

Systematic revision and species diversification of the genus *Episoriculus*
(Mammalia: Eulipotyphla: Soricidae), with descriptions of two new species

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ABSTRACT

Small insectivorous shrews of the genus *Episoriculus* (Soricidae: Nectogalini) are distributed primarily across the Himalaya-Hengduan Mountains. The taxonomy of the genus has remained unstable because earlier classifications relied mainly on morphology and geographically restricted materials. We conducted extensive field surveys across the region, sequenced two mitochondrial and six nuclear genes, and generated complete mitogenomes for representative operational taxonomic units (OTUs) to evaluate phylogenetic relationships. We also measured five external and 19 craniodental characters to evaluate morphometric variation. The analyses identify two previously unrecognized species, *E. gaoligongensis* sp. nov. from the Gaoligong Mountains of Yunnan and Medog

in southeastern Xizang, and *E. damuensis* sp. nov. endemic to Medog. Our integrative evidence further supports recognition of eight valid species within *Episoriculus*: *E. caudatus*, *E. leucops*, *E. macrurus*, *E. sacratus*, *E. soluensis*, *E. umbrinus*, *E. gaoligongensis* sp. nov., and *E. damuensis* sp. nov. We treat *E. baileyi* as a subspecies of *E. leucops* and clarify morphological delimitation criteria and distribution ranges for these taxa. Divergence-time estimates suggest that major splits within *Episoriculus* occurred from the Miocene to the Pleistocene, broadly consistent with a history shaped by interacting geological, climatic, ecological, and geographic processes in the Himalaya-Hengduan Mountains. More broadly, our results highlight the importance of integrative taxonomy and caution against relying on short mitochondrial fragments alone when delimiting species in rapidly diversifying montane mammals.

Keywords: Small mammals; Taxonomy; Phylogeny; New species; Himalaya; Hengduan Mountains

INTRODUCTION

Global biodiversity is under increasing pressure, making the discovery, delimitation, and formal description of species central to both taxonomy and conservation biology (Wilson, 2005). This task is especially important in regions where faunal inventories remain incomplete, and species diversity is still being rapidly revised. China, which harbors one of the richest mammalian faunas in the world, exemplifies this pattern: the number of recognized mammal species has increased from 572 in 2005 (Hutterer, 2005) to 736 in the most recent national catalogue (Wei et al., 2025). Much of this increase reflects continued taxonomic revision and the discovery of previously unrecognized diversity, particularly in topographically complex regions.

The Himalaya-Hengduan Mountains (HHM) region represents one of the world's most important biodiversity hotspots and forms the core area of both the Himalaya and Mountains of Southwest China hotspots, while its southern extension also overlaps with the Indo-Burma biodiversity hotspot (Mittermeier et al., 2011). This region served as an important refugium for many organisms during Quaternary glaciations and preserves exceptionally high levels of endemism (Zhang, 2002). In addition, the north-south-oriented mountain systems of the Hengduan Mountains likely functioned as major dispersal corridors for montane biota during glacial-interglacial climatic oscillations (Zhang, 2002). Despite extensive recent work, the HHM region remains a major center of unresolved small-mammal diversity, where species limits and distributions are still poorly understood for many taxa (Jiang et al., 2015; Li et al., 2024). Continued surveys in this region have revealed numerous previously unrecognized taxa (Chen et al., 2021, 2024; Wang et al., 2024; Li et al., 2025; Song et al., 2025; Zhu et al., 2025), indicating that its mammalian diversity remains substantially underestimated. At the same time, the historical processes associated with small-mammal diversification in the HHM region remain incompletely understood, particularly the relative roles of climatic oscillations, ecological heterogeneity, and geographic isolation.

The genus *Episoriculus* Ellerman and Morrison-Scott, 1951 (Mammalia: Eulipotyphla: Soricidae) represents an excellent model for investigating the influence of Neogene environmental and climatic change on the evolution of Himalayan and Hengduan

Mountain small mammals. Species of *Episoriculus* are small insectivorous shrews distributed mainly throughout the Himalaya-Hengduan Mountains, and are among the most common small mammals in this region. Most *Episoriculus* species inhabit montane and subalpine forests at elevations of approximately 1000-4000 m and exhibit strong habitat associations. However, the remoteness and topographic complexity of much of their range have constrained geographically comprehensive sampling. Consequently, *Episoriculus* remains one of the most taxonomically problematic small mammal lineages in China.

Episoriculus was originally treated by Ellerman and Morrison-Scott (1951) as a subgenus of *Soriculus*, and was elevated to full generic rank in the revised second edition of their checklist (Ellerman & Morrison-Scott, 1966). Repenning (1967) also noted substantial cranial and dental differences among *Episoriculus*, *Chodsigoa*, and *Soriculus* and gave *Episoriculus* a generic status. Nevertheless, several subsequent classifications continued to treat *Episoriculus* as a subgenus of *Soriculus* (Corbet, 1978; Hoffmann, 1985; Corbet & Hill, 1992; Wang, 2003). Hutterer (1994) again emphasized the morphological distinction between *Episoriculus* and *Soriculus*, and the generic status of *Episoriculus* has since been widely accepted in major taxonomic treatments (Hutterer, 2005; Burgin & He, 2018; Wei et al., 2025). Liu et al. (2025) largely followed Wei et al. (2022) while accepting the validity of *Pseudosoriculus* and further suggested that an undescribed species may occur in Xizang. These contrasting treatments mainly reflect differences in geographic sampling, specimen coverage, and the relative weight given to morphology, mitochondrial data, nuclear loci, karyotypes, and nomenclatural history; a geographically broad integrative reassessment is therefore required.

The main obstacle to resolving *Episoriculus* taxonomy has been the limited availability of geographically representative and reliably identified materials. Earlier studies were based largely on restricted local samples and morphology alone, conditions that likely contributed to misidentifications and unstable species boundaries. Over the past several decades, we conducted extensive small mammal surveys across the Himalaya-Hengduan Mountains, with particular attention to previously under-sampled localities, and assembled a large series of *Episoriculus* specimens. This material substantially expands current knowledge of the genus's distribution and habitat associations and provides a basis for reassessing species limits. Here, we integrate morphological and molecular evidence to

revise the taxonomy of *Episoriculus* and formally describe two new species from the Himalaya-Hengduan region.

MATERIALS AND METHODS

Specimen sampling

We examined 132 specimens assigned to *Episoriculus sensu lato*, including six specimens of *Pseudosoriculus fumidus*. Sampling localities are shown in Figure 1A. Specimens are deposited in the Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences, and Anhui Normal University. All animal handling procedures followed the ethical standards of Anhui Normal University and KIZ, and were approved by the Animal Ethics Committee of Anhui Normal University under approval number AHNU-ET2025028.

Initial specimen identifications followed Hoffmann (1985), Motokawa and Lin (2005), and Motokawa et al. (2008). To reduce errors associated with morphology-based identification, we sequenced the mitochondrial cytochrome b gene (*Cyt b*), reconstructed a gene tree together with published GenBank sequences, and then re-examined the morphology of each lineage. Based on the combined evidence from morphology and the *Cyt b* tree, specimens were assigned to 10 operational taxonomic units (OTUs) of *Episoriculus sensu lato* for comparative analyses: (1) *E. leucops* (n = 20), (2) *E. caudatus* (n = 7), (3) *E. umbrinus* (n = 23), (4) *E. sacratulus* (n = 5), (5) *E. soluensis* (n = 6), (6) *E. macrurus* (n = 46), (7) *P. fumidus* (n = 6), (8) six specimens from Medog, Xizang, and the Gaoligong Mountains, Yunnan, that were morphologically distinct from all known species and were assigned to a putative new species, *E. sp. 1*, (9) eight specimens from the Medog area that formed the sister lineage to *E. soluensis* but differed in body size and coloration and were assigned to a putative new species, *E. sp. 2*, and (10) five specimens of *E. macrurus* from Jiaozi Snow Mountain, Yunnan, which were morphologically similar to *E. macrurus* from other regions but formed a deeply divergent clade and were treated as a tentative species, *E. sp. 3*.

Morphological measurements and analyses

Ninety specimens with intact skulls were included in the morphological analyses. Only adult individuals were used, as confirmed by the full eruption of the permanent molars. Specimens with damaged skulls were excluded from the craniodental PCA and DA.

Because pronounced cranial sexual dimorphism sufficient to confound species-level comparisons has not been reported as a major issue in comparable taxonomic studies of soricids and other small insectivores, and because sample sizes for several rare taxa were limited, males and females were pooled in all morphometric analyses (Motokawa & Lin, 2005; Liu et al., 2025). Weight (W) and four external measurements-head and body length (HB), tail length (TL), hind foot length (HF), and ear length (EL)-were recorded in the field. Nineteen craniodental measurements were taken with digital calipers to the nearest 0.01 mm. These included: condyloincisive length (CIL), palatoincisive length (PIL), postpalatal length (PPL), rostral length (RL), postpalatal depth (PPD), interorbital breadth (IOB), cranial breadth (CB), maxillary breadth (MB), maximum width across the upper second molars (M^2 - M^2), upper toothrow length (UTL), distance from the anterior edge of the upper fourth premolar to the posterior edge of the upper third molar (P^4 - M^3), cranial height (CH), breadth of the foramen magnum (BMF), lower toothrow length (LTR), mandibular length (MdL), lower molar length (LM), height of the coronoid process (HCP), height of the coronoid valley (HCV), and height of the articular condyle (HAC). All craniodental measurements were taken by the first author. Measurement terminology and procedures followed Repenning (1967), Motokawa and Lin (2005), and Pan et al. (2007).

For each OTU, we calculated the range, mean, and standard deviation for each measured variable when sample size allowed (Table 1). For *E. sp. 3*, represented by only two intact skulls, we report only the observed values/range and did not calculate mean or standard deviation. We evaluated patterns of morphometric differentiation among OTUs using principal component analysis (PCA) and discriminant analysis (DA) performed in IBM SPSS Statistics for Windows, version v.19.0 (IBM Corp., Armonk, N.Y., USA). The PCA and DA were performed on the craniodental measurements only. All craniodental variables were $\log_{10}$ -transformed before analysis to improve normality. DA classification success was evaluated using both apparent/resubstitution classification and leave-one-out cross-validation.

Molecular data collection

Sixty-two specimens were selected for molecular analyses based on initial morphological screening and assignment. Total genomic DNA was extracted from tissue samples using a Tiangen tissue DNA extraction kit (TIANGEN Biotech Co., Ltd., Beijing,

China). We amplified two mitochondrial genes [*Cyt b* (1,140 bp) and 12S (816 bp)] and six nuclear genes [APOB (582 bp), BRCA1 (768 bp), RAG2 (675 bp), IRBP (1,233 bp), TTN (930 bp), and ATP7A (669 bp)] from newly sampled individuals. Homologous sequences from 21 *Episoriculus* individuals were downloaded from GenBank (Ohdachi et al., 2006; He et al., 2010; Liu et al., 2025), together with representative sequences from 11 other soricid genera, including all five other nectogaline genera (Supplementary Table S1).

Because mitochondrial gene trees reconstructed from *Cyt b* and 12S indicated that *E. macrurus* was not monophyletic with respect to other *Episoriculus* species, and because support values for some relationships were low (see Results), we generated complete mitochondrial genome data for at least one representative of each operational taxonomic unit (OTU), except *E. soluensis*, by combining our newly generated resequencing data with published GenBank sequences (Supplementary Table S2).

Phylogenetic analyses and molecular dating

Phylogenetic analyses were conducted in PhyloSuite (Zhang et al., 2020). Maximum-likelihood (ML) trees were reconstructed in IQ-TREE, and Bayesian inference (BI) trees were reconstructed in MrBayes using three concatenated datasets: (1) a two-gene mitochondrial dataset comprising *Cyt b* and 12S, with a final aligned length of 1,956 bp; (2) a six-gene nuclear dataset comprising APOB, BRCA1, RAG2, IRBP, TTN, and ATP7A, with a final aligned length of 4,857 bp; and (3) a mitochondrial genome dataset comprising 13 protein-coding genes and two rRNA genes, 12S and 16S. The best-fit substitution model for each partition was selected in PartitionFinder 2 under the Bayesian Information Criterion (BIC; Lanfear et al., 2017), and the partition schemes and models are provided in Supplementary Table S3.

Divergence-time analyses were based on the concatenated six-gene nuclear dataset. Following Yuan et al. (2024), three secondary calibrations were applied to the corresponding higher-level soricid nodes: (1) the Soricinae-Crocidurinae split at approximately 51.06 Ma, with mean = 51.38 and SD = 0.113; (2) the Blarinellini-Blarinini split at approximately 26.82 Ma, with mean = 27.20 and SD = 0.171; and (3) the earliest divergence within Nectogalini at approximately 28.04 Ma, with mean = 28.04 and SD = 0.147. Lognormal priors were used to incorporate uncertainty in the source estimates. Analyses used a random starting tree, an uncorrelated lognormal relaxed clock, and a birth-

death tree prior. Each BEAST analysis was run twice independently for 100 million generations and sampled every 10,000 generations. Convergence was assessed in Tracer, with the first 10% discarded as burn-in and effective sample size values exceeding 200. Phylogenetic trees were visualized and formatted in FigTree v.1.4.3.

RESULTS

Morphological variation

External and craniodental measurements for each OTU are provided in Table 1. Based on mean condyloincisive length (CIL), used here as an index of overall cranial size, we divided the sampled taxa into three size classes. The large-sized taxa, with mean CIL > 19.00 mm, included *E. leucops* and *E. caudatus*; *E. leucops* has a broader braincase and narrower rostrum than *E. caudatus*. The medium-sized taxa, with mean CIL between 18.00 and 19.00 mm, include *E. soluensis*, *E. sacratius*, *E. sp. 2*, and *P. fumidus*. Within this group, *E. soluensis* has a longer tail than the other three taxa. The small-sized taxa, with mean CIL < 18.00 mm, include *E. macrurus*, *E. umbrinus*, *E. sp. 1*, and *E. sp. 3*. These taxa differ mainly in relative tail length: *E. macrurus* and *E. sp. 3* have tail lengths 130-170% of head and body length; *E. sp. 1* has a tail slightly longer than head and body length; and *E. umbrinus* generally has a tail length less than or equal to head and body length. More detailed comparisons of external and craniodental morphology are provided in the Systematic account.

