *Solisorex* is sister to all other crocidurines in the mitochondrial gene tree. In contrast, all phylogenetic trees inferred from UCE data are relatively well-supported overall, with *P. muscorum* sister to all other crocidurines sequenced (note that *Solisorex* was not available in our UCE sampling). Analyses of our comprehensive (Fig. 11; Supplementary Data SD3) and restricted (Supplementary Data SD4) UCE data sets produced nearly identical topologies, with the only notable difference being lower nodal support values resulting from analysis of the restricted data set. In the ASTRAL trees, the placement of *Palawanosorex* is strongly supported by local posterior probabilities (Fig. 11; Supplementary Data SD4). In the concatenated UCE trees, crocidurine relationships consist of a basal relationship that is essentially a polytomy among *Palawanosorex*, *Scutisorex* + *Sylvisorex* + *Ruwenzorisorex*, and all remaining crocidurines (Supplementary Data SD3 and SD4). This same ambiguity is illustrated in our time-calibrated tree (concatenated

Table 3.—Cranial measurements of *Palawanosorex muscorum*, *Crocidura palawanensis*, and *Suncus murinus luzoniensis*. Mean \pm SD (top), range (middle), and sample size (bottom). Measurements defined in the text and in Fig. 2.

Measurement	<i>Palawanosorex muscorum</i>	<i>Crocidura palawanensis</i>	<i>Suncus murinus</i>
GLS	24.61 \pm 0.44 23.81–25.29 13	23.82 \pm 0.64 22.61–25.37 23	26.47 \pm 0.58 25.25–27.26 10
CIL	24.49 \pm 0.46 23.77–25.25	23.74 \pm 0.63 22.44–25.37	26.70 \pm 0.60 25.46–27.46
PL	10.13 \pm 0.38 9.38–10.70 16	10.04 \pm 0.33 9.58–10.99 23	11.34 \pm 0.39 10.65–11.79 10
MB	7.39 \pm 0.21 7.07–7.78 17	7.07 \pm 0.20 6.73–7.50 24	8.48 \pm 0.45 7.77–9.29 10
RW	2.65 \pm 0.15 2.45–2.99 16	2.61 \pm 0.12 2.43–2.86 23	3.13 \pm 0.23 2.76–3.49 10
WAB	1.79 \pm 2.05 1.10–1.55 18	1.25 \pm 0.11 1.09–1.47 23	1.53 \pm 0.19 1.19–1.83 10
IO	5.43 \pm 0.15 5.19–5.71 15	5.06 \pm 0.14 4.82–5.39 24	5.11 \pm 0.15 4.88–5.48 10
GW	10.89 \pm 0.22 10.63–11.29 15	9.88 \pm 0.19 9.43–10.16 24	10.88 \pm 0.29 10.39–11.34 10
HCC	6.23 \pm 0.15 6.01–6.52 15	5.70 \pm 0.21 5.24–6.09 24	6.05 \pm 0.19 5.74–6.35 10
PGL	7.32 \pm 0.19 7.02–7.76 16	6.81 \pm 0.22 6.42–7.47 24	7.59 \pm 0.78 6.77–7.89 10
UTR	10.90 \pm 0.23 10.47–11.26 16	10.52 \pm 0.34 10.06–11.36 23	11.60 \pm 0.38 11.12–12.21 10
P4–M3	6.02 \pm 0.17 5.87–6.33 17	5.83 \pm 0.20 5.45–6.33 23	6.34 \pm 0.20 6.06–6.54 10
M3L	0.82 \pm 0.06 0.72–0.91 17	0.84 \pm 0.05 0.72–0.94 23	0.86 \pm 0.11 0.66–1.02 10
M3W	1.47 \pm 0.14 1.29–1.83 17	1.52 \pm 0.09 1.37–1.70 23	1.68 \pm 0.08 1.57–1.82 10
LI1	2.27 \pm 0.16 2.00–2.64 17	2.44 \pm 0.26 1.90–2.81 21	3.04 \pm 0.32 2.42–3.53 10
ML	15.62 \pm 0.33 15.18–16.12 17	14.87 \pm 0.52 14.08–16.07 24	16.53 \pm 0.51 15.60–17.30 10
COR	5.78 \pm 0.21 5.42–6.19 17	5.45 \pm 0.21 5.12–6.09 24	6.42 \pm 0.38 6.07–7.35 10
CONW	1.65 \pm 0.10 1.44–1.84 17	1.64 \pm 0.15 1.33–1.89 24	2.15 \pm 0.18 1.89–2.86 10
CONH	1.91 \pm 0.18 1.66–2.32 17	2.28 \pm 0.25 1.72–2.77 24	2.68 \pm 0.30 2.25–3.39 10
LTR	10.16 \pm 0.28 9.60–10.82 17	9.82 \pm 0.33 9.32–10.57 24	10.66 \pm 0.35 10.19–11.12 10
m1–m3	5.07 \pm 0.17 4.83–5.46 17	4.91 \pm 0.17 4.52–5.24 24	5.32 \pm 0.19 5.06–5.57 10
Li1	3.95 \pm 0.29 3.33–4.44 17	4.13 \pm 0.25 3.75–4.51 23	4.80 \pm 0.32 4.32–5.37 10

Table 4.—Component loadings of the principal component analysis (PCA) comparing *Palawanosorex muscorum*, *Crocidura palawanensis*, and *Suncus murinus* (see Fig. 15).

