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THE SHREW OF NAGALAND: A REMARKABLE NEW GENUS AND SPECIES FROM NORTHEAST INDIA, WITH A DISCUSSION OF THE PHYLOGENY AND CLASSIFICATION OF THE SORICIDAE (MAMMALIA)

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ABSTRACT

A new genus and species of extant shrew, *Nagasorex albidens,* is described based on a single specimen obtained in Nagaland, northeastern India, in 1950. The new species shows novel characters, such as a total tooth number of 34, not found in any extant genus though they are found in extinct genera such as †*Miosorex*, †*Lartetium*, †*Pseudotrimylus*, and †*Domnina*. To determine the phylogenetic relationships of the new species, we first analyzed craniodental characters from all extant and many extinct genera of Soricidae. Although statistical support for most nodes was low, the nearest relatives of the new taxon appear to be certain Miocene and Pliocene taxa from Europe and Asia—†*Dobenflorinia* (new name), †*Clapasorex*, †*Miosorex*, and †*Crocidosorex*—followed by the extant African genera *Congosorex, Myosorex,* and *Surdisorex*, all of which we treat as members of the Myosoricinae. We then conducted a molecular phylogenetic study of extant genera using mitochondrial and nuclear genes. Although the genetic data we obtained from the new shrew are limited, our results place *Nagasorex* as the sister taxon of Crocidurinae (mitochondrial genes), or sister to Myosoricinae + Crocidurinae (nuclear genes). We tentatively place the new genus in the Myosoricinae. Additionally, we replace the preoccupied generic name *Soricella* with a new name, *Dobenflorinia*. Based on these results, we present a new systematic arrangement of the Soricidae.

INTRODUCTION

To an attentive naturalist, shrews may be nervous, high-strung little beasts with the energy of junior executives, a view reflecting the unique physiological constraints of these small mammals (Genoud, 1988). To a paleontologist, a shrew may be just that special piece of bone or tooth that finally appears in the sieve after laboriously shoveling, washing, and screening tons of sediment. People in ancient Egypt included shrews and other animals in their religious beliefs and practices; they embalmed and wrapped them carefully in cloth and placed them in small sarcophagi (Brunner-Traut, 1965; Woodman et al., 2017). Millennia later, other people removed the shrews from their ceremonial tombs and placed them equally carefully in museum collections, where they provide a unique record of animal life in ancient Egypt (Heim de Balsac and Mein, 1971; Hutterer, 1994a). There are obviously many different ways of looking at these animals.

Human mythology often is joined by scientific myth. Generations of textbooks (e.g., Romer, 1971) have delivered the opinion that shrews are among the most primitive mammals from which all other mammals may have been derived, despite the fact that in the Eocene, the earliest geological period from which remains of shrews are known (Yuan et al., 2024), most other mammal orders were already present (Simpson, 1953). Although we now know much more about the diversity of shrews than was the case only a decade or two ago (fig. 1), we know little about the origin or the general phylogenetic interrelationships of the approximately 29 extant (Wilson and Mittermeier, 2018; Burgin et al., 2020) and 90 extinct genera that are currently included in this family (if Heterosoricinae Viret and Zapfe (1951) are included; but see Yuan et al., 2024).

A unique specimen of unidentified shrew from Nagaland, a remote area of India, that had remained unstudied in hold-up collections of the Field Museum first received our attention more than three decades ago. Because this specimen contains a unique mix of traits not seen in any other living taxa, it expands the known morphological diversity of shrews and may provide a key for a better understanding of the relationships among the Soricidae G. Fischer, 1814 (Hutterer and Heaney, 1994). Our analyses, described below, show that this shrew does not fit well into the current taxonomic system of the family, but instead it combines characters of two subfamilies, and also exhibits characters known from Tertiary shrews believed to have been extinct since the Pliocene (Reumer, 1987). Although only one specimen is available for study, we conducted morphologically and genetically based analyses that provide critical information for the current discussion on the evolution of shrews. We begin this paper with a review of prior studies of shrew classification and phylogeny and describe the new shrew from Nagaland. We then assemble and analyse a set of craniodental characters from all extant and many extinct genera of shrews to place the new shrew into a broad phylogenetic context. Finally, we present a phylogenetic analysis of molecular data in an effort to clarify relationships of the living genera. On this basis, we propose a new classification of shrews and discuss future research needs.