The PCA of 19 log₁₀-transformed craniodental variables from 90 intact skulls recovered two principal components with eigenvalues greater than 1.0 (Table 2). Together, these two axes explained 78.21% of the total variation. The first axis, PC1, explained 63.54% of the variance and was positively associated with all measured variables except PPD and BMF, with loadings > 0.61, indicating that this axis primarily reflects overall skull size. The second axis, PC2, explained 14.67% of the variance and was driven mainly by PPD and BMF, with loadings > 0.78.

In the PC1-PC2 morphospace (Figure 1B), *E. sp. 3* overlapped broadly with *E. macrurus*, and together they occupied the negative region of PC1 and the positive region of PC2, indicating a relatively small skull combined with larger PPD and BMF values. *Episoriculus leucops* and *E. caudatus* occupied the far positive region of PC1, consistent with their larger skulls. *Episoriculus leucops* also scored higher on PC2 than *E. caudatus*,

reflecting larger PPD and BMF values. *Episoriculus umbrinus* had the lowest PC2 scores and overlapped partly with *E. soluensis*, indicating smaller PPD and BMF values. *Pseudosoriculus fumidus*, *E. sacratu*s, and *E. sp. 2* overlapped broadly, whereas *E. soluensis* showed wide dispersion, suggesting substantial cranial variation within it. *Episoriculus sp. 1* occupied the central region of the morphospace close to *E. sacratu*s but did not overlap with any other taxon.

In the discriminant analysis, the apparent/resubstitution classification rate was 96.6%, whereas the leave-one-out cross-validated classification rate was 79.8% (Supplementary Table S4). These results indicate substantial but incomplete morphometric separation among OTUs. Therefore, the discriminant analysis was treated as an exploratory summary of craniodental variation rather than as independent diagnostic validation, and its results were interpreted together with external morphology, molecular data, and other taxonomic evidence.

Phylogeny, genetic distances, and molecular dating

We generated eight genes for 62 newly sampled specimens of *Episoriculus sensu lato*. After integration with GenBank data, 83 *Episoriculus sensu lato* individuals were included in the molecular analyses. All newly generated sequences have been deposited in GenBank (Supplementary Table S1) and uploaded to ScienceDB (<https://doi.org/10.57760/sciencedb.j00139.000a9>).

Within each dataset, BI and ML analyses recovered broadly congruent topologies (Figure 1C, D; Supplementary Figure S1). However, the mitochondrial and nuclear datasets produced substantially different phylogenetic patterns. In the mitochondrial tree based on *Cyt b* and 12S, *E. macrurus* was recovered as the sister of all other sampled Nectogalini (PP = 1.00). *Pseudosoriculus fumidus* formed a weakly supported sister relationship with *E. sp. 1* (PP = 0.43), and this pair clustered with *Soriculus*, *Neomys*, *Nectogale*, and *Chimarrogale*. The remaining *Episoriculus* species formed a separate clade that clustered with *Chodsigoa*, although support for this relationship was weak (PP = 0.54). Within this topology, *E. sp. 2* was recovered as sister to *E. soluensis* with weak support (PP = 0.49), whereas *E. sp. 3* formed a distinct lineage sister to *E. macrurus* with strong support (PP = 1.00).

The nuclear tree recovered a different arrangement. *Pseudosoriculus fumidus* fell outside *Episoriculus* and grouped with a clade containing *Soriculus* and *Chodsigoa*, although this placement was weakly supported (PP = 0.25). The remaining *Episoriculus* OTUs formed a monophyletic group comprising three principal clades: *E. sp. 1* as Clade I, *E. macrurus* as Clade II, and the remaining species as Clade III. In this nuclear topology, *E. sp. 2* was strongly supported as sister to *E. soluensis* (PP = 1.00), whereas *E. sp. 3* was clustered in *E. macrurus*.

The mitochondrial-genome phylogeny differed from the *Cyt b* and 12S trees. In the mitogenomic tree (Figure 1E), *P. fumidus* was recovered as the basal lineage of Nectogalini (PP = 1.00), while all remaining *Episoriculus* species formed a monophyletic group. Within *Episoriculus*, the topology was congruent with the nuclear tree, except that *Episoriculus sp. 3* formed a distinct lineage sister to *E. macrurus* (PP = 1.00).

Pairwise *Cyt b* distances among OTUs ranged from 5.3% to 16.6% (Table 3). The smallest interspecific distance was between *E. umbrinus* and *E. sacratus* (5.3%). Distances between *P. fumidus* and all other taxa exceeded 12.8%. The minimum distance between *E. sp. 1* and any other sampled species was 12.2%, from *E. macrurus*. *Episoriculus sp. 2* differed from *E. soluensis*, its sister lineage, by 11.7%, whereas *E. sp. 3* differed from *E. macrurus* by 6.6%.

The BEAST time-calibrated tree was topologically congruent with the concatenated nuclear-gene tree and generally received strong posterior support (Figure 1F). Divergence-time estimation placed the most recent common ancestor of *Episoriculus*, excluding *P. fumidus*, at approximately 12.17 Ma (95% CI = 9.49-15.76 Ma), near the middle-late Miocene transition. *Episoriculus sp. 1* diverged from the remaining *Episoriculus* lineages at approximately 11.52 Ma. The split between *E. macrurus* and Clade III occurred at approximately 9.87 Ma (95% CI = 7.19-12.68 Ma). The remaining OTUs' divergences occurred mainly from the early Pliocene to early Pleistocene, approximately 2.02-5.25 Ma.

Based on our morphological comparisons and mitochondrial and nuclear phylogenetic analyses, and the species comparisons provided in the Systematic account, we recognize *Pseudosoriculus* as a morphologically diagnosable genus distinct from *Episoriculus*, while acknowledging that its deeper phylogenetic placement within Nectogalini remains

unresolved. Within *Episoriculus*, following the diagnosis-and-monophyly-based phylogenetic species concept (Gutiérrez & Garbino, 2018), we recognize the validity of *E. caudatus*, *E. leucops*, *E. macrurus*, *E. soluensis*, *E. sacratus*, and *E. umbrinus* as distinct species. We treat *E. baileyi* as a subspecies of *E. leucops* because available evidence does not show stable morphological differentiation or deep molecular divergence comparable to species-level taxa in this genus. Our data also support *E. sp. 1* and *E. sp. 2* as distinct new species, but retain *E. sp. 3* within *E. macrurus* because its mitochondrial divergence is not matched by nuclear separation or consistent diagnostic morphology. On this basis, we provide a systematic review of *Pseudosoriculus* and *Episoriculus* and formally describe the two new species below.

Systematic account

Order Eulipotyphla

Family Soricidae

Subfamily Soricinae

Tribe Nectogalini

Genus *Pseudosoriculus* Abramov et al., 2017

Type species: *Pseudosoriculus fumidus* (Thomas, 1913).

Diagnosis: The dental formula could be expressed as $I^1 I^2 I^3 C P^1 P^4 M^1 M^2 M^3 / I_1 I_2 P_4 M_1 M_2 M_3$ following Hutterer (2005b). Because the homology of the unicuspid teeth may be interpreted differently, we here use the conventional unicuspid notation $I^1 U^1 U^2 U^3 U^4 P^4 M^1 M^2 M^3 / I_1 U_1 U_4 M_1 M_2 M_3$, equivalent to $1.4.1.3/1.1.1.3 = 30$. *Pseudosoriculus* resembles *Episoriculus* in external and cranial morphology but differs from it in several diagnostic characters. The tail is short, less than 80% of head and body length, whereas the tail of *Episoriculus* is usually more than 80% of head and body length. The posterior margins of P^4 and M^1 are only shallowly concave, rather than deeply excavated as in *Episoriculus*. The coronoid process is high and broad and curves slightly anteriorly, whereas in *Episoriculus* it rises more nearly vertically. Tooth pigmentation is weak, with only faint pigment on the molar tips; pigmentation is stronger in *Episoriculus* and absent in *Chimarrogale*, *Nectogale*, and *Neomys*. *Pseudosoriculus* has four upper unicuspid, in

contrast to the three upper unicuspid present in *Chodsigoa*, *Chimarrogale*, and *Nectogale*.
The foreclaws are slender and not enlarged as in *Soriculus*. The genus is endemic to Taiwan.

Remarks: *Pseudosoriculus* is monotypic. The generic diagnosis largely follows the
species diagnosis below.

Pseudosoriculus fumidus (Thomas, 1913) (Figure 2; Table 1)

Common name: Taiwanese Brown-toothed Shrew; 台湾长尾鼯鼠

Soriculus fumidus Thomas, 1913. Annals and Magazine of Natural History, 11 (62): 217.

Type locality: Mt. Arisan (= Alishan), Taiwan, China.

Soriculus caudatus fumidus. Ellerman and Morrison-Scott, 1951. Checklist of Palaearctic
and Indian mammals 1758 to 1946: 59.

Episoriculus fumidus. James and Jones, 1977. Proceedings of the Biological Society of
Washington, 90: 474, part.

Soriculus fumidus. Hoffmann, 1985. The Journal of the Bombay Natural History Society,
82: 468, part.

Pseudosoriculus fumidus. Abramov et al., 2017. Russian Journal of Theriology, 16: 123.

Diagnosis: Same as the generic diagnosis above, because *P. fumidus* is the only recognized
species of *Pseudosoriculus*.

Remarks: *Chodsigoa sodalis* was formerly treated as a junior synonym of *P. fumidus*
(James & Jones, 1977), but later studies showed that the two are distinct species
(Motokawa et al., 1997; Chen et al., 2017). *Pseudosoriculus fumidus* was also long treated
as a subspecies of *E. caudatus* (Ellerman & Morrison-Scott, 1951). James and Jones (1977)
restored it to species rank on the basis of its distinctive geographic range and cranial
morphology, including its short and narrow rostrum. Molecular studies later showed that
fumidus does not cluster with mainland species of *Episoriculus* (Ohdachi et al., 2006; He
et al., 2010), and Abramov et al. (2017) therefore placed it in the separate genus
Pseudosoriculus. Some later taxonomic treatments, however, continued to list this species
within *Episoriculus*.

Our phylogenetic analyses consistently show that *P. fumidus* does not form a clade with the remaining species of *Episoriculus*, although the exact placement of *Pseudosoriculus* within Nectogalini differs among datasets and remains weakly supported. Direct comparison of specimens identifies several external, cranial, and dental characters that distinguish *P. fumidus* from mainland *Episoriculus*. Externally, *P. fumidus* has brown dorsal pelage and a short tail, with tail length averaging 48 mm and ranging from 45 to 50 mm. The tail is less than 80% of head and body length, unlike most *Episoriculus*, except for a small number of *E. umbrinus* individuals. Cranially, the posterior margins of the premolars and molars are only shallowly concave and are much less excavated than in *Episoriculus*, providing one of the clearest osteological distinctions between the genera. In addition, tooth pigmentation is weak and nearly absent on the molars, and the coronoid process is high and broad, with convergent anterior and posterior margins. We therefore recognize *Pseudosoriculus* as a morphologically diagnosable genus distinct from *Episoriculus*, while its deeper phylogenetic placement within Nectogalini remains unresolved.

Distribution and habitat: *Pseudosoriculus fumidus* is known only from Alishan and adjacent montane areas of central Taiwan, at 1000-3600 m elevations. It inhabits montane broad-leaved forest, coniferous forest, and arrow-bamboo thickets. At some high-elevation localities it occurs sympatrically with *Chodsigoa sodalis*, although the latter appears to be uncommon.

Genus *Episoriculus* Ellerman and Morrison-Scott, 1951

Type species: *Sorex caudatus* Horsfield, 1851.

Diagnosis. Dentition 1.4.1.3/1.1.1.3 = 30. Tail usually longer than 80% of head and body length; claws not enlarged. Compared with *Pseudosoriculus*, the rostrum is more slender and elongate. The posterior margins of P⁴ and M¹ are deeply concave, forming a crescent-shaped excavation. Four upper unicuspid are present on each side. Except for the fourth upper unicuspid, the tooth tips bear yellow-brown to reddish-brown pigment. The

mandibular coronoid process is nearly vertical or only weakly curved anteriorly and is relatively narrow at the base.

Episoriculus caudatus (Horsfield, 1851) (Figures 2, 3; Table 1)

Common name: Hodgson's Brown-toothed Shrew; 褐腹长尾鼯鼠

Sorex caudatus Horsfield, 1851. A catalogue of the Mammalia in the Museum of the Hon. East-India Company: 135. Type locality: Darjeeling, India.

Sorex homourus Gray, 1863. Catalogue of the specimens and drawings of mammals, birds, reptiles and fishes of Nepal and Tibet, presented by BH Hodgson to the British Museum. 2nd Edition: 8. *nomen nudum*.

Soriculus gracilicauda Anderson, 1877. Journal of the Asiatic Society of Bengal, 46: 282. Type locality: Darjeeling, India.

Soriculus caudatus. Ellerman and Morrison-Scott, 1951. Checklist of Palaearctic and Indian Mammals 1758 to 1946: 59.

Episoriculus caudatus. Hutterer, 2005. Order Soricomorpha. In: Wilson & Reeder, Mammal Species of the World (3rd ed.): 277.

Diagnosis: One of the largest species of *Episoriculus*, with condyloincisive length 19.03-19.72 mm. Dorsal pelage dark brown; venter slightly paler. Tail equal to or slightly shorter than head and body length. Dorsal and ventral surfaces of the tail dark brown; forefeet and hindfeet also dark brown. Rostrum broad. The first three upper unicuspid are nearly quadrangular, with basal width greater than or approximately equal to basal length.

Remarks: The taxonomic history of *E. caudatus* is complex. *Pseudosoriculus fumidus*, *E. sacratus*, *E. soluensis*, and *E. umbrinus* have all been treated at different times as subspecies or synonyms of *E. caudatus* (Ellerman & Morrison-Scott, 1951; Gruber, 1969; Hoffmann, 1985). James and Jones (1977) restored *E. fumidus* to species rank. The lectotype of *E. caudatus* (BMNH 79.11.21.479) is badly damaged and preserves only the upper toothrow and mandible. Motokawa et al. (2008) measured its mandibular length at 11.93 mm and found it markedly larger than *E. soluensis*, *E. sacratus*, and *E. umbrinus*,

supporting the distinctness of *E. caudatus*. Karyotypic data also distinguish *E. caudatus* (2N = 60, FN = 118) from *E. soluensis* (2N = 74, FN = 126), *E. sacratus* (2N = 58, FN = 108), and *E. umbrinus* (2N = 58, FN = 112) (Motokawa et al., 2009; Wan et al., 2026).