Axis	1	2	3
CIL	0.977	0.001	-0.026
GSL	0.972	0.044	-0.027
PL	0.907	-0.166	-0.083
MB	0.939	-0.074	-0.225
RW	0.854	-0.290	-0.080
IO	0.279	0.827	0.153
GW	0.755	0.553	-0.111
HCC	0.585	0.637	0.039
PGL	0.734	0.326	-0.363
UTR	0.962	0.081	0.139
P4–M3	0.915	0.126	0.135
LI1	0.673	-0.555	0.257
ABW	0.683	-0.119	0.012
M3L	0.235	-0.069	-0.399
M3W	0.565	-0.359	-0.312
ML	0.940	0.222	0.023
Li1	0.723	-0.433	0.102
COR	0.888	0.024	-0.030
LTR	0.897	0.148	0.175
LM13	0.841	0.099	0.347
COW	0.842	-0.206	-0.059
COH	0.471	-0.666	0.120
Eigenvalue	13.6	2.9	1.3
Variance explained	61.6%	13.0%	5.9%

analysis of *Cytb*, *Bdnf*, and *Rag1*, where after the divergence of *Solisorex* from all other crocidurines, the relationships among *Palawanosorex*, *Scutisorex* + *Ruwenzorisorex*, and *Suncus* + *Feroculus* + *Crocidura* + *Paracrocidiura* + *Diplomesodon* are unclear (Fig. 12). Nonetheless, the time-calibrated tree illustrates that *P. muscorum* diverged from its closest living relative approximately 9.6 Ma (95% highest posterior density interval: 7.4–11.9 Ma). Overall, the phylogenetic placement of *Palawanosorex* is strongly supported only in the ASTRAL trees (Fig. 11; Supplementary Data SD4). All DNA sequences generated as part of this project are available online as individual GenBank accessions (Table 1) or as part of NCBI BioProject PRJNA433997.

Distribution.—*Palawanosorex muscorum* is currently known only from Mt. Mantalingahan in southern Palawan Island, in the southwestern portion of the Philippines (Fig. 1; Mallari et al. 2001). Mt. Mantalingahan is an isolated highland area composed principally of Cretaceous igneous rock that originated as an ophiolite (i.e., material from the ocean floor that has been emplaced on land—Mines and Geosciences Bureau 2010). The soils produced by ophiolites are low in silica and rich in magnesium and iron, which results in low rates of plant growth and generally low nutrients and plant productivity (Fernando et al. 2008). Maximum elevation of the peak is 2,086 m.

Habitats and ecology.—From 19 June to 25 July 2007, our field team (led by DSB) sampled small mammals at 7 locations along the elevational gradient (Table 5). These localities encompassed substantial variation in vegetative composition and structure. Forest was largely absent below about 700 m due to intensive logging and agriculture; above 1,100 m, the terrain was steep (Supplementary Data SD5). We failed to detect *P. muscorum*