A Brief Review of Soricid Classification and Phylogeny

The statement of Butler (1972: 253), "How to classify the insectivores is perhaps the most controversial problem of mammalian taxonomy," may equally apply to one component, the family Soricidae. Attempts to classify shrews began more than 200 years ago. In 1814 G. Fischer (who adopted the title "von Waldheim" only in 1835; see Mearns and Mearns, 1988) proposed the name Soricini for a group of mammals that Linnaeus (1758) had included in his "Bestiae" and Kerr (1792) and many others in the "Ferae," artificial clusters that embraced such diverse groups as carnivores, pigs, armadillos, opossums, and insectivores. G. Fischer's grouping was soon adopted as the family Soricidae by Bowdich (1821) and Gray (1821), to whom original authorship of the name often is mistakenly credited (e.g., Yates, 1984). Other early pathways of shrew classification have been reviewed in detail by Gill (1875) and Gregory (1910). A milestone was reached by Milne-Edwards (1872) and Dobson (1890) who, based on red or white coloration of the teeth, divided the Soricidae into the two subfamilies Soricinae G. Fischer, 1814 ("teeth red-tipped") and Crocidurinae Milne-Edwards 1872 ("teeth white"). Their view was subsequently adopted by Trouessart (1897), Cabrera (1925), Simpson (1945), and others, and constituted the principal classification of shrews for almost a century. However, subsequent studies have shown that all these authors grouped one or more genera incorrectly by constructing paraphyletic or polyphyletic groups.

In two interesting papers, Winge (1877, 1917, both translated into English in 1942) expressed a somewhat different view. His concept of the Soricidae was rather broad and included what is currently known as the Plesiosoricidae Winge, 1917, an extinct group of mole- or hedgehoglike creatures. The primary merit of Winge's work was that he tried to find new characters to determine their states in all of the species available to him and to discuss their polarities. He introduced the position of the foramen ovale as a new character, which allowed him to characterize the "Soriculi" (neomyine shrews in the current classification). With this new character he correctly recognized that *Chimarrogale* Anderson (1877) and *Nectogale* Milne-Edwards, 1870, are soricines, rather than crocidurine shrews as all former authors had classified them because they appeared to have unpigmented teeth.

One should bear in mind that at the time of Winge's publications only about 25% of the living genera of Soricidae known today had been discovered, and that the scientific study and description of fossil shrews was still in its infancy (fig. 1). It is interesting to recognize that the discovery of new genera of extant shrews was almost completed in the 1950s with the description of *Episoriculus* Ellerman and Morrison-Scott (1951), *Paracrocidura* Heim de Balsac, 1956, and *Congosorex* Heim de Balsac and Lamotte, 1956. Since then, four further genera of extant shrews have been named, *Ruwenzorisorex* Hutterer, 1986a, *Pseudosoriculus* Abramov et al. (2017a), *Palawanosorex* Hutterer et al., 2018, and *Parablarinella* Bannikova et al., 2019. A fifth new genus will be described in this report. However, this does not mean that the inventory of shrew diversity is complete. New discoveries are common at the species level, due to intensive field studies and new techniques that allow recognition of cryptic species. The total number of known extant shrew species increased from 1 in 1758 to 48 in 1858 and 265 in 1958; in 1993, it was 316 (Hutterer, 1993a), increased to 376 (Hutterer, 2005a), then to 448 (Wilson and Mittermeier, 2018), and recently to 488 species (Burgin et al., 2020; Esselstyn et al., 2021; Mammal Diversity Database, 2024) that are placed in 29 genera, and still there is no end to be seen (fig. 1). The discovery of fossil shrew genera also increased considerably; our list (below) contains a total of 80 genera of extinct shrews, 71 (89%) of which were named after 1950.

One of the significant discoveries of Winge's time was the African armored shrew, *Scutisorex somereni* Thomas (1910) (see also Thomas, 1913a, 1913b), a species with interlocking vertebrae, for which Allen (1917) erected a new subfamily Scutisoricinae Allen, 1917, a view also tentatively held by Simpson (1945). The fossil record was enriched by the description of a superbly preserved skull of a large Miocene shrew from Europe, †*Heterosorex* Gaillard (1915), which later served as the basis for the distinctive new subfamily Heterosoricinae Viret and Zapfe, 1951 (Wilson, 1960; Engesser, 1972, 1975, 1979). From Miocene sediments of North America, Stirton (1930) described the new genus, †*Limnoecus* Stirton, 1930, which apparently was related to Eurasian crocidurines but had pigmented teeth that are more typical of soricines. Stirton summarized what was known at his time about fossil and recent shrews and proposed five species groups for the latter.

In a short but significant paper entitled "On the phylogeny of the Soricidae," the paleontologist Stehlin (1940) described a new genus *Saturninia* Stehlin, 1940, that, for generations to follow, was considered to be the most primitive shrew known from the fossil record. More recently, this genus has been shown to be more distantly related to the Soricidae, and is now generally included in the family Nyctitheriidae Simpson et al. (1928) (Robinson, 1968; Krishtalka, 1977). He also presented new material of the little-known shrew †*Sorex antiquus* Pomel (1853) (= †*Crocidosorex antiquus*; see Crochet, 1975) from the Miocene of France, which in his view held an intermediate position between the Eocene and Oligocene †*Saturninia* and the modern shrews. Stehlin developed the hypothesis that over the course of the evolution of shrews a stepwise reduction in tooth number had taken place.