Our specimens from Medog, Xizang, agree well with the description of Motokawa et al. (2008) and have large mandibles (MdL = 12.01-12.36 mm; Table 1). We also examined the sequence of specimen HA7083, identified by Motokawa et al. (2008), and found that it represents the same species as our Xizang material, namely *E. caudatus*. Liu et al. (2025) suggested that two specimens from Medog might represent an undescribed species, but our re-analysis indicates that those specimens are referable to *E. caudatus*. By contrast, the taxon treated as “*E. caudatus*” by Liu et al. (2025) shows only shallow divergence from *E. umbrinus* (*Cyt b* distance = 2.7%), and we assign that material to *E. umbrinus*.

In addition to the names listed above, *homourus* and *gracilicauda* have also been treated as synonyms of *E. caudatus* (Corbet & Hill, 1992; Hutterer, 2005). *Homourus* is a nomen nudum and is therefore unavailable. *Soriculus gracilicauda* was described by Anderson (1877) from material collected at Darjeeling. Blanford later re-examined the specimens and regarded *gracilicauda* as a synonym of *E. caudatus* (Blanford, 1888), a conclusion followed here.

Based on the newly available complete specimens, and consistent with Motokawa et al. (2008), *E. caudatus* is a large species, with CIL usually exceeding 19.0 mm. *Episoriculus caudatus* overlaps with *E. leucops* in overall cranial size but differs from it in having a relatively shorter tail, with TL/HB $\leq$ 100% in all eight examined specimens of *E. caudatus*, compared with TL/HB $>$ 100% in 11 of 15 examined specimens of *E. leucops*. It also differs from *E. leucops* in having a narrower braincase (CB = 9.12-9.49 mm in *E. caudatus* vs. 9.53-10.36 mm in *E. leucops*), a relatively shorter and broader rostrum, broader first three upper unicuspid teeth that are wider than long, and a larger fourth upper unicuspid with a distinct medial notch.

Distribution and habitat: *Episoriculus caudatus* is known from Xizang, China; Sikkim, India; and Nepal. In Medog, Xizang, it occurs in the forest at 950-2000 m. In Nepal, it has been recorded mainly from 2500-2700 m and appears to be uncommon.

Episoriculus leucops (Horsfield, 1855) (Figures 2, 3; Table 1)

456

457 **Common name:** Long-tailed Brown-toothed Shrew; 大长尾鼯鼠

458 *Sorex leucops* Horsfield, 1855. The Annals and Magazine of Natural History, 2 (16) :

459 111. Type locality: Nepal.

460 *Soriculus baileyi* Thomas, 1914. Journal of the Bombay Natural History Society, 22: 683.

461 Type locality: Mishmi Hills.

462 *Soriculus leucops*. Ellerman and Morrison-Scott, 1951. Checklist of Palearctic and

463 Indian Mammals 1758 to 1946: 59.

464 *Soriculus caudatus baileyi*. Ellerman and Morrison-Scott, 1951. Checklist of Palearctic

465 and Indian Mammals 1758 to 1946: 59.

466 *Soriculus gruberi* Weigel, 1969. Systematische übersicht über die insektenfresser und

467 nager Nepals nebst bemerkungen zur tiergeographie, Khumbu Himal, 3(2): 170.

468 *Soriculus leucops baileyi*. Hoffmann, 1985. Journal of the Bombay Natural History

469 Society, 82: 466.

470 *Episoriculus leucops*. Hutterer, 2005. Order Soricomorpha. In: Wilson & Reeder,

471 Mammal Species of the World (3rd ed.): 278.

472 *Episoriculus baileyi*. Motokawa and Lin, 2005. Mammal Study, 30(2): 118.

473 **Diagnosis:** One of the largest species of *Episoriculus*, with condyloincisive length 19.15-

474 20.09 mm. Tail long, usually equal to or slightly longer than head and body length. Dorsal

475 surfaces of the feet light brown centrally, with dirty-white margins. Rostrum slender. The

476 first three upper unicuspid are rectangular and longer than wide at the base.

477 **Remarks:** The names *E. leucops* and *E. macrurus* were long confused. Large, pale-gray

478 shrews with very long tails were previously misidentified as *E. leucops* (Anthony, 1941;

479 Abe, 1971, 1982). Hoffmann (1985) showed that the holotype of *E. leucops* is a large, dark-

480 brown shrew with a tail only slightly longer than head and body length, and that the

481 specimens described by Anthony (1941) and Abe (1971, 1982) are referable to *E. macrurus*.

482 *Episoriculus leucops* is among the largest species in the genus and overlaps in CIL

483 only with *E. caudatus*. It differs from *E. caudatus* by its longer tail, broader braincase, and

484 narrower rostrum. Specimens collected in April and November have long, dense pelage

485 approximately 6 mm in length, distinctly longer than that observed in other examined

486 species of *Episoriculus*, in which pelage length is approximately 4 mm.

Episoriculus baileyi was described by Thomas (1914) from the Mishmi Hills, northeastern India, whereas the type locality of *E. leucops* lies farther west in Nepal. The taxon was long treated as a subspecies of *E. leucops* (Hoffmann, 1985; Corbet & Hill, 1992; Hutterer, 2005), but Motokawa and Lin (2005) elevated it to species rank after examining the type series, mainly on the basis of auditory-bulla morphology. We did not examine the holotype or obtain molecular data from type material, and our treatment should therefore be regarded as a conservative reassessment based on published descriptions and photographs, available comparative material, and available sequences. Geographically, our Medog material is closer to the Mishmi Hills than to the type locality of *E. leucops*, and specimens from farther east in Yunnan show little or no mitochondrial differentiation from the Medog specimens. These eastern populations are therefore more plausibly referable to the *baileyi* form than to nominate *E. leucops*. However, the auditory-bulla characters proposed to distinguish *E. baileyi* show marked individual variation in the specimens examined, and the available molecular evidence does not provide independent support for species-level separation. We therefore retain *baileyi* as a valid subspecies, *Episoriculus leucops baileyi*, while acknowledging that its status should be reassessed when the type series and molecular data from topotypic material become available.

Weigel (1969) described *Soriculus gruberi* from northeastern Nepal. Abe (1977) regarded this name as a synonym of *E. leucops*, a treatment followed by later authors. On geographic grounds, *gruberi* is referred here to the nominotypical subspecies, *E. l. leucops*.

Distribution and habitat: The nominotypical subspecies, *E. l. leucops*, occurs in Nepal. The Mishmi subspecies, *E. l. baileyi*, occurs in China, including Xizang and Yunnan, northeastern India, Myanmar, and Vietnam. It inhabits mountain forests at elevations of approximately 1500-3500 m, including evergreen broad-leaved, rhododendron, and moist coniferous forests. Most examined specimens were captured at night.

Episoriculus macrurus (Blanford, 1888) (Figures 2, 3; Table 1)

Common name: Arboreal Brown-toothed Shrew; 小长尾鼯鼠

Sorex macrurus Hodgson, 1863. In: Gray, Catalogue of the Specimens and Drawings of Mammals, Birds, Reptiles and Fishes of Nepal and Thibet (2nd ed.), 90: 9. *nomen nudum*.

Soriculus macrurus Blanford, 1888. The Fauna of British India, including Ceylon and
Burma. Mammalia, Part I: 231. Type locality: Darjeeling, India.

Soriculus irene Thomas, 1911a. Abstracts of the Proceedings of the Zoological Society of
London, 100: 49. Type locality: Yingjing, Sichuan, China.

Episoriculus macrurus. Hutterer, 2005. Order Soricomorpha. In: Wilson & Reeder,
Mammal Species of the World (3rd ed.): 118.

Diagnosis: A small species of *Episoriculus*, with condyloincisive length 16.58-18.46 mm.
Dorsal pelage grayish brown; venter pale gray; dorsal surfaces of the feet pale whitish. Tail
very long, 72-101 mm, corresponding to approximately 130-170% of head and body length.
Braincase strongly domed and nearly semicircular in lateral profile. The first three upper
unicuspids are broader than long at the base.

The population from Jiaozi Snow Mountain, referred to here as *E. sp. 3*, forms a
distinct lineage in the mitochondrial tree but is not recovered as a separate lineage in the
nuclear tree. Additionally, PCA analysis shows that it clusters with *E. macrurus* from other
regions (Figure 1B), although this inference is limited by the availability of only two intact
skulls. Therefore, we tentatively retain it within *E. macrurus*. Thomas (1911a) described
Soriculus irene from Sichuan. This name has subsequently been treated either as a synonym
of *E. macrurus* (Allen, 1938; Hoffmann, 1985; Hutterer, 2005) or as a subspecies (Smith
and Xie, 2009; Burgin & He, 2018; Wei et al., 2022). Our analyses reveal that populations
of *E. macrurus* from different regions exhibit pronounced population structure in the
mitochondrial tree. However, the phylogenetic relationships within *E. macrurus* are
inconsistent between mitochondrial and nuclear datasets, suggesting a complex history of
population structure within this species. As a result, we refrain from proposing any
subspecific classification for this species in the present study. Further genomic and
geographic sampling will be needed to clarify the evolutionary history and taxonomy of
this species.

Distribution and habitat: *Episoriculus macrurus* is distributed in central Nepal,
northeastern India, northern Myanmar, northern Vietnam, and southwestern China,
including Sichuan, Xizang, Yunnan, and Chongqing. It inhabits mountain forests at
approximately 1100-4400 m. The very long tail can coil around branches, consistent with
a semi-arboreal habit.

549

550 *Episoriculus sacratus* (Thomas, 1911) (Figures 2, 3; Table 1)

551

552 **Common names:** Sichuan Brown-toothed Shrew; 灰腹长尾鼯鼠

553 *Soriculus sacratus* Thomas, 1911. Thomas, 1911b. Abstracts of the Proceedings of the
554 Zoological Society of London 90: 4. Type locality: Emei Mountain, Sichuan, China.

555 *Soriculus caudatus sacratus*. Allen, 1923. American Museum Novitates: 5.

556 *Episoriculus sacratus*. Wang, 2003. A Complete Checklist of Mammal Species and
557 Subspecies in China and Their Distribution: 16.

558 *Episoriculus caudatus sacratus*. Hutterer, 2005: Order Soricomorpha. In: Wilson &
559 Reeder, Mammal Species of the World (3rd ed.): 277.

560 **Diagnosis:** A medium-sized species of *Episoriculus*, with condyloincisive length 17.81-
561 18.79 mm. Tail shorter than head and body length. Talon of the upper incisor small and
562 lower than the second upper unicuspid. The first three upper unicuspid are nearly
563 quadrangular, with basal width greater than or approximately equal to basal length.
564 Mandible robust; ascending ramus high and broad, with an almost square dorsal tip. Height
565 of coronoid process 4.00-4.42 mm; height of coronoid valley 2.72-2.83 mm.

566 **Remarks:** Thomas (1911b) described *sacratus* from Emei Mountain, Sichuan. Allen (1938)
567 treated it as a subspecies of *E. caudatus*. Although Anthony (1941) regarded *sacratus* as a
568 distinct species, Allen's arrangement was followed for several decades (Ellerman &
569 Morrison-Scott, 1951; Hoffmann, 1985; Hutterer, 2005). Motokawa et al. (2008) showed
570 that *E. caudatus* is substantially larger than the taxa then treated as its subspecies, including
571 *sacratus*, *soluensis*, and *umbrinus*, and separated *E. caudatus* from that complex.
572 Following this separation, *sacratus* had priority as the species-level name for the remaining
573 complex that included *sacratus*, *soluensis*, and *umbrinus*.

574 Motokawa et al. (2009) subsequently reported clear karyotypic differences between
575 *E. sacratus* and *E. soluensis*, supporting their recognition as separate species. *Episoriculus*
576 *sacratus* from Sichuan has been reported with $2N = 58$ and $FN = 108$, whereas Nepalese
577 *E. soluensis* has $2N = 74$ and $FN = 126$. *Episoriculus umbrinus* was separated primarily by
578 its smaller size. On this basis, Motokawa et al. (2009) treated *E. caudatus*, *E. sacratus*, *E.*

soluensis, and *E. umbrinus* as distinct species, an arrangement that was followed by Burgin and He (2018).

In our analyses, *E. sacratus* is closely related to *E. umbrinus* and is externally similar to it, but it is larger and differs in cranial and mandibular proportions. The diagnostic differences between these two species are discussed further under *E. umbrinus*.

Distribution and habitat: *Episoriculus sacratus* is endemic to western Sichuan, China. It occurs mainly in evergreen broad-leaved, coniferous, and rhododendron forests at approximately 1500-4000 m and appears to occupy humid, shaded microhabitats.

Episoriculus soluensis (Gruber, 1969) (Figures 2, 3; Table 1)

Common names: Nepalese Brown-toothed Shrew; 尼泊尔长尾鼯鼠

Soriculus caudatus soluensis Gruber, 1969. Tiergeographische, ökologische und bionomische Untersuchungen an kleinen Säugetieren in Ost-Nepal. Khumbu Himal, 3: 309.

Episoriculus sacratus soluensis. Motokawa et al., 2008. Integrative Zoology, 3: 183.

Episoriculus soluensis. Motokawa et al., 2009. Zoological Science, 26: 796.

Diagnosis: A medium-sized species of *Episoriculus*, with condyloincisive length 17.75-18.88 mm. Tail shorter than head and body length and weakly bicolored. Dorsal surfaces of the feet light brown centrally, with dirty-white margins. Talon of the upper incisor high, nearly equal in height to the second upper unicuspid. The first three upper unicuspid are rectangular and longer than wide at the base.

Remarks: *Episoriculus soluensis* was originally described as a subspecies of *Soriculus caudatus* by Gruber (1969). Hoffmann (1985) considered it a synonym of *E. caudatus*, a treatment later followed by Hutterer (2005). Motokawa et al. (2008) argued that *E. caudatus* is much larger than the smaller taxa then included under it and should be separated. After this separation, they elevated *sacratus* to species rank and treated *soluensis* and *umbrinus* as subspecies of *E. sacratus*. Motokawa et al. (2009) subsequently showed that *E. soluensis* differs karyotypically from *E. sacratus* and elevated it to species rank, a treatment followed by later authors.