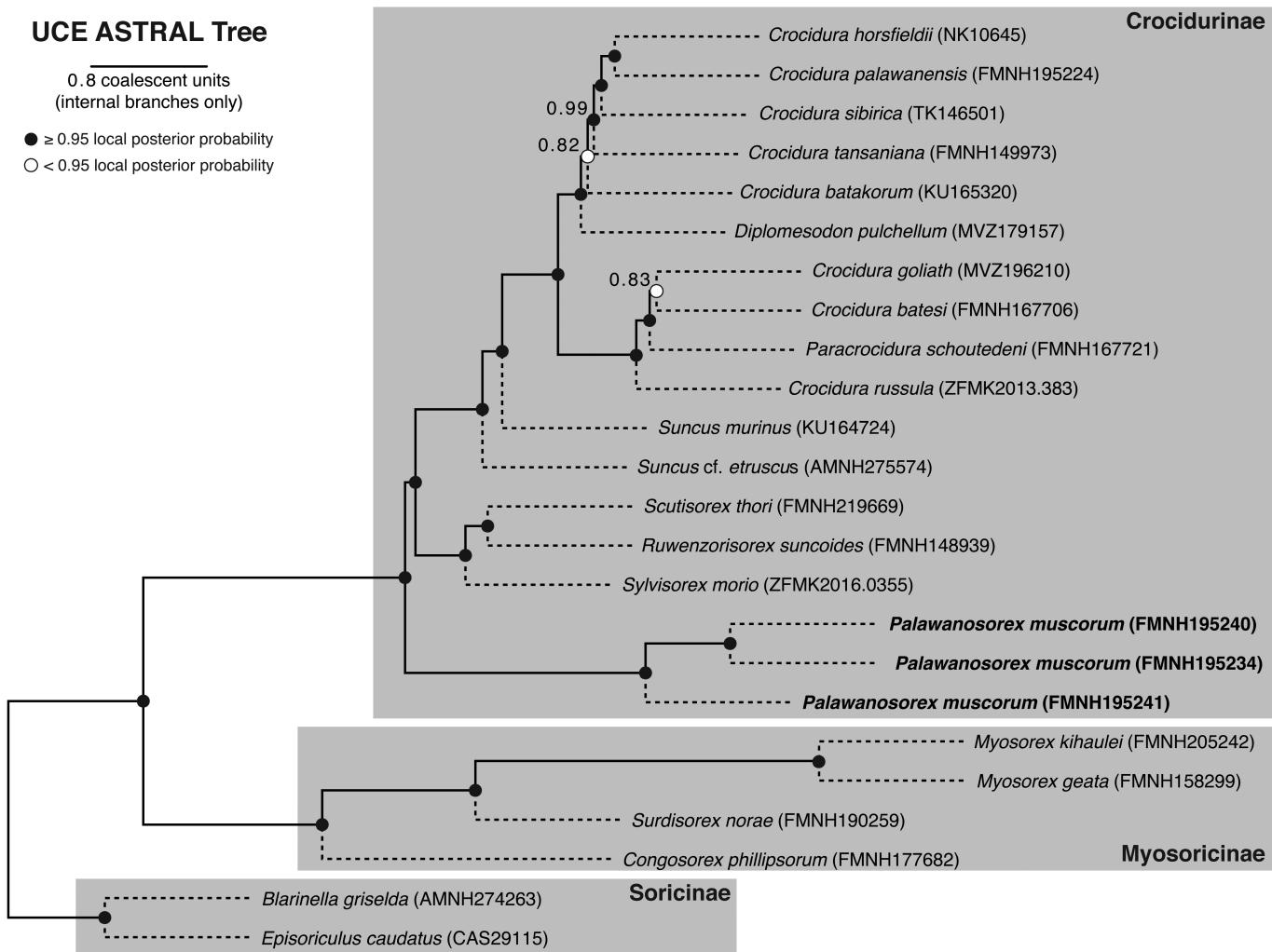


Fig. 11.—Coalescent species tree estimate derived from ASTRAL analysis of ultraconserved elements (comprehensive data set of 3,630 loci). Numbers at nodes denote local posterior probabilities. Tip branches (dotted lines) have arbitrary lengths, whereas internal branches (solid lines) are in coalescent units. The outgroup *Hylomys suillus* was included in the analysis but has been pruned from the figure.

from 700 to 1,300 m (Table 5). At 700 m, patches of 2nd growth forest were interspersed among agricultural areas. We sampled in areas of previously logged, regenerating lowland forest in which dipterocarps (Dipterocarpaceae), figs (*Ficus*), and wild banana (*Musa* spp.) predominated, and bamboos were common along trails. Moss was scarce and leaf litter was nearly absent. At 900 m, previously logged transitional lowland-montane forest dominated by dipterocarps and figs had some montane elements (e.g., *Tristaniopsis* and *Quercus*); moss was scarce but leaf litter was somewhat more common. Forest at 1,100 m was similar to that at 900 m, but less disturbed, some larger trees were present, and some moss on tree trunks and a thin layer of leaf litter were present. At our 1,300 m sampling area, the vegetation was montane forest lightly disturbed by a few clearings and some trails, with *Tristaniopsis*, *Dacrycarpus*, and *Agathis* commonly reaching 20 m. Figs were rare, and wild bananas absent; *Freyinetia* vines were common. Moss cover on trees, fallen logs, and exposed rock was common, and viney bamboos (genus *Dinnochloa* or *Schizostachyum*), ferns, begonias, and orchids were abundant in the understory; leaf litter thinly covered the ground.

Palawanosorex muscorum was among the most common species from 1,550 to 1,950 m (Table 5). Along this portion of the gradient, anthropogenic disturbance was largely absent. At 1,550 m, mature montane forest on ultramafic soil had a canopy at 7–10 m, with areas of heath forest with canopy at only 2–3 m. *Callophylum*, *Dacrycarpus*, *Leptospermum*, *Podocarpus*, *Quercus*, and *Tristaniopsis* were the most common trees; epiphytes included mosses, ferns, and lichens, with few vines. Understory plants included *Medinilla*, *Ardizia*, viney bamboo, *Dracaena*, and *Rhododendron*. Ground cover consisted of sedges, ferns, orchids, pitcher plants, and viney bamboo. Leaf litter was continuous and moderately thick, and moss was abundant on the ground and up to 2 m on tree trunks. The vegetation at 1,750 m was similar, but nearly all was brushy, heath-like forest with canopy of 1–3 m, and moss was even more abundant. At 1,950 m, we sampled in low heath forest; a few emergents (*Dacrycarpus*, *Callophylum*) reached 5 m in sheltered terrain, but most trees (also including *Quercus* and *Syzygium*) were 2–3 m tall. *Psychotria*, *Rhododendron*, and bamboo were common. Moss covered many of the tree trunks and branches,