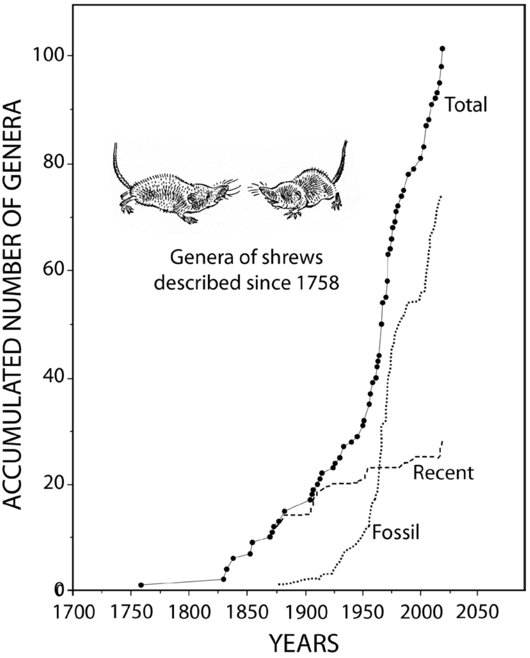


FIG. 1. Accumulated number of new genera of shrews described since Linnaeus, 1758, living and fossil. Synonyms have not been included. The graph shows that the inventory of extant genera was almost complete around 1960, at which time the study of fossil genera was in its prime. Sketch of fighting shrews by artist Erik Thorn, from Peter Crowcroft's (1957: 66) "The Life of the Shrew."

Simpson (1945) summarized what had been learned since the time of Linnaeus; he recognized 21 living and six extinct genera of shrews and arranged them in three subfamilies, as mentioned earlier. His study was followed by a prosperous period of new discoveries (see fig. 1), mainly from Africa (see Butler, 1998). At the same time, Bate (1945) discussed the fossil and extant shrews and substantiated why the genera

Chimarrogale and *Nectogale* belonged to the soricine shrews. Heim de Balsac (1956) described the remarkable genus *Paracrocidura* from Zaire (now Democratic Republic of the Congo), and Meester (1953) and Heim de Balsac and Lamotte (1956) produced important studies on the relationships of African genera. In a series of notes presented before the French Academy of Sciences, Heim de Balsac (1955, 1958, 1966a, 1966b) discussed evolutionary traits in characters of the skull and dentition of shrews. He pointed out that certain ancestral characters of the Eocene †*Saturninia* and the Miocene †*Heterosorex* also were present in extant African genera such as *Myosorex* Gray, 1838, *Congosorex*, *Surdisorex* Thomas (1906), and *Paracrocidura*. Other important contemporary contributions to the understanding of shrew evolution were Landry's (1957, 1989) articles on skull foramina and McDowell's (1958) comparative study of insectivore morphology. The latter author concluded that the Solenodontidae Gill, 1872, are the sister group of the Soricidae, a novel view.

In 1965 Kretzoi published a short paper on †*Drepanosorex* Kretzoi (1941), a genus of fossil shrew subsequently reduced to a subgenus of *Sorex* Linnaeus, 1758 (Reumer, 1985), in which he discussed classification problems of extant Soricidae and also proposed several new tribes, such as Soriculini Kretzoi, 1965, Crocidurini Kretzoi, 1965, Myosoricini Kretzoi, 1965, and Blarinini Kretzoi, 1965. Shortly thereafter, Repenning (1967) published his study of the systematic relationships among living and fossil genera of shrews that served as the basic classification of that group until recently. Repenning's work is outstanding for its clarity and consistency; characters are clearly defined, and all genera are described and figured in the same way. He recognized five subfamilies, the extinct †Heterosoricinae, †Allosoricinae Fejfar, 1966, the newly named †Limnoecinae Repenning, 1967, and the extant Soricinae and Crocidurinae. His conclusions were summarized in the form of a phylogenetic tree (fig. 2) that for the first time allowed easy orientation among the tangled diversity of shrews. Probably no other paper had such an impact on the further study of shrew phylogeny and evolution; generations of students have tested their findings since against Repenning's framework. However, neither he nor other authors before him presented their results within a cladistic framework, differing from cladistic methodology in such ways as using primitive characters to define relationships, explicitly constructing paraphyletic taxa, and recognizing grades as taxa.

In the same year, Van Valen (1967) published a comprehensive paper on the evolution of Insectivora in which the Soricidae played a minor role. Van Valen updated Simpson's (1945) list of genera and suggested that †Plesiosoricidae or †Adapisoricidae Schlosser, 1887 (now †Dormaaliidae Quinet, 1964; see Novacek et al., 1985) may be sister taxa of the Soricidae, a view held earlier by Winge (1917) and subsequently by Butler (1988) and others.