The skull of *E. soluensis* is variable in size. Two specimens from Yadong, Xizang, are larger (CIL = 18.82-18.88 mm) than specimens from Gyirong (CIL = 18.36-18.75 mm). In overall cranial length, *E. soluensis* is smaller than *E. leucops* and *E. caudatus*, but overlaps with *E. sacratus* and *E. umbrinus*. This cranial overlap is also reflected in the discriminant analysis, in which *E. soluensis* showed relatively low classification success and was most often confused with *E. umbrinus*, indicating that craniodental measurements alone do not reliably distinguish these two species. It differs from *E. sacratus* and *E. umbrinus* in several dental and external characters. The talon of the upper incisor is high and nearly as tall as the second upper unicuspid, whereas in *E. sacratus* and *E. umbrinus* it reaches less than half that height. The first three upper unicuspids are rectangular and longer than wide at the base, whereas in *E. sacratus* and *E. umbrinus* they are nearly quadrangular. The feet of *E. soluensis* are paler, especially the forefeet, which are dirty white rather than brown. The fourth upper unicuspid is distinctly larger and medially notched, whereas it is minute and dot-like in *E. sacratus* and *E. umbrinus*. In addition, postpalatal depth is smaller than in *E. sacratus*.

Distribution and habitat: *Episoriculus soluensis* is known from Nepal, northeastern India, and Xizang, China, including Gyirong, Yadong, and Dingjie. It occurs mainly above 2300 m and has been recorded to elevations above 4300 m. It appears to occupy damp, shaded habitats with thick leaf litter.

Episoriculus umbrinus (Allen, 1923) (Figures 2, 3; Table 1)

Common name: Hidden Brown-toothed Shrew; 云南长尾鼯鼠

Soriculus caudatus umbrinus Allen, 1923. American Museum Novitates, 100: 5. Type locality: Muchang, Zhenkang, western Yunnan, China.

Soriculus sacratus umbrinus. Anthony, 1941. Field Museum of Natural History: 69.

Episoriculus caudatus umbrinus. Hutterer, 2005. Order Soricomorpha. In: Wilson & Reeder, Mammal Species of the World (3rd ed.): 278.

Episoriculus sacratus umbrinus. Motokawa et al., 2008. Integrative Zoology, 3: 184.

Episoriculus umbrinus. Motokawa et al., 2009. Zoological Science: 796.

Diagnosis: Similar to *E. sacratus* but smaller, with condyloincisive length 16.68-18.55 mm. Tail slightly shorter than head and body length. The first three upper unicusps are nearly quadrangular, with basal width greater than or approximately equal to basal length. Mandible less robust than in *E. sacratus*; ascending ramus narrower; coronoid process tapering to a triangular tip. Height of coronoid process 3.61-3.99 mm; height of coronoid valley 2.31-2.66 mm.

Remarks: *Episoriculus umbrinus* was long treated as a subspecies of *E. caudatus* (Allen, 1923; Hoffmann, 1985; Hutterer, 2005), although some authors placed it under *E. sacratus* (Anthony, 1941; Motokawa et al., 2008). Motokawa et al. (2009) elevated *umbrinus* to species rank because it is smaller than both *E. caudatus* and *E. sacratus*. This treatment was later followed by Burgin and He (2018), although Wei et al. (2022) retained it as a subspecies of *E. caudatus*. More recently, Chen et al. (2025) reported a karyotype for the Yunnan taxon that differs from those reported for *E. soluensis* and *E. sacratus*, further supporting its recognition as a distinct species.

Our phylogenetic analyses recover *E. umbrinus* as sister to *E. sacratus*, and PCA separates the two taxa. We therefore recognize *E. umbrinus* as a valid species. The relatively small *Cyt b* distance between *E. umbrinus* and *E. sacratus* (5.3%) is interpreted in the context of their stable morphological differences, strong phylogenetic separation in the available trees, geographic structure, and distinct karyotypic reports. The material from Medog, Xizang, that clusters with the “*E. caudatus*” of Liu et al. (2025) shows little *Cyt b* divergence from our Yunnan material (2.7%) and no obvious morphological difference. We therefore assign that material to *E. umbrinus*. Morphologically, *E. umbrinus* is similar to *E. soluensis* and *E. sacratus*. Its differences from *E. soluensis* are discussed under the account of that species. Compared with *E. sacratus*, *E. umbrinus* is smaller overall and differs in the shape and proportions of the coronoid process. In *E. sacratus*, the coronoid process is high and broad, with an almost square tip; in *E. umbrinus*, it is narrower and tapers to a triangular tip. Corresponding mandibular measurements are also smaller in *E. umbrinus*: HCP 3.61-3.99 mm versus 4.00-4.42 mm in *E. sacratus*, and HCV 2.31-2.66 mm versus 2.72-2.83 mm in *E. sacratus*.

Distribution and habitat: *Episoriculus umbrinus* is known from Guizhou, Yunnan, and Xizang in China, and from northeastern India, northern Myanmar, and northern Vietnam.

It occurs mainly in evergreen broad-leaved, rhododendron, and coniferous forests at approximately 1800-3500 m and appears to be relatively common within its range.

Episoriculus gaoligongensis sp. nov. (Figures 2, 3; Table 1, = *Episoriculus* sp. 1)

ZooBank registration: urn:lsid:zoobank.org:act:11B80BCA-FF9A-481A-8111-7858210DC12F

Suggested common name: Gaoligong Brown-toothed Shrew; 高黎贡长尾鼯鼠

Holotype: KIZ: 040393, adult female, collected by Jing Luo on 26 November 2023. Dried skin, cleaned skull, and muscle tissue deposited in KIZ.

Type locality: Shiyueliang Town, Fugong County, Gaoligong Mountains, Yunnan, China, 27.169°N, 98.486°E, 2682 m a.s.l.

Paratypes: KIZ: 040394, adult male, collected by Changzhe Pu on 28 November 2023 at 2199 m from the type locality; KIZ: 040392, adult female, collected on 10 April 2014 from Mangkuan, Baoshan, Gaoligong Mountains, Yunnan, China, 25.292 °N, 98.744 °E, 2829 m a.s.l. Both paratypes are deposited in KIZ.

Additional specimens: KIZ: 040391, KIZ: 040395, and KIZ: 040396 collected from Medog, Xizang, China. All are deposited in KIZ.

Etymology: The specific epithet refers to the Gaoligong Mountains, where the type locality is situated. The Latin suffix *-ensis* denotes origin or belonging.

Diagnosis: A small species of *Episoriculus*, with condyloincisive length 17.76-18.08 mm, mean 17.87 ± 0.15 mm. Dorsal pelage yellowish brown to grayish brown, venter pale gray. Tail slightly longer than head and body length, TL/HB = 103-120%, and distinctly bicolored, with a gray dorsal surface and pale ventral surface. Talon of the upper incisor much lower than the second upper unicuspid. The first three upper unicuspid are nearly quadrangular, with basal width greater than or approximately equal to basal length.

Description: Dorsal pelage yellowish brown to grayish brown; ventral pelage pale gray. Tail slender, slightly longer than head and body length, and distinctly bicolored, with a gray dorsal surface and pale ventral surface. Dorsal surfaces of the hands and feet dirty white, with a light-brown central area.

Skull generally triangular in dorsal view, with a moderately long rostrum, strongly domed and smooth braincase, and weak lambdoidal and sagittal crests. Mandible slender. Coronoid process short, with a triangular tip, and rising almost vertically. Condylloid process short; angular process long, thin, and straight. Dentition 1.4.1.3/1.1.1.3 = 30. Talon of the upper incisor small and much lower than the second upper unicuspid. Four upper unicuspids present; The first three upper unicuspids are nearly quadrangular, with basal width greater than or approximately equal to basal length. U^1 - U^3 decrease gradually in size; U^4 is greatly reduced, but larger than those in *E. sacratus* and *E. umbrinus*. P^4 and M^1 deeply excavated posteriorly. All teeth except U^4 have dark chestnut pigment on the cusp tips.

Comparison: *Episoriculus gaoligongensis* sp. nov. has a tail slightly longer than head and body length, similar to *E. leucops*, but much shorter than that of *E. macrurus*, in which TL/HB exceeds 130%. It differs from *E. caudatus*, *E. sacratus*, *E. soluensis*, and *E. umbrinus* by having a relatively longer tail. Its pale-gray ventral pelage resembles that of *E. macrurus* but differs from the darker or less contrasting ventral pelage of most other species in the genus. The distinctly bicolored tail also resembles that of *E. macrurus*, but differs from the dark or only weakly bicolored tails of most other *Episoriculus* species.

In cranial size, *E. gaoligongensis* sp. nov. is much smaller than *E. leucops* and *E. caudatus*. Its mean CIL is 17.87 mm, compared with 19.61 mm in *E. leucops* and 19.38 mm in *E. caudatus*. The first three upper unicuspids are nearly quadrangular, with basal width greater than or approximately equal to basal length, unlike those of *E. leucops* and *E. soluensis*, in which they are longer than wide. The talon of the upper incisor is much lower than the second upper unicuspid, unlike in *E. soluensis*, where the talon is high and nearly reaches the height of the second upper unicuspid. A concise comparison of external, dental, and cranial diagnostic characters is provided in Supplementary Table S5.

Distribution and habitat: *Episoriculus gaoligongensis* sp. nov. is known from Baoshan and Fugong in the Gaoligong Mountains, Yunnan, and from Medog, Xizang, China. Specimens were collected in evergreen broad-leaved forest at 2100-2829 m. Under natural conditions, the tail is sometimes curved, and several specimens were captured in trees, suggesting a semi-arboreal habit similar to that of *E. macrurus*.

Episoriculus damuensis sp. nov. (Figures 2, 3; Table 1, = *Episoriculus* sp. 2)

ZooBank registration: urn:lsid:zoobank.org:act:A5B9C738-7976-453F-B98E-7173EDFBCFA5

Suggested common name: Damu Brown-toothed Shrew. 达木长尾鼯鼠

Holotype: KIZ: 040418, adult female, collected by Jing Luo on 30 October 2018. Dried skin, cleaned skull, and muscle tissue deposited in KIZ.

Type locality: Damu Town, Medog, southeastern Xizang, China, 29.701° N, 95.527° E, 2617 m a.s.l.

Paratypes: KIZ: 040397, adult female; KIZ: 040398, adult female; KIZ: 040419, adult male, collected in October 2018; and KIZ: 040420, adult male, collected in May 2019. All paratypes were collected from the type locality and are deposited in KIZ.

Etymology: The specific epithet refers to Damu Town, Medog, the type locality. The Latin suffix *-ensis* denotes origin or belonging.

Diagnosis: A medium-sized species of *Episoriculus*, with mean condyloincisive length 18.63 ± 0.10 mm. Pelage dense and soft, with guard hairs approximately 6 mm long, among the longest observed in the genus. Tail uniformly dark brown, approximately equal to or slightly longer than head and body length. Rostrum long and narrow. The first three upper unicuspid are rectangular and longer than wide at the base. Talon of the upper incisor high, nearly equal in height to the second upper unicuspid.

Description: Mean external measurements are approximately as follows: body mass 5.4 g, head and body length 62 mm, tail length 69 mm, and condyloincisive length 18.63 mm. Pelage uniformly dark brown over the body. Fur dense and soft, with hairs approximately 6 mm long, among the longest observed in *Episoriculus*. Tail approximately equal to or slightly longer than head and body length, with TL/HB = 96-120%, and uniformly dark brown. Dorsal surfaces of the hands and feet also dark brown.

Rostrum relatively longer and narrower than in other species of *Episoriculus*. Braincase strongly domed and smooth, with weak lambdoidal and sagittal crests. Mandible slender. Coronoid process high, with a rounded tip, and rising nearly vertically. Dentition 1.4.1.3/1.1.1.3 = 30. Talon of the upper incisor high, nearly equal in height to the second

upper unicuspid. Four upper unicuspid present; the first three upper unicuspid are rectangular and longer than wide at the base, U^1 - U^3 decreasing gradually in size; U^4 minute and dot-like. P^4 and M^1 deeply excavated posteriorly. All tooth tips except U^4 pigmented dark chestnut.

Comparison: *Episoriculus damuensis* sp. nov. has pelage hairs approximately 6 mm long, similar to *E. leucops* but longer than those observed in most other species of the genus, in which hair length is approximately 4 mm. The tail is approximately equal to or slightly longer than head and body length, making it relatively longer than in *E. caudatus*, *E. sacratus*, *E. soluensis*, and *E. umbrinus*, but shorter than in *E. macrurus*. Its uniformly dark brown pelage is much darker than that of *E. gaoligongensis* sp. nov. and *E. macrurus*.

In cranial size, *E. damuensis* sp. nov. is similar to *E. sacratus* and *E. soluensis*, with mean CIL values of 18.63 mm, 18.28 mm, and 18.29 mm, respectively. It is smaller than *E. leucops* and *E. caudatus*, with mean CIL values of 19.61 mm and 19.38 mm, respectively, but larger than *E. gaoligongensis* sp. nov., *E. macrurus*, and *E. umbrinus*, with mean CIL values of 17.87 mm, 17.59 mm, and 17.68 mm, respectively. The rostrum is relatively longer and narrower than in other species of *Episoriculus*. The first three upper unicuspid are longer than wide at the base, as in *E. leucops* and *E. soluensis*, rather than nearly quadrangular as in most other species. The talon of the upper incisor is nearly as high as the second upper unicuspid, similar to *E. soluensis* and unlike the lower talon observed in *E. caudatus*, *E. gaoligongensis* sp. nov., *E. macrurus*, *E. sacratus*, and *E. umbrinus*. The fourth upper unicuspid is minute, as in *E. sacratus* and *E. umbrinus*, but smaller than in most other species. A concise comparison of external, dental, and cranial diagnostic characters is provided in Supplementary Table S5.

Distribution and habitat: *Episoriculus damuensis* sp. nov. is known only from Medog, Xizang, China. Specimens were collected in evergreen broad-leaved forest at 2560-2700 m.