**CYTB, BDNF, and RAG1
Concatenated**

● ≥ 0.95 PP
○ < 0.95 PP

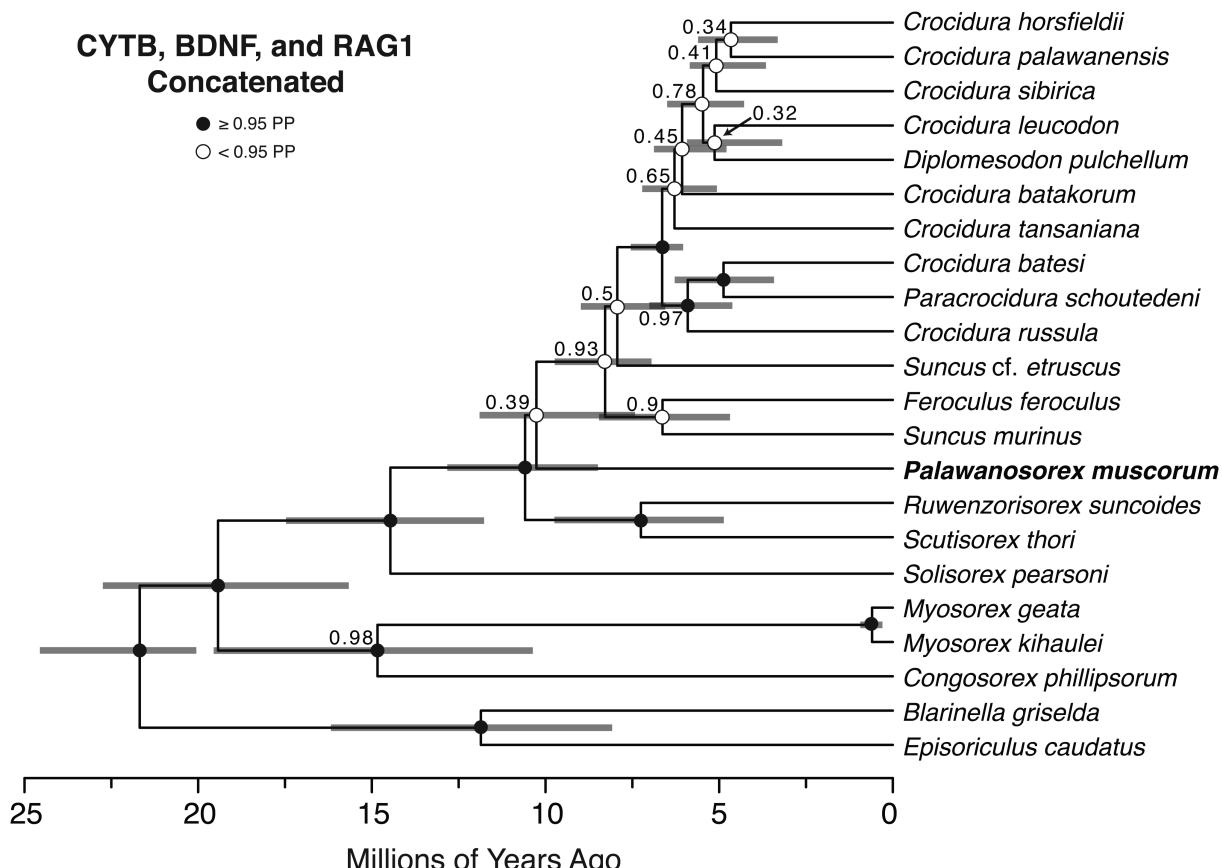


Fig. 12.—Time-calibrated phylogeny estimated from a partitioned, fossil-calibrated BEAST analysis of concatenated *Cytb*, *Bdnf*, and *Rag1* sequences. Nodes without numbers have posterior probabilities = 1.0. Gray bars denote the 95% highest posterior density intervals for node age.

and nearly the entire forest floor was covered with moss. Ferns and orchids grew abundantly on the ground and as epiphytes.