Only a few years later, Gureev (1971, 1979) presented his view of shrew phylogeny from a different perspective (fig. 3). Apparently due to information access and language barriers, his work has received much less attention in the English-speaking community than it deserves. Although part of his phylogeny warrants skepticism, it has the advantage that it offers clear branching patterns where Repenning operated with broad and unresolved tribal and subtribal "branches." Gureev's phylogeny constitutes a hypothesis that can easily be tested down to the level of the genus. As regards the ancestry of the shrews, he adopted once more Stehlin's (1940) idea of †*Saturninia* being the closest relative. He went even further and included this genus into the Soricidae under the new subfamily name †Saturniinae Gureev, 1979 (= †Nyctitheriidae).

One of the most conclusive systems to be proposed was established by Jammot (1983). Based on sound knowledge of both fossil and living shrews, he evaluated a number of characters for evolutionary trends and integrated information on fossil and extant genera, as had Repenning (1967) and Gureev (1971, 1979). Jammot treated the Heterosoricinae and Soricinae as sister taxa and consequently Crocidurini and Soricini as tribes. Repenning's subfamily †Limnoecinae appears in Jammot's system as a

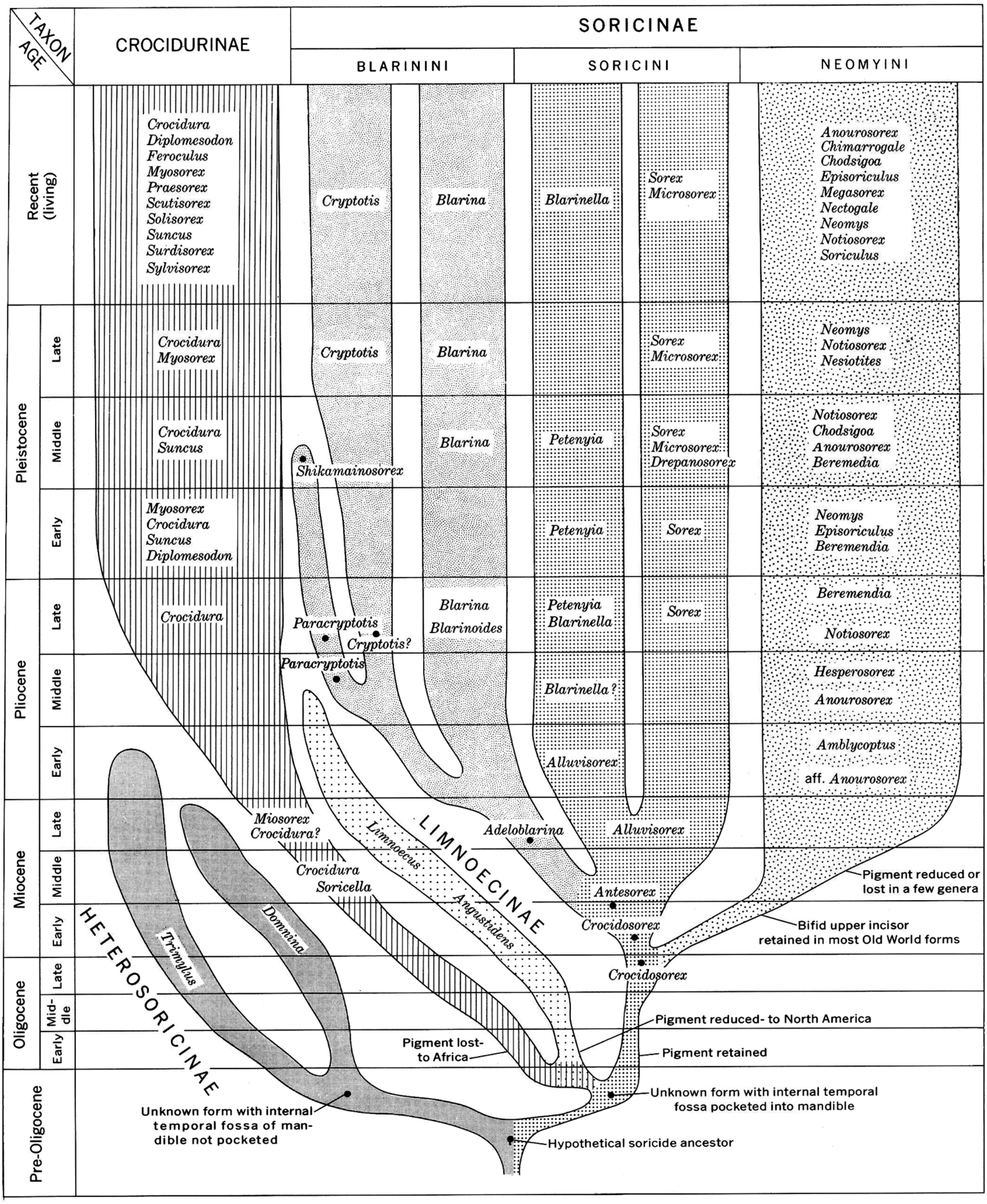


FIG. 2. Repenning's classical phylogeny of the Soricidae (Repenning, 1967: 61). The almost simultaneously published subfamily †Allosoricinae (Fejfar, 1966) does not appear in the graph.