Key to the species of *Episoriculus* and *Pseudosoriculus*

1. Posterior margins of P^4 and M^1 only weakly concave; known only from Taiwan *Pseudosoriculus fumidus*
- Posterior margins of P^4 and M^1 deeply concave; not known from Taiwan 2

793	2. Tail very long, exceeding 130% of head and body length	<i>Episoriculus macrurus</i>
794	Tail shorter, less than 130% of head and body length	3
795	3. Larger species, CIL > 19.0 mm	4
796	Smaller species, CIL < 19.0 mm	5
797	4. Braincase narrower, CB < 9.5 mm; first three upper unicuspid nearly quadrangular or	
798	broader than long at the base.....	
799	<i>Episoriculus caudatus</i>	
800	Braincase broader, CB > 9.5 mm; first three upper unicuspid rectangular and longer	
801	than wide at the base.....	
802	<i>Episoriculus leucops</i>	
803	5. Talon of upper incisor large, nearly equal in height to the second upper unicuspid; first	
804	three upper unicuspid longer than wide	6
805	Talon of upper incisor small, clearly lower than the second upper unicuspid; first three	
806	upper unicuspid broader than long	7
807	6. Tail approximately equal to or longer than head and body	
808	length	<i>Episoriculus damuensis</i>
809	sp. nov.	
810	Tail shorter than head and body length	<i>Episoriculus soluensis</i>
811	7. Tail longer than head and body length; tail distinctly bicolored, with gray dorsal surface	
812	and pale ventral surface	<i>Episoriculus gaoligongensis</i> sp. nov.
813	Tail shorter than head and body length; tail uniformly dark or only weakly bicolored	8
814	8. Coronoid process high and broad; HCP $\geq$ 4.0 mm; HCV > 2.7	
815	mm	<i>Episoriculus sacratus</i>
816	Coronoid process lower and narrower, tapering to a triangular tip; HCP < 4.0 mm; HCV	
817	< 2.7 mm	<i>Episoriculus umbrinus</i>

819 DISCUSSION

820 Implications for taxonomy

821 The taxonomy of *Episoriculus* has long been contentious because several nominal
 822 taxa lack consistent morphological diagnoses and previous studies were based on limited
 823 geographic sampling (Motokawa et al., 2009; Abramov et al., 2017; Burgin & He, 2018;

Liu et al., 2025). Following a diagnosis-and-monophyly-based phylogenetic species concept (Gutiérrez & Garbino, 2018), we treated species as diagnosable lineages supported by morphological evidence and phylogenetic separation in mitochondrial and/ or nuclear datasets, with geographic structure, karyotypic information where available, nomenclatural history, and sequence divergence used as additional context rather than as fixed species-delimitation thresholds. By integrating broad sampling across the Himalaya-Hengduan Mountains with morphological, mitochondrial, and nuclear data, including complete mitochondrial genomes for representative OTUs, we provide a comprehensive reassessment of the genus.

At the generic level, *Pseudosoriculus* is retained as a morphologically diagnosable genus distinct from *Episoriculus*, although its deeper phylogenetic placement within Nectogalini remains unresolved. Within *Episoriculus*, we recognize eight valid species, including the two new species described here, *E. gaoligongensis* sp. nov. and *E. damuensis* sp. nov. Several controversial cases are treated conservatively under the same framework: *E. baileyi* is retained as a subspecies of *E. leucops* because available evidence does not show stable diagnostic morphology or independent molecular support comparable to recognized species, and the Jiaozi Snow Mountain population (*E. sp. 3*) is retained within *E. macrurus* because its mitochondrial distinctiveness is not corroborated by nuclear or consistent morphological evidence. Our analyses also clarify previous taxonomic misinterpretations. For instance, specimens from Medog previously suggested as a potentially undescribed species are confirmed as *E. caudatus*, whereas other material assigned to *E. caudatus* in Liu et al. (2025) is more appropriately referred to *E. umbrinus*.

Despite clear genetic differentiation among species, morphological variation within *Episoriculus* is relatively subtle, likely reflecting rapid diversification and morphological conservatism. Nevertheless, several traits, including body size, tail length, pelage coloration, and dental morphology, provide reliable diagnostic characters for species delimitation. Interestingly, early-diverging lineages such as *E. gaoligongensis* sp. nov. and *E. macrurus* share several traits, including relatively small body size, long tails, and paler pelage, which may reflect morphological conservatism among some early lineages of the genus. Collectively, these results demonstrate that an integrative taxonomic framework is essential for resolving species limits in morphologically conservative montane mammals.

Inconsistency between mitochondrial and nuclear phylogenies

In our study, we observed substantial discordance between mitochondrial and nuclear phylogenies. One notable example involves the phylogenetic position of *P. fumidus* (Figure 1C, D). In the mitochondrial-genome phylogeny, *P. fumidus* was recovered as the basal lineage of Nectogalini, whereas in the nuclear tree it grouped with a clade containing *Soriculus* and *Chodsigoa*, although this relationship received weak support. This conflict illustrates the uncertainty in resolving the deeper placement of *P. fumidus* within Nectogalini using the present datasets. In addition, the internal structure of *E. macrurus* differed markedly between mitochondrial and nuclear datasets. Such mito-nuclear incongruence appears to be widespread in small mammals and has been attributed to rapid speciation, incomplete lineage sorting (ILS), and, in some cases, introgression or historical hybridization (He et al., 2010; Chen et al., 2022; Zhang et al., 2022; Li et al., 2026). Our divergence-time analyses suggest that Nectogalini underwent rapid radiation during the middle Miocene, whereas *E. macrurus* populations diversified rapidly during the early Pleistocene. During rapid diversification, multiple lineages split within short evolutionary intervals, leaving insufficient time for ancestral polymorphisms to sort completely among descendant taxa. Such conditions frequently generate discordant gene trees across loci and are widely recognized as a major cause of mito-nuclear incongruence (Steenwyk et al., 2023). Therefore, the conflicting placement of *P. fumidus* and the discordant internal structure of *E. macrurus* are plausibly explained by incomplete lineage sorting associated with rapid diversification.

We also found that phylogenies inferred from short mitochondrial fragments (*Cyt b* + 12S) placed *E. macrurus* and *E. gaoligongensis* sp. nov. outside the main *Episoriculus* clade, whereas both complete mitochondrial genomes and nuclear loci recovered these taxa within a monophyletic *Episoriculus*. Similar inconsistencies between short mitochondrial markers and multilocus datasets have also been reported in *Soriculus* (Jiang et al., 2023; Chen et al., 2024). One important contributing factor is the inherent limitation of short mitochondrial fragments. Compared with complete mitochondrial genomes or multilocus datasets, short mtDNA sequences contain relatively few informative sites and therefore provide limited phylogenetic signal, particularly in rapidly diversifying taxa with shallow divergence histories. In addition, because mitochondrial DNA reflects only maternal

lineage history, mitochondrial divergence may overestimate species-level differentiation and exaggerate phylogenetic structure relative to the nuclear genome. Overreliance on short mitochondrial markers or DNA barcodes may therefore lead to unstable taxonomy, misleading phylogenetic inference, and even taxonomic inflation (Thomson et al., 2018; Raposo et al., 2020). Our results therefore highlight the need for caution when interpreting phylogenetic patterns inferred from short mitochondrial sequences alone, particularly in rapidly diversifying montane systems characterized by recent radiation and complex geographic histories. Integrative approaches combining morphology with multilocus or genomic-scale evidence are likely essential for robust species delimitation and phylogenetic inference in these groups.

Diversification and biogeography

The discovery of *E. gaoligongensis* sp. nov. has important implications for understanding the biogeographic history of *Episoriculus*, because this species represents the earliest-diverging lineage recovered in our analyses. Previous studies have proposed contrasting hypotheses regarding the origin and dispersal of Nectogalini. Based partly on fossil evidence, He et al. (2010) suggested that the tribe originated in Europe, dispersed eastward through western Siberia, and subsequently entered southwestern China via a high-latitude route. However, this hypothesis is difficult to reconcile with the occurrence of older *Soriculus*-like fossils from Kashmir (Storch et al., 1998). Alternatively, Yuan et al. (2013), using *Cyt b* data from *Neomys*, proposed a low-latitude dispersal route through Central Asia into the southern Himalayan foothills and suggested that *Soriculus*, *Nectogale*, and *Episoriculus* may have followed a similar pathway. Additional support for this scenario was provided by Bover et al. (2018), who recovered a relatively close relationship between the Mediterranean fossil *Nesiotites hidalgo* and the Himalayan endemic *Soriculus nigrescens*. Our divergence estimates place the split between *E. gaoligongensis* sp. nov. and the remaining *Episoriculus* lineages at approximately 11.52 Ma, indicating that the ancestral lineage had already reached southwestern China by the middle Miocene. This timing is therefore more consistent with a low-latitude dispersal scenario than with a later high-latitude colonization of the Himalaya-Hengduan region. Our results further suggest that Medog and the Gaoligong Mountains represent major centers of diversification and persistence for *Episoriculus*. Species richness is highest in Medog, where six species occur

(*E. macrurus*, *E. gaoligongensis* sp. nov., *E. damuensis* sp. nov., *E. umbrinus*, *E. caudatus*, and *E. leucops*), although *E. leucops* appears to be rare in the region, with only a single specimen recorded. The Gaoligong Mountains also harbor multiple species, including the earliest-diverging lineage, *E. gaoligongensis* sp. nov.

Diversification within *Episoriculus* may have been shaped by multiple interacting mechanisms, including tectonic reorganization, climatic oscillations, ecological differentiation, and geographic isolation. Our divergence-time estimates indicate that the most recent common ancestor of *Episoriculus* (excluding *Pseudosoriculus*) dates to approximately 12.17 Ma (95% CI = 9.49-15.76 Ma), whereas the earliest internal split occurred at approximately 11.52 Ma. These events broadly coincide with tectonic and climatic changes near the middle-late Miocene transition (Spicer et al., 2020), suggesting a possible temporal association between environmental change in the Himalaya-Hengduan region and the initial diversification of the genus. The subsequent divergence of the *E. soluensis* + *E. damuensis* sp. nov. lineage at approximately 5.25 Ma falls near the Miocene-Pliocene boundary, whereas later divergences involving *E. caudatus*, *E. soluensis*, and populations of *E. macrurus* cluster near the Pliocene-Pleistocene transition. Taken as an approximate temporal framework, rather than a set of precise divergence dates, these estimates suggest that diversification in *Episoriculus* may have coincided with Neogene environmental change and later Quaternary climatic oscillations in the Himalaya-Hengduan biodiversity hotspot (Spicer et al., 2020; Lu et al., 2025). This interpretation is necessarily cautious because formal sensitivity analyses using alternative calibration schemes were not performed. Ecological differentiation may also have contributed to coexistence and diversification within the genus. *E. macrurus* and *E. gaoligongensis* sp. nov. exhibit semi-arboreal habits, whereas the remaining species are predominantly terrestrial, suggesting possible niche partitioning that may reduce direct competition among sympatric taxa. In addition, *E. damuensis* sp. nov., *E. umbrinus*, and *E. caudatus* occupy distinct elevational zones in Medog, with *E. damuensis* sp. nov. primarily distributed at 2560-2700 m, *E. umbrinus* at 2080-2230 m, and *E. caudatus* mainly below 1960 m. Comparable elevational segregation has also been documented in *Soriculus* (Chen et al., 2024). Such patterns are consistent with the hypothesis that steep altitudinal gradients in the Himalaya-Hengduan region facilitate ecological differentiation across elevational

belts. In addition to ecological differentiation, major river systems may have acted as barriers to dispersal and gene flow within *Episoriculus*. In particular, the Jinsha River is a plausible historical barrier associated with the divergence between the sister species *E. umbrinus* and *E. sacratulus*, which split during the early Pleistocene (~2.02 Ma). *Episoriculus sacratulus* is restricted to western Sichuan north of the upper Yangtze River, whereas *E. umbrinus* occurs primarily south of the Jinsha River. Similar riverine barriers have been implicated in diversification processes in many other montane mammals from the Hengduan Mountains, where deep valleys and river systems frequently restrict dispersal and promote allopatric divergence (Chen et al., 2017; He et al., 2019).

Taken together, these patterns suggest that diversification within *Episoriculus* is consistent with historical influences of geological, climatic, ecological, and geographic processes across the southeastern Himalaya-Hengduan Mountains. The concentration of both extant diversity and deep phylogenetic lineages in this region further suggests that it may have functioned as both a long-term refugium and a center of diversification for montane small mammals. Long-term environmental stability, complex topography, repeated climatic oscillations, ecological heterogeneity, and riverine barriers are plausible contributors to lineage persistence and diversification, but their relative roles remain to be tested explicitly with denser genomic, ecological, and biogeographic analyses. Similar patterns have been documented in other montane vertebrates from southwestern China, where heterogeneous habitats have generated high levels of cryptic diversity and phylogeographic structure (Wan et al., 2018; He et al., 2019; Song et al., 2025; Zhu et al., 2025; Li et al., 2026).

DATA AVAILABILITY

All newly generated sequences have been deposited in GenBank and uploaded to ScienceDB (<https://doi.org/10.57760/sciencedb.j00139.000a9>).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Z.Z.C. contributed to the study design, proposed the research concept and overall objectives, performed data analysis, and led the writing of the manuscript. Y.C.S., M.Z., X.X.P., and Y.F.X. performed specimen collection, molecular experiments, and data analysis. Q.L., W.Y.S., Z.X.Z. conducted specimen collection, manuscript review, and editing. O.O.K., X.Y.L. conducted manuscript review and editing. X.L.J. proposed the research concept, provided specimens and tissue samples, reviewed and edited the manuscript, and secured project funding. All authors read and approved the final version of the manuscript.