We had a total of 7,083 trap-nights along our transect (Table 5). The 4 middle sampling localities had similar trapping efforts, but the limited area of forest at 700 m, and limited accessibility of our localities at 1,750 and 1,950 m, resulted in about one-half the number of trap-nights (Table 5). In total, we captured 8 species of small mammals, all of which are native and 7 of which are endemic to the Palawan faunal region (Heaney 1986), with only *Sundamys muelleri* being more widespread (Table 5). Species richness (documented or inferred from presence above and below on the elevational gradient) varied from 3 to 5, with the maximum species richness at 1,750 m. The non-endemic *S. muelleri* was uncommon, occurring only from 700 to 1,300 m in areas with anthropogenic disturbance. Two species (*Tupaia palawanensis* and *Chiropodomys calamianensis*) occurred only in disturbed lowland forest, which is consistent with prior records (Esselstyn et al. 2004). *Maxomys panglima*, a Palawan faunal region endemic, was the most abundant species overall and occurred at all localities, but was less abundant at the 2 highest localities. *Crocidura palawanensis*, which is known to occur down to sea level in the vicinity of Mt. Mantalingahan (Esselstyn et al. 2004; Heaney et al. 2010), probably also occurred along the entire gradient. Three species occurred only at medium to high elevations (*P. muscorum*, *Sundasciurus rabori*, and *Palawanomys furvus*; Table 5 and prior records in Esselstyn

et al. 2004); all 3 are known only from Mt. Mantalingahan and are likely endemic to the mountain.

We recorded whether each mammal captured was taken on the ground or above the ground surface, captured with fried coconut or live earthworms as bait, and whether the captures occurred during daylight or at night. Both shrew species were captured predominantly on the ground, but *C. palawanensis* was taken more frequently above the ground (8 of 30 captures) than *Palawanosorex* (2 of 21 captures); field notes indicate that some *Crocidura* were captured on tree trunks up to 2 m above ground, while the *Palawanosorex* were captured at most 0.5 m above ground. Additionally, *Palawanosorex* was captured proportionately more frequently (11 of 22) with earthworm bait than was *C. palawanensis* (7 of 30 captures). Both were captured predominantly at night, with no difference evident.

Reproduction.—Of 12 female *Palawanosorex*, 7 had enlarged nipples. Three pairs of teats were present, always in the inguinal region and equally spaced. An adult female captured on 1 July 2007 carried a single embryo (7 mm length). In 1 male (FMNH 195239) the penis was visible; the glans was rounded, wrinkled, and 3 mm long.

DISCUSSION

Morphology.—*Palawanosorex muscorum* is a distinctive, uniformly dark shrew with long dorsal pelage, a short tail,

Table 5.—Summary of captures and trapping effort on Mt. Mantalingahan, Palawan Island, Philippines. For descriptions of the habitats, see text.

Species	Elevation (m) of sampling locality							
	700	900	1,100	1,300	1,550	1,750	1,950	Total
<i>Tupaia palawanensis</i>	0	1	0	0	0	0	0	1
<i>Crocidura palawanensis</i>	0	0	0	0	11	7 ^c	4	22
<i>Palawanosorex muscorum</i>	0	2	0 ^a	5	14 ^b	6	3	30
<i>Chiropodomys calamianensis</i>	2	0	0	0	0	0	0	2
<i>Sundasciurus rabori</i>	0	0	0	0	0	1	0	1
<i>Maxomys panglima</i>	22	37	27	32	27	5	6	156
<i>Palawanomys furvus</i>	0	0	0	0	12	8	8	28
<i>Sundamys muelleri</i>	2	5	1	1	0	0	0	9
Total captures	26	45	28	38	64	27	21	249
Trap-nights—ground	491	1,176	1,202	968	1,233	614	418	6,102
Trap-nights—arboreal	206	133	79	329	62	40	132	981
Total trap-nights	697	1,309	1,281	1,297	1,295	654	550	7,083

^a Inferred to be present from presence above and below along the transect.^b One hand-captured specimen excluded from tally.^c Includes one discarded specimen that had been partially consumed.

broad feet, and long claws (Figs. 4A and 5; Supplementary Data SD2). Its external ears are small but well visible, indicating a terrestrial lifestyle with a tendency toward subterranean habits (Hutterer 1985). In Southeast Asia, the new genus has no counterpart; there are other middle-sized, blackish shrews on Borneo (*S. ater*, *Crocidura baluensis*, *C. foetida*), Sumatra (*C. lepidura*), and Java (*C. brunnea*, *C. orientalis*), but they all have tails with at least a portion near the base covered by long bristle hairs and limbs without long claws; all have the plantar surface granulated (Ruedi 1995), except that of *S. ater*, in which it is scaly. The structures on the palm and sole of shrews are highly variable (Hutterer 1985) and may serve to distinguish between genera, and sometimes also between species. These structures clearly discriminate between *Palawanosorex*, *Crocidura*, and *Suncus*. In all *Crocidura* species, be it in the Philippines (Heaney and Ruedi 1994:figure 5) or in Africa (Stanley et al. 2015:figure 7), the space between the interdigital pads and the thenar and hypothenar are covered by numerous small granule-like bumps. In *Palawanosorex*, the same area is smooth, and in *S. murinus* it is covered by large scales (Figs. 4 and 6; Supplementary Data SD2). Future work may show whether all species of *Suncus* have this pattern. Externally similar, but phylogenetically distant shrews occur in Africa (*Myosorex*; see Hutterer 2005a; Kerbis Peterhans et al. 2011) and South America (*Cryptotis*; see Woodman and Péfau 2008). Most of those species occur in montane forests or grasslands at higher elevation, suggesting an element of morphological convergence in the feet, tails, and pelage of these distant relatives.