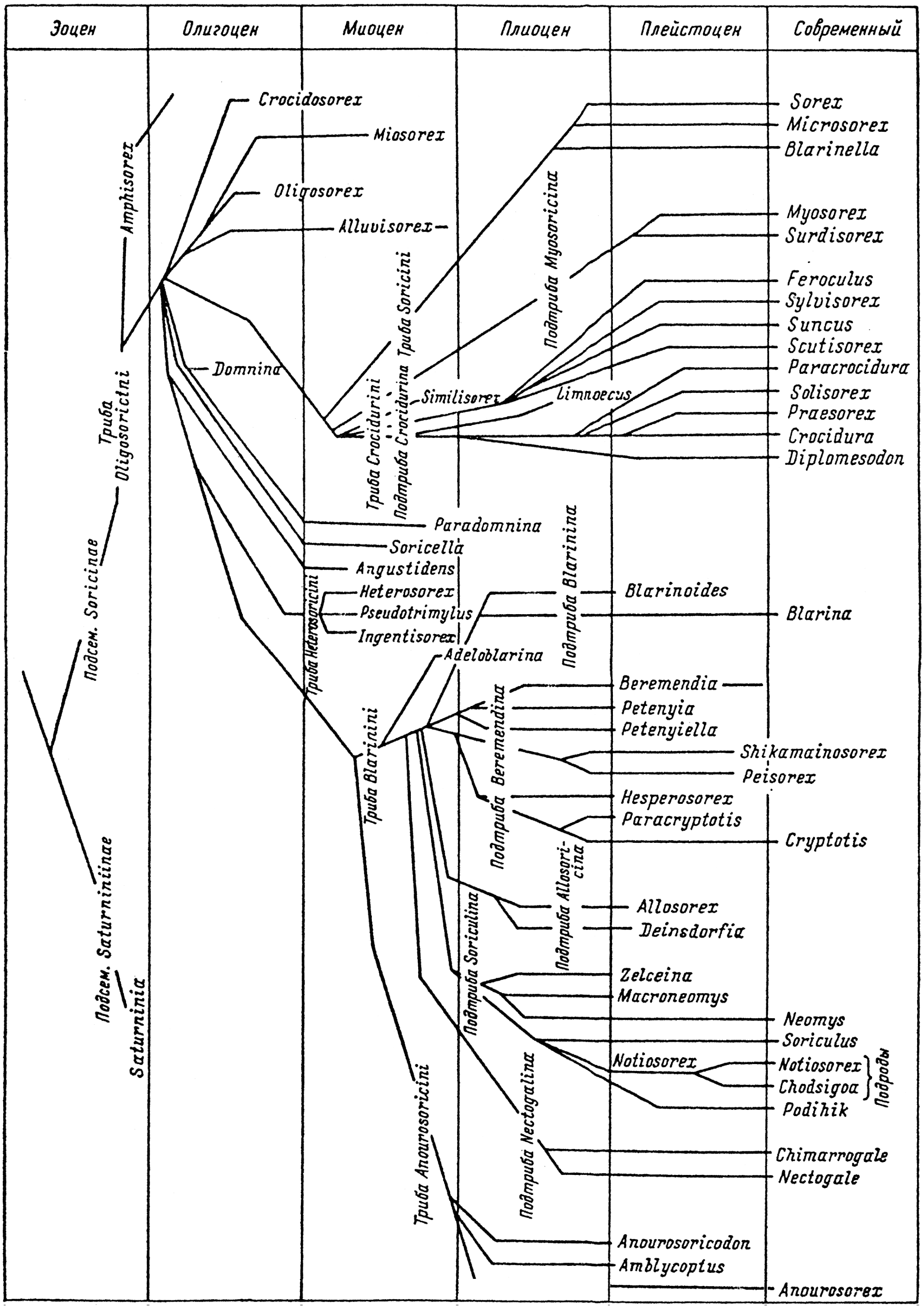


FIG. 3. Phylogeny proposed by Gureev (1979: 301) in which the †Saturniinae (= Nyctitheriidae) are treated as a subfamily of the Soricidae. The geological periods labeled in Russian letters are Eocene, Oligocene, Miocene, Pliocene, Pleistocene, and Holocene.