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REFERENCES

- Abe H. 1971. Small mammals of central Nepal. *Journal of the Faculty of Agriculture*, **56**(4): 367–423.
- Abe H. 1977. Variation and taxonomy of some small mammals from central Nepal. *Journal of the Mammalogical Society of Japan*, **7**(2): 63–74.
- Abe H. 1982. Ecological distribution and faunal structure of small mammals in central Nepal. *Mammalia*, **46**(4): 477–504.
- Abramov AV, Bannikova AA, Chernetskaya DM, et al. 2017. The first record of *Episoriculus umbrinus* from Vietnam, with notes on the taxonomic composition

- 1010 of *Episoriculus* (Mammalia, Soricidae). *Russian Journal of Theriology*, **16**(2):
1011 117–128.
- 1012 Allen GM. 1923. New Chinese insectivores. *American Museum Novitates*, **100**: 1-11.
- 1013 Allen GM. 1938. The Mammals of China and Mongolia. New York: The American
1014 Museum of Natural History.
- 1015 Anderson J. 1877. Description of some new and little known Asiatic shrews in the Indian
1016 Museum, Calcutta. *Journal of the Asiatic Society of Bengal*, **46**: 261-283.
- 1017 Anthony HE. 1941. Mammals collected by the Vernay-Cutting Burma expedition. In
1018 Papers on Mammalogy, Published in Honor of Wilfred Hudson Osgood. Chicago:
1019 Field Museum of Natural History.
- 1020 Blanford WT. 1888. The fauna of British India: including Ceylon and Burma-Mammalia.
1021 London: Taylor and Francis.
- 1022 Bover P, Mitchell KJ, Llamas B, et al. 2018. Molecular phylogenetics supports the origin
1023 of an endemic Balearic shrew lineage (*Nesiotites*) coincident with the Messinian
1024 Salinity Crisis. *Molecular Phylogenetics and Evolution*, **125**: 188–195.
- 1025 Burgin CJ, He K. 2018. Family Soricidae (shrew). In: Wilson DE, Russell AM (eds),
1026 Handbook of the Mammals of the World: Insectivores, Sloths and Colugos.
1027 Barcelona: Lynx Editions.
- 1028 Chen ZZ, He K, Huang C, et al. 2017. Integrative systematic analyses of the genus
1029 *Chodsigoa* (Mammalia: Eulipotyphla: Soricidae), with descriptions of new
1030 species. *Zoological Journal of the Linnean Society*, **180**(3): 694–713.
- 1031 Chen ZZ, He SW, Hu WH, et al. 2021. Morphology and phylogeny of scalopine moles
1032 (Eulipotyphla: Talpidae: Scalopini) from the eastern Himalayas, with descriptions
1033 of a new genus and species. *Zoological Journal of the Linnean Society*, **193**(2):
1034 432–444.
- 1035 Chen ZZ, Pei XX, Hu JX, et al. 2024. Multilocus phylogeny and morphological analyses
1036 illuminate overlooked diversity of *Soriculus* (Mammalia: Eulipotyphla:
1037 Soricidae), with descriptions of two new endemic species from the eastern
1038 Himalayas. *Zoological Journal of the Linnean Society*, **201**(2): 534–548.
- 1039 Corbet GB. 1978. The mammals of the Palearctic region: a taxonomic review. London:
1040 British Museum (Natural History), 1-314.
- 1041 Corbet GB, Hill JE. 1992. The Mammals of the Indomalayan Region: a Systematic
1042 Review. Natural History Museum Publications, Oxford University Press, Oxford,
1043 488 pp.
- 1044 de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology*,
1045 **56**(6): 879–886.
- 1046 Ellerman JR, Morrison-Scott TCS. 1951. Checklist of Palaearctic and Indian mammals
1047 1758 to 1946. London: British Museum.



- 1048 Ellerman JR, Morrison-Scott TCS. 1966. Checklist of Palaearctic and Indian Mammals
1049 1758 to 1946 (2nd ed.). London: British Museum (Natural History).
- 1050 Gray JE. 1863. Catalogue of the Specimens and Drawings of Mammalia, Birds, Reptiles
1051 and Fishes of Nepal and Tibet. London: British Museum (Natural History).
- 1052 Gruber U. 1969. Tiergeographische, ökologische und bionomische Untersuchungen an
1053 kleinen Säugetieren in Ost-Nepal. *Khumbu Himal*, **3**(2): 149-312. (in German).
- 1054 Gutiérrez EE, Garbino GST. 2018. Species delimitation based on diagnosis and
1055 monophyly, and its importance for advancing mammalian taxonomy. *Zoological
1056 Research*, **39**(5): 301–308.
- 1057 He K, Li YJ, Brandley MC, et al. 2010. A multi-locus phylogeny of Nectogalini shrews
1058 and influences of the paleoclimate on speciation and evolution. *Molecular
1059 Phylogenetics and Evolution*, **56**(2): 734–746.
- 1060 He K, Gutiérrez EE, Heming NM, et al. 2019. Cryptic phylogeographic history sheds
1061 light on the generation of species diversity in sky-island mountains. *Journal of
1062 Biogeography*, **46**(10): 2232–2247.
- 1063 Hoffmann RS. 1985. A review of the genus *Soriculus* (Mammalia: Insectivora). *Journal
1064 of the Bombay Natural History Society*, **82**: 459–481.
- 1065 Honacki JH, Kinman KE, Koepl JW. 1982. Mammal Species of the World: A
1066 Taxonomic and Geographic Reference (1st ed.). Kansas: Allen Press, Inc. and
1067 The Association of Systematic Collection.
- 1068 Horsfield T. 1851. A catalogue of the Mammalia of the Museum of the Hon. East India
1069 Company. London: W.H. Allen and Co., 212 pp.
- 1070 Horsfield T. 1855. Brief notices of several new or little known species of Mammalia,
1071 lately discovered and collected in Nepal by Brian Houghton Hodgson. *The Annals
1072 and Magazine of Natural History*, **2**(16): 101-114.
- 1073 Hutterer R. 1993. Order Insectivora. In: Wilson DE, Reeder DM (eds), Mammal Species
1074 of the World: A Taxonomic and Geographic Reference (2nd ed.). Washington and
1075 London: Smithsonian Institution Press, 69-130.
- 1076 Hutterer R. 1994. Generic limits among Neomyine and Soriculine shrews (Mammalia:
1077 Soricidae). Neogene and Quaternary Mammals of the Palaearctic: Conference in
1078 Honour of Professor Kazimierz Kowalski, Kraków, Poland.
- 1079 Hutterer R. 2005a. Order Erinaceomorpha, Order Soricomorpha. In: Wilson DE, Reeder
1080 DM (eds), Mammal Species of the World: A Taxonomic and Geographic
1081 Reference (3rd ed.). Baltimore: Johns Hopkins Press, 212-311.
- 1082 Hutterer R. 2005b. Homology of unicuspid and tooth nomenclature in shrews. In:
1083 Merritt JF, Churchfield S, Hutterer R, Sheftel B, eds. Advances in the Biology of
1084 Shrews II. Special Publication No. 1. New York: International Society of Shrew
1085 Biologists, 379–404.



- 1086 James EW, Jones GS. 1977. The Soricidae of Taiwan. *Proceedings of the Biological*
1087 *Society of Washington*, **90**: 459-482.
- 1088 Jiang ZG. 2015. Diversity and Geographical Distribution of Mammals in China. Beijing:
1089 Science Press. (in Chinese).
- 1090 Jiang HJ, Fu CK, Tang KY, et al. 2023. Molecular phylogenetics and diversity of the
1091 Himalayan shrew (*Soriculus nigrescens* Gray, 1842) (Eulipotyphla, Soricidae) in
1092 Southwest China. *Zootaxa*, **5263**(1): 061–078.
- 1093 Lanfear R, Frandsen PB, Wright AM, et al. 2017. PartitionFinder 2: new methods for
1094 selecting partitioned models of evolution for molecular and morphological
1095 phylogenetic analyses. *Molecular Biology and Evolution*, **34**(3): 772–773.
- 1096 Li Q, Li XY, Hu WQ, et al. 2024. Mammals of Gaoligong Mountain in China: diversity,
1097 distribution, and conservation. *Zoological Research: Diversity and Conservation*,
1098 **1**(1): 3–19.
- 1099 Li Q, Jackson SM, Li XY, et al. 2025. Discovery of a new species of giant flying squirrel
1100 (*Petaurista*) from northwest Yunnan, China, sheds light on the origin and
1101 diversification of the genus. *Zoological Journal of the Linnean Society*, **205**(1):
1102 zlaf106.
- 1103 Li YX, Chen ZZ, Li Q, et al. 2026. Species diversification in the sky islands of
1104 southwestern China revealed by genomic, introgression, and demographic
1105 analyses of Asian shrew moles. *Systematic Biology*, **75**(2): 221–235.
- 1106 Liu YX, Wang XM, Wan T, et al. 2025. Integrative phylogenetic analysis of the genus
1107 *Episoriculus* (Mammalia: Eulipotyphla: Soricidae). *PLoS ONE*, **20**(1): e0299624.
- 1108 Lu C, Ding W, Xu W, et al. 2025. Contrasting evolutionary trajectories of terrestrial
1109 vertebrates in the Hengduan Mountains hotspot. *National Science Review*, **12**(8):
1110 nwaf157.
- 1111 Mittermeier RA, Turner WR, Larsen FW, et al. 2011. Global biodiversity conservation:
1112 the critical role of hotspots. In: Mittermeier RA, Turner WR, Larsen FW, Brooks
1113 TM, Gascon C (eds), *Biodiversity Hotspots*. Berlin: Springer, 3–22.
- 1114 Motokawa M, Harada M, Lin LK, et al. 1997. Karyological study of the gray shrew
1115 *Crocidura attenuata* (Mammalia: Insectivora) from Taiwan. *Zoological Studies*,
1116 **36**(1): 70-73.
- 1117 Motokawa M, Lin LK. 2005. Taxonomic status of *Soriculus baileyi* (Insectivora,
1118 Soricidae). *Mammal Study*, **30**(2): 117–124.
- 1119 Motokawa M, Harada M, Mekada K, et al. 2008. Karyotypes of three shrew species
1120 (*Soriculus nigrescens*, *Episoriculus caudatus* and *Episoriculus sacratu*) from
1121 Nepal. *Integrative Zoology*, **3**(3): 180–185.
- 1122 Motokawa M, Wu Y, Harada M. 2009. Karyotypes of six soricomorph species from Emei
1123 Shan, Sichuan Province, China. *Zoological Science*, **26**(11): 791–797.



- 1124 Ohdachi SD, Hasegawa M, Iwasa MA, et al. 2006. Molecular phylogenetics of soricid
1125 shrews (Mammalia) based on mitochondrial cytochrome *b* gene sequences: with
1126 special reference to the Soricinae. *Journal of Zoology*, **270**(1): 177–191.
- 1127 Pan QH, Wang YX, Yan K. 2007. A Field Guide to the Mammals of China. Beijing:
1128 China Forestry Publishing House. (in Chinese)
- 1129 Raposo MA, Kirwan GM, Lourenço ACC, et al. 2021. On the notions of taxonomic
1130 'impediment', 'gap', 'inflation' and 'anarchy', and their effects on the field of
1131 conservation. *Systematics and Biodiversity*, **19**(3): 296–311.
- 1132 Repenning CA. 1967. Subfamilies and Genera of the Soricidae. Washington, D.C.:
1133 United States Government Printing Office.
- 1134 Smith AT, Xie Y. 2009. A Guide to the Mammals of China. Changsha: Hunan Education
1135 Publishing House. (in Chinese)
- 1136 Song WY, Chen ZZ, Li Q, et al. 2025. Taxonomic revision of the long-tailed mole
1137 (Talpidae: *Scaptonyx*) with description of a new species from the Gaoligong
1138 Mountains. *Journal of Mammalogy*, **106**(3): 782–797.
- 1139 Spicer RA, Su T, Valdes PJ, et al. 2021. Why 'the uplift of the Tibetan Plateau' is a myth.
1140 *National Science Review*, **8**(1): nwaa091.
- 1141 Steenwyk JL, Li YN, Zhou XF, et al. 2023. Incongruence in the phylogenomics era.
1142 *Nature Reviews Genetics*, **24**(12): 834–850.
- 1143 Storch G, Qiu ZD, Ziegler S. 1998. Fossil history of shrews in Asia. In: Wójcik JM,
1144 Wolsan M (eds), *Evolution of Shrews*. Białowieża: Mammal Research Institute,
1145 Polish Academy of Sciences, 93–120.
- 1146 Thomas O. 1911a. On mammals collected in the provinces of Szechwan and Yunnan, W.
1147 China, by Malcolm Anderson, for the Duke of Bedford's exploration. *Abstracts of*
1148 *the Proceedings of the Zoological Society of London*, **100**: 48–50.
- 1149 Thomas O. 1911b. Mammals collected in the provinces of Kan-su and Sze-chwan,
1150 western China, by Mr. Malcolm Anderson, for the Duke of Bedford's exploration
1151 of Eastern Asia. *Abstracts of the Proceedings of the Zoological Society of London*,
1152 **90**: 3–5.
- 1153 Thomas O. 1913. Four new shrews. *The Annals and Magazine of Natural History*, Ser. 8,
1154 **11**(62): 214–218.
- 1155 Thomas O. 1914. A new *Soriculus* from the Mishmi Hills. *Journal of the Bombay*
1156 *Natural History Society*, **22**: 683.
- 1157 Thomson SA, Pyle RL, Ahyong ST, et al. 2018. Taxonomy based on science is necessary
1158 for global conservation. *PLoS Biology*, **16**(3): e2005075.
- 1159 Wan T, He K, Jin W, et al. 2018. Climate niche conservatism and complex topography
1160 illuminate the cryptic diversification of Asian shrew-like moles. *Journal of*
1161 *Biogeography*, **45**(10): 2400–2414.



- 1162 Wan Y, Qing P, Su WT, et al. 2026. Karyotypes of three shrew species and implication
1163 of their taxonomic states. *Acta Theriologica Sinica* (in press).
1164 <https://doi.org/10.16829/j.slxb.151106>.
- 1165 Wang YX. 2003. A Complete Checklist of Mammal Species and Subspecies in China and
1166 Their Distribution. Beijing: China Forestry Publishing House. (in Chinese).
- 1167 Wang SY, Li YX, Li Q, et al. 2024. A new species of mountain vole (Rodentia,
1168 Cricetidae, *Neodon*) from south Xizang, China. *Zoological Research: Diversity
1169 and Conservation*, **1**(4): 282–289.
- 1170 Wei FW, Yang QS, Wu Y, et al. 2022. Taxonomy and Distribution of Mammals in
1171 China. Beijing: Science Press. (in Chinese).
- 1172 Wei FW, Yang QS, Wu Y, et al. 2025. Catalogue of mammals in China (2024). *Acta
1173 Theriologica Sinica*, **45**(1): 1–16. (in Chinese).
- 1174 Weigel I. 1969. Systematische Übersicht über die Insektenfresser und Nager Nepals nebst
1175 Bemerkungen zur Tiergeographie. *Khumbu Himal*, **3**(2): 149–196. (in German).
- 1176 Wilson DE, Reeder DM. 2005. Mammal Species of the World: A Taxonomic and
1177 Geographic Reference (3rd ed.). Baltimore: Johns Hopkins University Press.
- 1178 Yuan SL, Jiang XL, Li ZJ, et al. 2013. A mitochondrial phylogeny and biogeographical
1179 scenario for Asiatic water shrews of the genus *Chimarrogale*: implications for
1180 taxonomy and low-latitude migration routes. *PLoS ONE*, **8**(10): e77156.
- 1181 Yuan HB, Dickson ED, Martinez Q, et al. 2024. The origin and evolution of shrews
1182 (Soricidae, Mammalia). *Proceedings of the Royal Society B: Biological Sciences*,
1183 **291**(2037): 20241856.
- 1184 Zhang RZ. 2002. Geological events and mammalian distribution in China. *Acta
1185 Zoologica Sinica*, **48**: 141–153.
- 1186 Zhang D, Gao F, Jakovlić I, et al. 2020. PhyloSuite: an integrated and scalable desktop
1187 platform for streamlined molecular sequence data management and evolutionary
1188 phylogenetics studies. *Molecular Ecology Resources*, **20**(1): 348–355.
- 1189 Zhang T, Lei ML, Zhou H, et al. 2022. Phylogenetic relationships of the zokor genus
1190 *Eospalax* (Mammalia, Rodentia, Spalacidae) inferred from whole-genome
1191 analyses, with description of a new species endemic to Hengduan Mountains.
1192 *Zoological Research*, **43**(3): 331–342.
- 1193 Zhu ZX, Li Q, Song WY, et al. 2025. Discovery of an ancient Himalayan birch mouse
1194 lineage illuminates the evolution of the family *Sicistidae* (Rodentia: Dipodoidea),
1195 with descriptions of a new genus and two new species. *Zoological Research*,
1196 **46**(4): 921–938.