Palawanosorex has highly unusual cranial characters. The most remarkable is the dorsal fissure of the skull, which is open or at least translucent in most specimens; posterior to the fissure, 2 dorsal foramina are closed by a thin bone layer in many of the specimens (Fig. 8). Dorsal foramina are present in all species of soricine, neomyine, and myosoricine shrews, but they are lacking in most crocidurine shrews (Repenning 1967), suggesting this is an ancestral trait retained in *Palawanosorex*,

but lost in other crocidurines. An open dorsal fissure has only been observed in the myosoricine *C. phillipsorum*, a Tanzanian endemic. Like in *Palawanosorex*, the fissure is present in adults of *C. phillipsorum* (Stanley et al. 2005). However, in contrast to *Palawanosorex*, the paired dorsal foramina of *C. phillipsorum* are placed anterior to the dorsal fissure (Stanley et al. 2005:figure 6). More variation exists in the number and position of these foramina within the Soricidae, but this trait has not been studied in detail. Another remarkable character is the additional small cusp, present at low frequency, on M1, just between the protocone and hypocone (Fig. 10), a feature not seen in any other shrew.

Molecular phylogeny.—Our phylogenetic results are derived from both small and large samples of the genome. They agree in that they place *Palawanosorex* on a long branch but disagree somewhat as to the sister group. Our species trees and concatenated analyses of thousands of UCE loci strongly supported a sister relationship to all other crocidurines (Fig. 11; Supplementary Data SD3 and SD4), but this data set lacked *Solisorex* and *Feroculus*. Our dated inference relying on 3 loci included these genera but also exhibited greater topological uncertainty (Fig. 12). If we treat the poorly supported nodes from this analysis as a polytomy, then *Palawanosorex* is sister to either *Ruwenzorisorex* + *Scutisorex*, or *Suncus* + *Feroculus* + *Crocidura* + *Paracrocidura* + *Diplomesodon*, or both (Fig. 12). In any event, these topologies document the phylogenetic uniqueness of *Palawanosorex*, with an estimated divergence from other genera some 10 Ma (Fig. 12). Interestingly, it is also clear that the sister group of *Palawanosorex* is either entirely, or largely dominated by, African species. As such, *Palawanosorex* seems to fit the pattern of a relictual lineage, isolated by great geographical and temporal distances from its closest living relatives. Similar, apparently relictual patterns with a single Southeast Asian species most closely related to African taxa have been noted in birds (e.g., Jónsson et al. 2007), but biogeographic explanations are necessarily speculative.



Fig. 13.—*Palawanosorex muscorum* (upper, FMNH 195235, a female) and *Crocidura palawanensis* (lower, FMNH 195215, a male) in their natural habitat on Mt. Mantalingahan. Photos taken on 21 and 22 June 2007 by DSB.

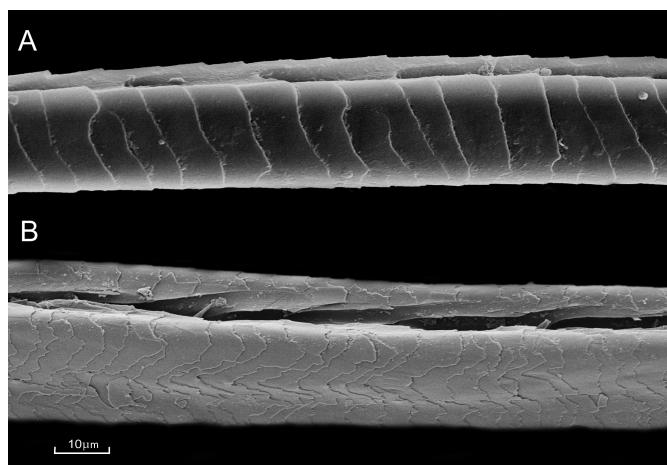


Fig. 14.—Scanning electron micrographs showing microstructure of curly overhairs of (A) *Palawanosorex muscorum* (FMNH 195238) and (B) *Crocidura palawanensis* (FMNH 195230).

Ecology and biogeography.—Of the 8 species we documented on Mt. Mantalingahan, none were non-native, even though our 3 lowest localities were in forest patches in areas

of extensive anthropogenic disturbance. This follows the pattern on Luzon, where non-native species are rare or absent in secondary or mature forest (Rickart et al. 2011; Heaney et al. 2016). Although the intensity of our sampling was uneven, we found that increasing species richness along the elevational gradient parallels that on Luzon, with maximum species richness at 1,750 m, potentially reflecting a mid-domain effect (McCain 2005). As such, *P. muscorum* occurs in a high-elevation small mammal community composed solely of native species, where species richness, and probably total abundance, are high. On the mountain as a whole, all but 1 of the species is endemic to the Palawan Faunal Region; the exception (*S. muelleri*) is widespread on Borneo and other portions of the Sunda Shelf (Musser and Newcomb 1983). Over the documented elevational range of *P. muscorum*, it and 2 other species (*S. rabori* and *P. furvus*) are probably endemic exclusively to Mt. Mantalingahan. *Palawanosorex* is thus a member of a distinctive fauna that reaches its greatest richness in mossy forest at high elevation. Because our survey is the 1st comprehensive study of the small terrestrial mammal fauna on any high peak on Palawan, we do not know if other high-elevation areas of endemism are present, as is the case on larger islands (Heaney et al. 2016).