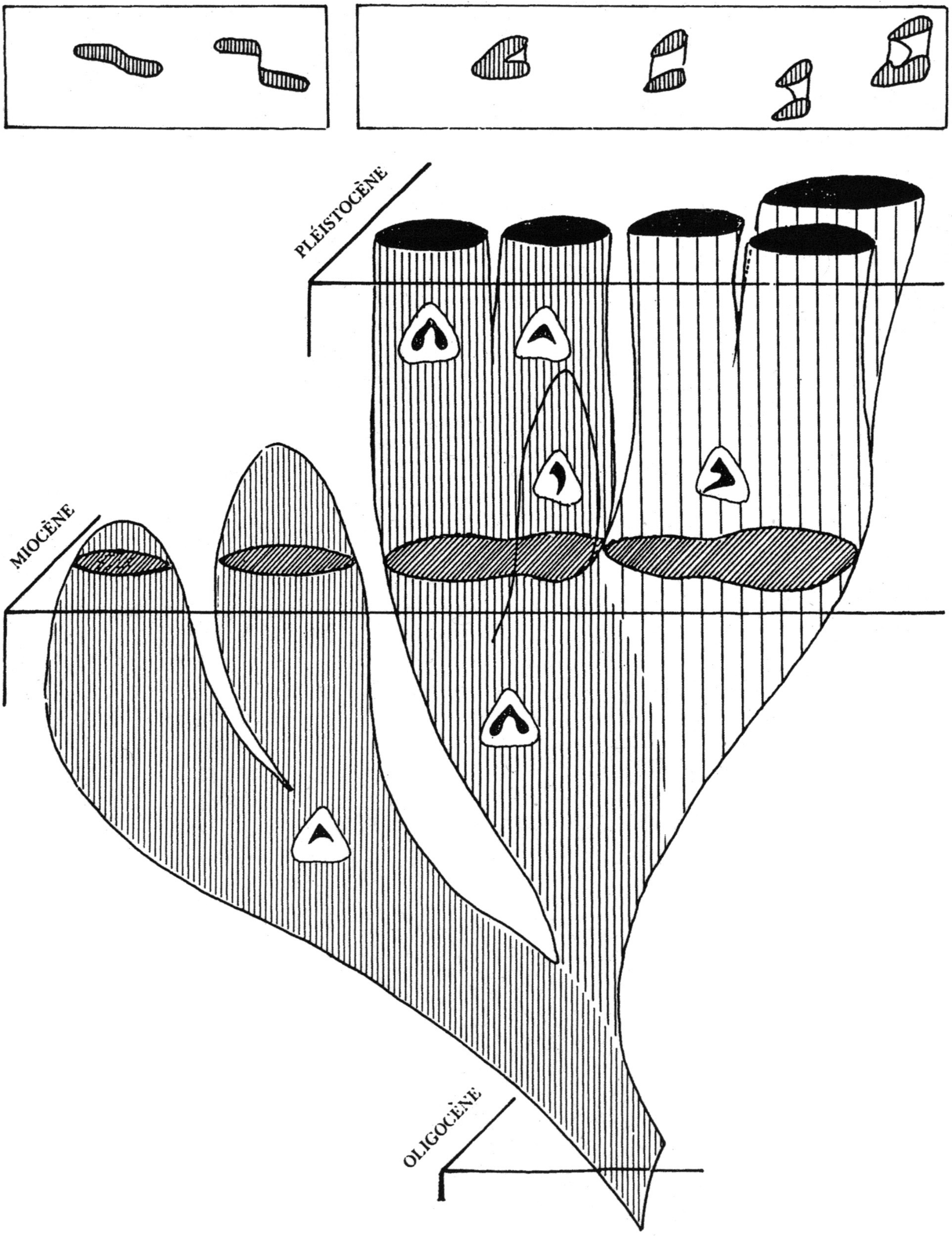


FIG. 4. Jammot's (1983: 270) design of the general evolutionary trends within the Soricidae based on characters of the mandibular condyle and the shape of the fourth lower premolar.