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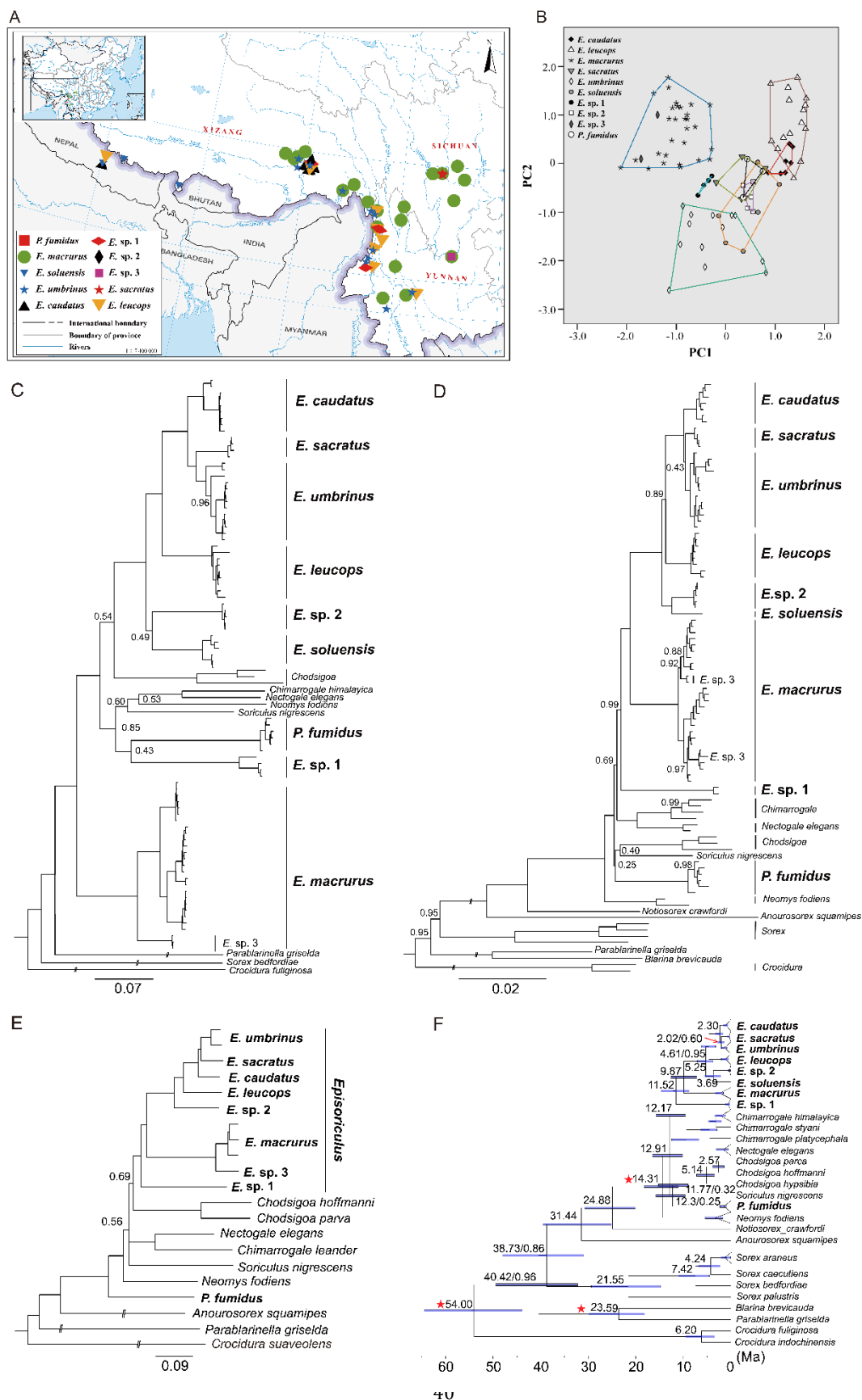


Figure 1. Sampling localities, PCA, phylogenetic relationships, and divergence-time estimation of *Episoriculus* and related taxa. (A) Geographic distribution of the sampled specimens. (B) Results of the principal component analysis (PCA). (C) Bayesian Phylogenetic tree based on the concatenated mitochondrial 12S rRNA and *Cyt b* genes. (D) Bayesian Phylogenetic tree based on the concatenated nuclear genes. (E) Bayesian phylogenetic tree based on mitochondrial genomes. (F) Divergence times estimated using BEAST. Red stars indicate secondary calibration points.

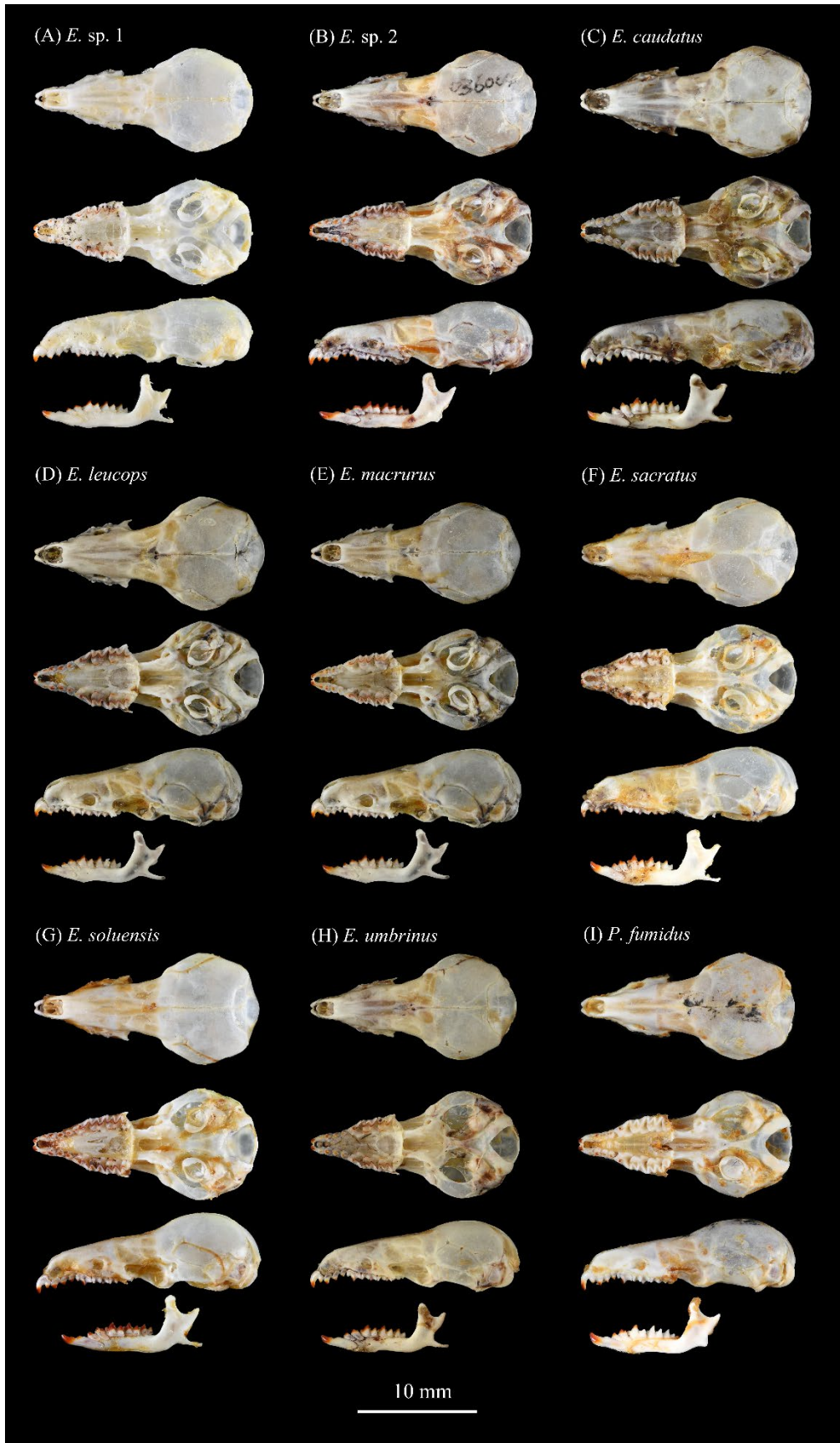


Figure 2. The ventral, dorsal, and lateral views of the skull of (A) *E. sp. 1* (KIZ: 040393), (B) *E. sp. 2* (KIZ: 040418), (C) *E. caudatus* (KIZ: 040425), (D) *E. leucops* (KIZ: 040424), (E) *E. macrurus* (KIZ: 040423), (F) *E. sacratus* (AHNU: SC2110093), (G) *E. soluensis* (KIZ: 040422), (H) *E. umbrinus* (KIZ: 040421), and (I) *P. fumidus* (KIZ: 040412).

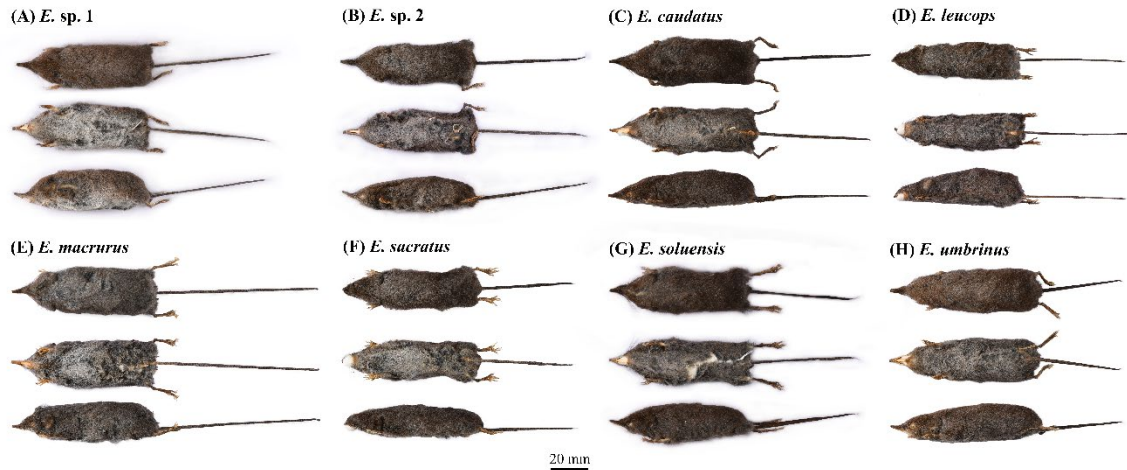


Figure 3. Dorsal and ventral views of the skin of (A) *E. sp. 1* (KIZ: 040393), (B) *E. sp. 2* (KIZ: 040418), (C) *E. caudatus* (KIZ: 040361), (D) *E. leucops* (KIZ: 040426), (E) *E. macrurus* (KIZ: 040427), (F) *E. sacratus* (AHNU: SC2110093), (G) *E. soluensis* (KIZ: 040422), and (H) *E. umbrinus* (KIZ: 040428).

1217 **Table**

1218 **Table 1.** Means (mm), standard deviations, ranges, and sample sizes of morphological measurements for different operational taxonomic
 1219 units (OTUs) of the genus *Episoriculus* and *Pseudosoriculus*.