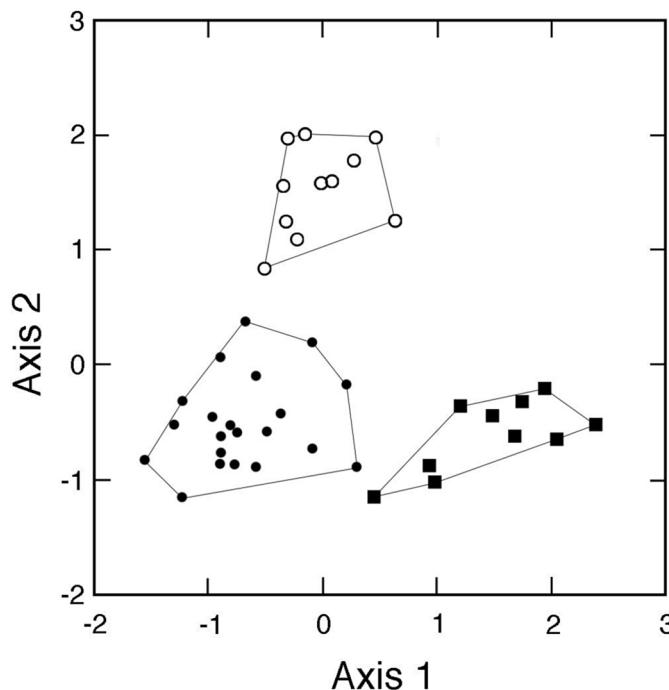


Fig. 15.—Bivariate plot of principal components 1 and 2 from analysis of 22 log-transformed craniodental variables for specimens of *Palawanosorex muscorum* (open circles), *Crocidura palawanensis* (black dots), and *Suncus murinus luzoniensis* (black squares).

The similar patterns of endemism with elevation are not the result of Palawan and Luzon sharing a closely related fauna. No species of small terrestrial mammals are shared by the islands and, at the generic level, only *Crocidura* and *Rattus* occur on both Luzon and Palawan. The non-volant mammals of Palawan show consistent evidence of having their closest relatives on Borneo and adjacent parts of continental Southeast Asia (Heaney 1986; Esselstyn et al. 2004, 2010; Piper et al. 2011; Supplementary Data SD6). In this regard, the relationships of *P. muscorum* are enigmatic. The species apparently has no extant, close relatives and its most likely sister groups are dominated by African species. The existence of *P. muscorum* in Southeast Asia implies that the Crocidurinae have been present in the region since perhaps 10 Ma, and that some level of exchange with Africa has been a fundamental feature of the history of this subfamily since its origin. Currently unassigned fossil shrews from Flores (Van den Hoek Ostende et al. 2007) may also provide evidence of an early Asian shrew fauna that differed dramatically from the extant fauna.

This leaves open the question of how this distinctive genus came to occur on Palawan. The geological history of the island is complex and uncertain in important respects. The primary geological units that now constitute Palawan originated as continental rock, rifting from what is now southern China ca. 40 Ma, and reaching the current position about 5 Ma (Hall 1998, 2013). Uplift of the current mountains probably began not more than 5 Ma, with Mt. Mantalingahan and other Palawan high peaks reaching their current elevations more recently. Given this history, it seems unlikely that *P. muscorum* occurred on Palawan before 5 Ma and may have arrived much more

recently. Given the biogeographic relationships of Palawan's other mammals, it seems likely that *Palawanosorex* arrived via Borneo within the last few million years. We hypothesize that *Palawanosorex* reached Palawan from Borneo during one of the periods of Pleistocene low sea level, when the 2 islands either were joined by a continuous land bridge or were separated by only a narrow channel (Esselstyn et al. 2004; Piper et al. 2011). If this was the case, a living relative may yet be found on Borneo or other nearby area. Given that shrews are currently rather poorly sampled on Borneo, especially at high elevation, we recommend that comprehensive surveys be conducted.