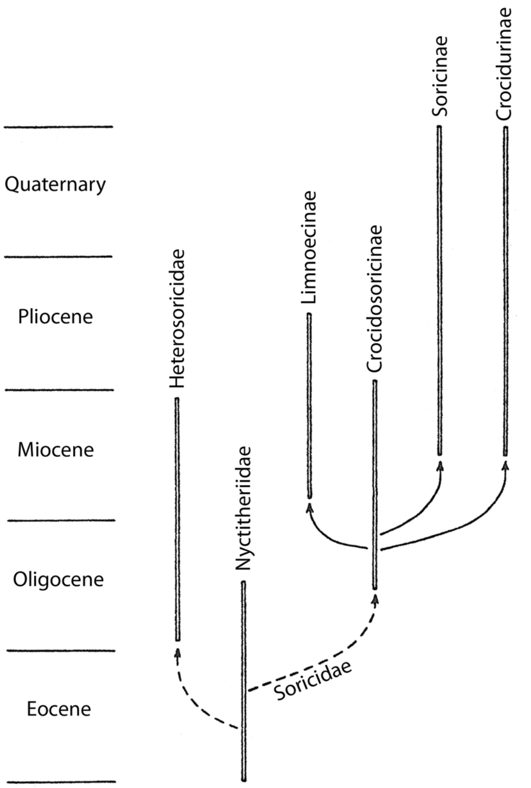


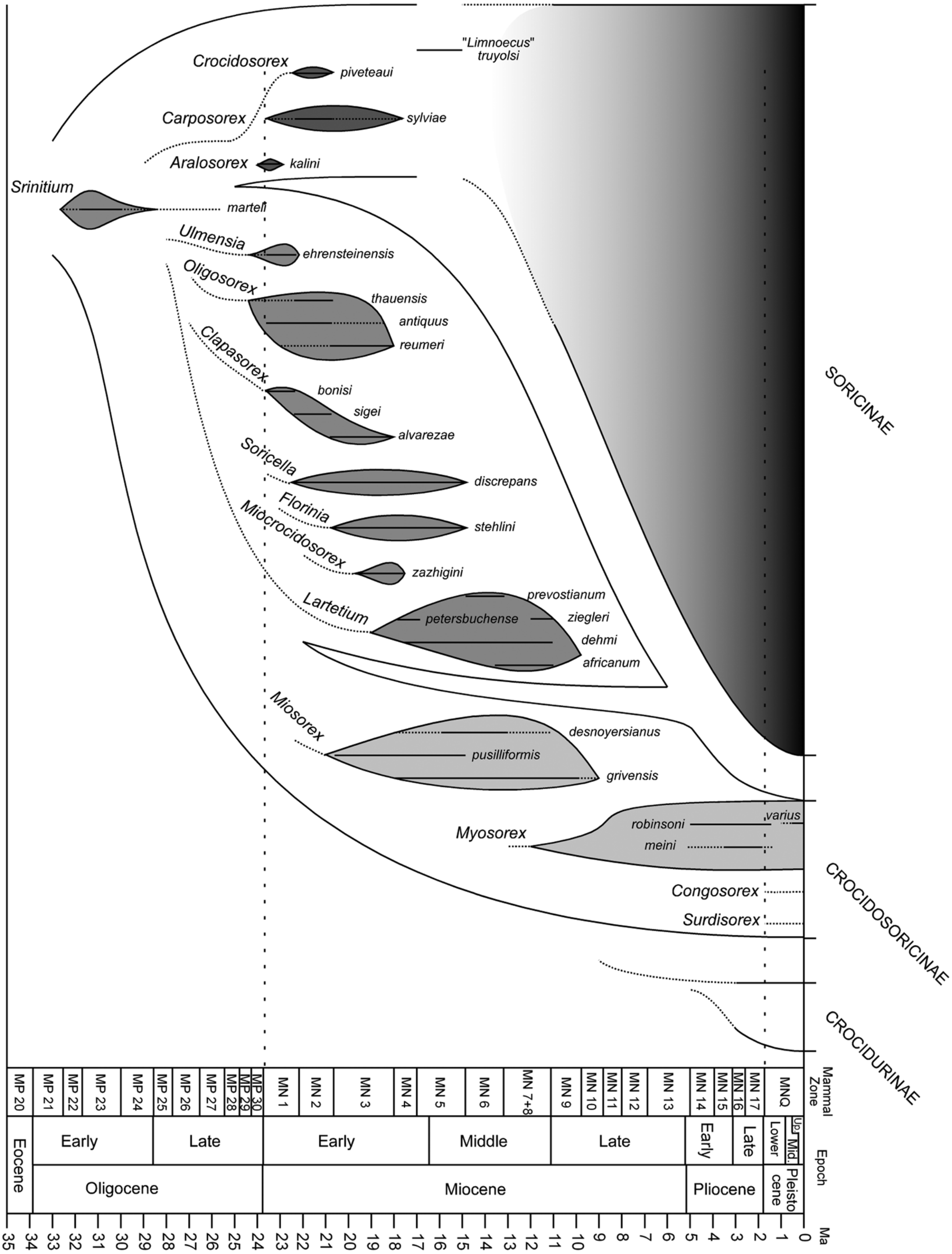
FIG. 5. Sketch taken from Reumer (1987: 191) in which the author derived both †Heterosoricinae (treated as a separate family) and Soricidae from the †Nyctitheriidae.

subtribe of Crocidurini, subfamily Soricinae (fig. 4), while the †Allosoricinae are not mentioned. He also adopted Kretzoi's (1965) proposal of a myosoricine group within the Crocidurini and expressly postulated a close relationship between the extant African genus *Myosorex* and extinct European genera such as †*Miosorex* Kretzoi (1959a), a conclusion relevant to the subject of this paper.