1220

Variable	<i>E. sp. 1</i>	<i>E. sp. 2</i>	<i>E. caudatus</i>	<i>E. leucops</i>	<i>E. macrurus</i>	<i>E. sp. 3</i>	<i>E. sacratulus</i>	<i>E. soluensis</i>	<i>E. umbrinus</i>	<i>P. fumidus</i>
	N=4	N=5	N=7	N=15	N=29	N=2	N=5	N=6	N=14	N=3
WT	4.4 ± 0.3 4.0-4.6; 4	5.4±1.7 4.3-8.4; 5	6.1±0.9 4.8-7.0; 7	7.5±1.4 5.9-10.6; 14	4.7±0.8 3.6-6.9; 29	2.9-3.7	5.7±0.9 4.7-6.9; 5	6.3±0.6 5.8-7.3; 6	4.7±0.8 3.1-6.3; 14	6.0±0.9 5.0-6.8; 3
HB	60±5 54-65; 4	62±4 60-68; 5	64±3 60-69; 7	68±4 60-77; 15	60±3 55-65; 29	47-52	64±2 62-67; 5	62±2 60-65; 6	60±5 52-70; 14	63±3 60-65; 3
TL	67±3 63-71; 4	69±3 65-72; 5	61±4 55-65; 7	71±7 55-82; 15	90±5 81-101; 29	72-82;	59±2 56-60; 5	55±2 53-57; 6	52±5 44-62; 14	48±3 45-50; 3
HF	14±1 13-15; 4	14±0 13-14; 5	13±3 5-15; 7	15±1 13-17; 15	15±1 12-17; 29	13-17	13±0 13-13; 5	13±1 12-14; 6	13±1 11-14; 14	13±1 12-13; 3
EL	8±1 7-9; 4	9±1 8-9; 5	8±1 7-10; 7	8±2 5-11; 14	8±2 4-11; 28	8-10	10±1 9-11; 5	8±1 6-9; 6	7±1 4-9; 14	8±0 8-9; 3
CIL	17.87±0.15 17.76-18.08; 4	18.63±0.10 18.53-18.79; 5	19.38±0.22 19.03-19.72; 7	19.61±0.30 19.15-20.09; 15	17.59±0.41 16.58-18.46; 29	16.86-16.93	18.28±0.36 17.81-18.79; 5	18.29±0.49 17.75-18.88; 6	17.68±0.58 16.68-18.55; 14	18.51±0.49 18.19-19.07; 3
PIL	7.89±0.11 7.80-8.03; 4	8.21±0.15 8.00-8.42; 5	8.61±0.05 8.56-8.68; 7	8.67±0.22 8.35-9.05; 15	7.57±0.23 7.02-7.90; 29	7.18-7.53	7.98±0.26 7.60-8.26; 5	8.17±0.26 7.80-8.40; 6	7.73±0.30 7.17-8.20; 14	8.12±0.26 7.95-8.42; 3
PPL	7.98±0.15 7.79-8.13; 4	7.74±0.12 7.59-7.90; 5	8.21±0.22 7.89-8.49; 7	8.31±0.24 7.82-8.57; 15	7.55±0.20 6.99-8.08; 29	7.00-7.48	7.88±0.11 7.79-8.07; 5	7.61±0.21 7.35-7.90; 6	7.50±0.22 7.15-7.89; 14	8.08±0.24 7.82-8.29; 3
RL	6.25±0.17 6.05-6.42; 4	6.99±0.34 6.77-7.58; 5	6.87±0.11 6.65-6.97; 7	7.10±0.17 6.77-7.38; 15	6.09±0.21 5.62-6.48; 29	5.58-5.66	6.36±0.30 6.08-6.82; 5	6.78±0.29 6.29-7.19; 6	6.36±0.22 6.04-6.81; 14	7.02±0.22 6.80-7.24; 3
PPD	3.48±0.12 3.33-3.61; 4	3.51±0.05 3.45-3.57; 5	3.68±0.10 3.53-3.84; 7	3.81±0.14 3.54-4.09; 15	3.68±0.11 3.43-3.91; 29	3.52-3.81	3.81±0.12 3.63-3.93; 5	3.51±0.09 3.37-3.61; 6	3.40±0.11 3.18-3.51; 14	3.55±0.05 3.51-3.60; 3
IOB	4.06±0.07 3.97-4.13; 4	4.19±0.12 4.00-4.31; 5	4.20±0.09 4.08-4.33; 7	4.43±0.14 4.22-4.61; 15	4.06±0.13 3.78-4.28; 29	3.93-3.98	4.13±0.08 4.02-4.23; 5	4.10±0.11 3.97-4.26; 6	3.97±0.12 3.79-4.13; 14	4.39±0.18 4.22-4.58; 3

CB	8.69±0.17	9.05±0.13	9.32±0.13	9.83±0.21	8.62±0.21		9.01±0.12	9.18±0.25	8.83±0.25	9.28±0.25
	8.43-8.82; 4	8.87-9.18; 5	9.12-9.49; 7	9.53-10.36; 15	8.22-8.95; 29	8.32-8.38	8.92-9.18; 5	8.89-9.52; 6	8.43-9.24; 14	9.13-9.57; 3
MB	5.07±0.13	5.13±0.11	5.58±0.17	5.93±0.20	5.08±0.15		5.41±0.11	5.36±0.16	5.13±0.30	5.31±0.07
	4.98-5.27; 4	5.03-5.30; 5	5.34-5.80; 7	5.59-6.22; 15	4.79-5.32; 29	4.82-4.95	5.26-5.56; 5	5.11-5.55; 6	4.67-5.74; 14	5.23-5.36; 3
M ² -M ²	4.69±0.14	4.69±0.08	5.24±0.14	5.35±0.19	4.61±0.15		5.02±0.14	4.90±0.13	4.68±0.19	4.93±0.01
	4.59-4.89; 4	4.56-4.79; 5	5.11-5.47; 7	4.98-5.74; 15	4.31-4.89; 29	4.40-4.60	4.82-5.17; 5	4.72-5.09; 6	4.45-4.95; 14	4.93-4.94; 3
UTL	7.64±0.12	7.90±0.16	8.32±0.09	8.45±0.21	7.35±0.23		7.65±0.24	7.95±0.28	7.51±0.36	7.95±0.33
	7.47-7.74; 4	7.71-8.13; 5	8.14-8.39; 7	7.95-8.77; 15	6.73-7.64; 29	7.11-7.49	7.33-8.00; 5	7.60-8.29; 6	6.98-8.12; 14	7.65-8.31; 3
P ¹ -M ³	4.52±0.08	4.72±0.12	4.98±0.05	5.02±0.11	4.60±0.15		4.69±0.12	4.74±0.12	4.49±0.19	4.85±0.11
	4.40-4.59; 4	4.55-4.84; 5	4.90-5.05; 7	4.76-5.16; 15	4.20-4.88; 29	4.40-4.67	4.57-4.82; 5	4.59-4.87; 6	4.16-4.79; 14	4.76-4.97; 3
CH	5.64±0.11	5.83±0.10	6.07±0.14	6.09±0.19	5.67±0.46		6.10±0.28	5.85±0.42	5.56±0.19	5.86±0.09
	5.54-5.77; 4	5.69-5.95; 5	5.84-6.24; 7	5.82-6.53; 15	3.76-6.29; 29	5.47-5.48	5.68-6.37; 5	5.42-6.38; 6	5.26-5.84; 14	5.78-5.95; 3
BMF	3.21±0.12	3.12±0.06	3.19±0.09	3.33±0.12	3.29±0.14		2.79±0.16	3.00±0.17	2.93±0.08	3.14±0.13
	3.06-3.34; 4	3.06-3.22; 5	3.05-3.28; 7	2.99-3.52; 15	3.09-3.59; 29	3.24-3.31	2.62-2.96; 5	2.85-3.31; 6	2.76-3.08; 14	3.00-3.26; 3
LTR	7.01±0.10	7.35±0.18	7.78±0.06	7.83±0.20	6.74±0.17		7.11±0.23	7.22±0.48	6.98±0.33	7.26±0.31
	6.93-7.15; 4	7.08-7.58; 5	7.71-7.85; 7	7.36-8.16; 15	6.34-7.01; 29	6.40-6.76	6.81-7.38; 5	6.36-7.69; 6	6.45-7.50; 14	7.03-7.61; 3
MdL	10.92±0.05	11.76±0.14	12.14±0.11	12.24±0.28	10.57±0.28		11.11±0.22	11.34±0.50	10.87±0.38	11.45±0.34
	10.85-10.97; 4	11.57-11.90; 5	12.01-12.36; 7	11.83-12.72; 15	9.88-11.19; 29	10.07-10.60	10.93-11.47; 5	10.61-11.97; 6	10.22-11.53; 14	11.12-11.79; 3
LLMn	3.71±0.13	3.93±0.07	4.18±0.09	4.21±0.13	3.86±0.10		3.99±0.15	3.86±0.14	3.76±0.16	3.99±0.19
	3.61-3.88; 4	3.87-4.04; 5	4.03-4.29; 7	3.93-4.42; 15	3.60-4.00; 29	3.73-3.93	3.78-4.14; 5	3.66-4.03; 6	3.45-4.00; 13	3.78-4.11; 3
HCP	3.98±0.13	4.16±0.05	4.20±0.12	4.27±0.13	3.98±0.13		4.19±0.16	4.11±0.18	3.82±0.13	3.91±0.10
	3.83-4.12; 4	4.10-4.23; 5	4.08-4.36; 7	4.05-4.45; 15	3.74-4.24; 29	3.73-3.81	4.00-4.42; 5	3.85-4.31; 6	3.61-3.99; 14	3.83-4.02; 3
HCV	2.56±0.05	2.61±0.05	2.79±0.11	2.79±0.11	2.54±0.22		2.79±0.05	2.65±0.15	2.51±0.12	2.70±0.05
	2.50-2.61; 4	2.56-2.69; 5	2.62-2.92; 7	2.51-3.02; 15	2.30-3.55; 29	2.46-2.48	2.72-2.83; 5	2.38-2.83; 6	2.31-2.66; 14	2.64-2.74; 3
HAC	3.16±0.14	3.46±0.12	3.57±0.14	3.61±0.08	3.12±0.12		3.41±0.11	3.28±0.08	3.20±0.15	3.34±0.12
	3.02-3.33; 4	3.28-3.60; 5	3.30-3.68; 7	3.43-3.71; 15	2.85-3.30; 29	2.97-3.26	3.30-3.54; 5	3.22-3.42; 6	2.99-3.50; 14	3.27-3.48; 3

Table 2. Factor loadings, eigenvalues and percentage of variance explained by the first two principal components of the principal component analysis of 19 log₁₀-transformed craniodental measurements of *Episoriculus* and *Pseudosoriculus*.

Variables	Principal Component	
	1	2
MdL	0.965	0.120
PIL	0.956	0.148
UTL	0.945	0.166
LTR	0.945	0.124
CIL	0.944	0.240
RL	0.904	-0.012
M ² -M ²	0.888	0.252
CB	0.880	0.226
HAC	0.870	0.150
MB	0.858	0.316
P ⁴ -M ³	0.827	0.427
PPL	0.802	0.330
LLMn	0.766	0.495
HCP	0.705	0.432
HCV	0.650	0.129
IOB	0.638	0.519
CH	0.612	0.343
PPD	0.247	0.821
BMF	-0.052	0.783
Eigenvalue	0.965	0.120
Percent variance explained (%)	63.54	14.67

Table 3. Pairwise *Cyt b* uncorrected (*p*) genetic distances (%) among OTUs of *Episoriculus* and *Pseudosoriculus* based on the *Cyt b* gene.

	<i>E. sp. 1</i>	<i>E. sp. 2</i>	<i>E. sp. 3</i>	<i>E. caudatus</i>	<i>E. leucops</i>	<i>E. macrurus</i>	<i>E. sacratu</i>	<i>E. soluensis</i>	<i>E. umbrinus</i>
<i>E. sp. 1</i>									
<i>E. sp. 2</i>	0.153								
<i>E. sp. 3</i>	0.149	0.150							
<i>E. caudatus</i>	0.149	0.129	0.144						
<i>E. leucops</i>	0.138	0.122	0.142	0.107					
<i>E. macrurus</i>	0.122	0.140	0.066	0.128	0.124				
<i>E. sacratu</i>	0.148	0.123	0.138	0.081	0.112	0.131			
<i>E. soluensis</i>	0.140	0.117	0.148	0.113	0.115	0.131	0.107		
<i>E. umbrinus</i>	0.130	0.106	0.135	0.071	0.092	0.122	0.053	0.095	
<i>P. fumidus</i>	0.146	0.166	0.161	0.156	0.156	0.128	0.161	0.140	0.147

Supplementary Table S1. Samples, sampling localities and DNA sequences used for molecular analyses.

Supplementary Table S2. The complete mitochondrial genomes used for phylogenetic analyses.

Supplementary Table S3. The best-fit partitioning schemes and evolutionary models estimated using PartitionFinder.

Supplementary Table S4. Results of the discriminant analysis.

Supplementary Table S5. Diagnostic comparison of the two new species and related *Episoriculus* species.

Supplementary Figure S1. Maximum-likelihood phylogenetic tree of the genus *Episoriculus* based on the concatenated datasets of (A) mitochondrial 12S rRNA and *Cyt b* genes, (B) nuclear genes and (C) the mitochondrial genome. Numbers beside nodes indicate SH-aLRT support (%)/ultrafast bootstrap support (%), respectively; support values of 100/100 are not shown.

1250 须弥鼯鼠属（哺乳纲：劳亚食虫目：鼯鼠科）的系统学修订与物种演化，兼记两
1251 新种

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1260

1261 ZooBank ID: urn:lsid:zoobank.org:pub:486245C7-313C-4BAE-83D8-08C14C20F311

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1264 **摘要：**须弥鼯鼠属（*Episoriculus*）隶属于哺乳纲劳亚食虫目鼯鼠科，是一类主要
1265 分布于喜马拉雅—横断山地区的小型食虫类哺乳动物。由于早期分类研究主要依据
1266 形态特征或所用标本的地理覆盖范围有限，该属的分类体系长期不稳定。本研究在
1267 广泛野外调查的基础上，测定了 2 个线粒体基因和 6 个核基因的序列，并获得了代
1268 表性操作分类单元（OTUs）的完整线粒体基因组，以重建属内系统发育关系；同
1269 时测量了 5 项外部形态指标和 19 项颅齿指标，以分析形态变异特征。整合分析结
1270 果发现 2 个新物种：分布于云南高黎贡山和西藏墨脱的高黎贡长尾鼯鼠（*E.*
1271 *gaoligongensis* sp. nov.），以及墨脱特有分布的达木长尾鼯鼠（*E. damuensis* sp.
1272 nov.）。整合证据支持须弥鼯鼠属包含 8 个有效种：褐腹长尾鼯鼠（*E. caudatus*）、
1273 大长尾鼯鼠（*E. leucops*）、小长尾鼯鼠（*E. macrurus*）、灰腹长尾鼯鼠（*E.*

*sacratu*s)、尼泊尔长尾鼯鼠 (*E. soluensis*)、云南长尾鼯鼠 (*E. umbrinus*)、高黎
贡长尾鼯鼠 (*E. gaoligongensis* sp. nov.) 和达木长尾鼯鼠 (*E. damuensis* sp. nov.)。
同时, 我们将米什米长尾鼯鼠 (*E. baileyi*) 处理为大长尾鼯鼠 (*E. leucops*) 的亚种,
并厘清了各物种的形态鉴别特征和分布范围。分化时间估算表明, 须弥鼯鼠属内的
主要分化事件发生于中新世至更新世, 总体上与喜马拉雅—横断山地区地质、气候、
生态和地理过程相互作用所塑造的演化历史相吻合。本研究凸显了整合分类学的重要
性, 尤其强调在界定快速分化的山地哺乳动物物种时, 不应仅仅依赖短片段线粒
体序列, 此类标记的局限性不可忽视。

关键词: 小型哺乳动物; 分类学; 系统发育; 新种; 喜马拉雅; 横断山