ACKNOWLEDGMENTS

This work was funded by the Field Museum's Barbara Brown Fund for Mammal Research and the National Science Foundation (OISE-0965856, DEB-1343517, and DEB-1441634). We thank the late W. T. Stanley, J. C. Kerbis Peterhans (FMNH, Chicago), J. Decher (ZFMK, Bonn), J. Patton and C. Conroy (MVZ, Berkeley), R. Voss (AMNH, New York), J. Cook (MSB, Albuquerque), H. Garner (TTU, Lubbock), J. Dumbacher (CAS, San Francisco), and R. Timm (KU, Lawrence) for providing tissues, and M. Omura and H. Hoekstra (MCZ, Harvard) for access to collections. E. Rickart conducted the PCA analysis; K. Ulmen and B. Strack performed the SEM micrographs. L. Uí Dhalaigh and K. Kueffner assisted in designing the figures. Research permits were provided by the Palawan Council for Sustainable Development and the Department of Environment and Natural Resources. Field work was coordinated by the Katala Foundation and Conservation International, Palawan; our team included J. Sarmiento, N. Antoque, and H. Garcia. The work of RH at the Field Museum was supported by a Bass Senior Fellowship in 2017. This manuscript was improved by constructive criticism by 2 anonymous reviewers and the associate editor.

SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Mitochondrial cytochrome *b* (*Cytb*) Bayesian gene tree.

Supplementary Data SD2.—Additional photographs and figures of the new species; captured animals compared with *Crocidura palawanensis*; details of external features, ear, and feet of *Palawanosorex muscorum* and *C. palawanensis*.

Supplementary Data SD3.—Concatenated ultraconserved elements (UCEs) maximum likelihood tree based on comprehensive data set.

Supplementary Data SD4.—Coalescent species tree and concatenated ultraconserved elements (UCEs) maximum likelihood tree based on restricted data set.

Supplementary Data SD5.—Habitat photographs of capture sites on Mt. Mantalingahan at elevations 1,550, 1,750, and 1,950 m.

Supplementary Data SD6.—Checklist of native non-volant small mammals of Palawan Faunal Region, indicating which species occur on Palawan Island and on Mt. Mantalingahan.

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Submitted 29 November 2017. Accepted 27 March 2018.

Associate Editor was Ricardo Moratelli.

APPENDIX I

Specimens examined in this study ($n = 83$); acronyms are explained in the “Materials and Methods” section:

Crocidura batakorum ($n = 1$).—PHILIPPINES: Palawan, 60 km NE Puerto Princesa, Tanabag River valley near village Kalabayog, $10^{\circ}07'00.1''N$, $118^{\circ}53'09.3''E$, 200 m (ZFMK 1996.0411, holotype; type locality here corrected).

Crocidura palawanensis ($n = 31$).—PHILIPPINES: Palawan; Rizal Municipality, 4.14 km W, 0.75 km S Mt. Mantalingahan, 900

m, 08.81267°N, 117.63784°E (FMNH 195233, 195996); 3.4 km W, 0.6 km S Mt. Mantalingahan, 1,300 m, 08.81352°N, 117.64975°E (FMNH 195229–195232, 195995); 2.5 km W, 0.7 km S. Mt. Mantalingahan peak, 1,550 m, 08.81264°N, 117.65871°E (FMNH 195214–195222, 195225, 195986–195990); 2.0 km W, 0.7 km S. Mt. Mantalingahan peak, 1,750 m, 08.81301°N, 117.66313°E (FMNH 195223–195224, 195226, 195991, 195993).

Feroculus feroculus ($n = 2$).—SRI LANKA: Central Province, Nuwara Eliya, 7,000 feet (FMNH 99453–99454).

Palawanosorex muscorum ($n = 21$).—PHILIPPINES: Palawan, Rizal Municipality, 2.5 km W, 0.7 km S. Mt. Mantalingahan peak, 1,550 m, 08.81264°N, 117.65871°E (FMNH 195234–195239, 195242, 195997–196000); 2.0 km W, 0.7 km S. Mt. Mantalingahan peak, 1,750 m, 08.81301°N, 117.66313°E (FMNH 195240–195241, 195243–195244, 196001–196002); 1.7 km W, 0.9 km S. Mt. Mantalingahan peak, 1,950 m, 08.81130°N, 117.66699°E (FMNH 195245–195246, 196003–196004).

Solisorex pearsoni ($n = 1$).—SRI LANKA: Uva Province, Welimada, 5,000 feet (FMNH 108990).

Suncus ater ($n = 1$).—MALAYSIA: Sabah, Gunung Kinabalu, 5,500 feet (MCZ 36574, holotype).

Suncus montanus ($n = 10$).—SRILANKA: Central Province, Medamahanuwara, 3,500–3,750 feet (FMNH 99433–99435, 99437, 99439, 99441–99443); Central Province, NW Diyagama West, Agrapatana, 5,000–6,000 feet (FMNH 95042, 96285).

Suncus murinus ($n = 12$).—PHILIPPINES: Palawan, Puerto Princesa City (ZFMK 1996.0412); Taytay (FMNH 230754, paratype of *Pachyura palawanensis* Taylor, 1934); Luzon I., Cagayan Province, Penablanca Munic, 590 m (FMNH 216381, 216382); Bataan Province, 0.7 N, 0.2 km W Mt. Natib peak, 900 m (FMNH 183279–183286).

Suncus niger ($n = 4$).—INDIA: Tamil Nadu, S Kodaikanal, Pambar River, 6,000–7,000 feet (FMNH 82529–82532).