In a study of Plio-Pleistocene shrews of Europe, Reumer (1987) introduced a number of new genera and species and also rearranged the subfamily Soricinae, which he divided into seven tribes. He also provided valuable information on previously described genera from Asia and North America. In three further papers, Reumer (1989, 1992, 1994) discussed the taxonomic level of the Allosoricinae, which before Reumer (1984) was treated as a tribe, and he erected a new subfamily, †Crocidosoricinae Reumer, 1984, for †*Crocidosorex* Lavocat (1951) and a set of other extinct genera that were previously included in either Soricinae or Crocidurinae. Additionally, he excluded the †Heterosoricinae from the Soricidae. His hypothetical phylogenetic tree (Reumer, 1987: 191) differs from previous ones in that both Soricidae and †Heterosoricidae Viret and Zapfe, 1951, are supposed to stem from the Nyctitheriidae and the †Crocidosoricinae to give rise to the extinct †Limnoecinae and the extant Soricinae and Crocidurinae (fig. 5). This arrangement was subsequently accepted by Ziegler (1989). Hutterer (1993a) rejected the exclusion of the †Heterosoricinae from the Soricidae and critically remarked on the Crocidosoricinae. He pointed out, in accordance with Jammot (1983), that the characters used to define the "extinct" †Crocidosoricinae also apply to the extant African genera *Congosorex*, *Myosorex*, and *Surdisorex*, in which case the name Myosoricinae (Kretzoi, 1965) has priority.

An important new set of data was provided by Stephan et al. (1991), who analyzed the anatomy of the brain of 12 extant genera of shrews, providing the most comprehensive study of that kind to date. They found that the brains of the Crocidurinae were smaller than those of the Soricinae. They also corroborated the generic separation of the newly described genus *Ruwenzorisorex*, and pointed out the distant position of *Myosorex* and *Sylvisorex* Thomas (1904) in relation to *Crocidura* Wagler (1832).

FIG. 6. Hypothetical tree taken from Furió et al. (2007: 1027) in which the authors put the evolution of †Crocidosoricinae (and Myosoricinae) into a time frame. †Crocidosoricinae are found only at the base of the tree (genera †*Crocidosorex*, †*Carposorex*, and †*Aralosorex*), while the branch leading to *Myosorex*, *Congosorex* and *Surdisorex* should be named Myosoricinae. Hutterer et al. (2018) demonstrated that this branch originated almost 20 Ma before present.


"Limnoecus"
truyolsi
Crocidosorex
piveteaui
Carposorex
sylviae
Aralosorex
kalini
Srinitium
martell
Ulmensia
ehrensteinensis
Oligosorex
thauensis
antiquus
reumeri
Clapasorex
bonisi
sigei
alvarezae
Soricella
discrepans
Florinia
stehlini
Miocrocidosorex
zazhigini
prevostianum
petersbuchense
ziegleri
Lartetium
dehmi
africanum
Miosorex
desnoyersianus
pusilliformis
grivensis
Myosorex
robinsoni
varius
meini
Congosorex
Surdisorex
SORICINAE
CROCIDOSORICINAE
CROCIDURINAE
MP 20
MP 21
MP 22
MP 23
MP 24
MP 25
MP 26
MP 27
MP 28
MP 29
MP 30
MN 1
MN 2
MN 3
MN 4
MN 5
MN 6
MN 7+8
MN 9
MN 10
MN 11
MN 12
MN 13
MN 14
MN 15
MN 16
MN 17
MNQ
Mammal Zone
Eocene
Early
Late
Early
Middle
Late
Early
Late
Lower
Mid.
Up.
Epoch
Oligocene
Miocene
Pliocene
Pleisto cene
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The study of albumin and allozyme variation in shrews in the 1980s opened a new field of research. Results are available for a number of extant soricines (George, 1986, 1988; George et al., 1989) and some crocidurines (Maddalena, 1990; Maddalena and Bronner, 1992). However, in these studies only small portions of the entire diversity were analyzed, with the most comprehensive work that of George (1986: 153; 1988), who compared eight genera. Her results "support Repenning's (1967) classification rather than those proposed by Stirton (1930), Gureev (1971), and Reumer (1984)." She also discussed the fossil history and divergence times of the groups treated.

Near the end of the 20th and during the early 21st centuries, research on both extant and fossil shrews increased. Storch (1995), Storch and Qiu (1991, 2004), Storch and Zazhigin (1996) Reumer (1998), Lopatin (2002, 2004a, 2004b, 2005), and Woodman (2015, 2019) named a number of new extant and extinct taxa, but also discussed the phylogeny of the shrews. At the same time the techniques for the study of genetic relations between taxa improved, and numerous studies were published. Examples of research dealing with a wider spectrum of extant shrews are Queroil et al. (2001), and Dubey et al. (2007, 2008).

Furio at al. (2007) presented a synthetic view of the evolution of Soricinae, Crocidurinae, and what he called the Crocidosoricinae Reumer, 1987 (= Myosoricinae, as discussed below), starting with the extinct Oligocene genus †*Srinitium* Hugueney (1976) and ending with the extant genera *Myosorex*, *Congosorex*, and *Surdisorex* (fig. 6). We do not agree with all details of his hypothesis, but it was the first attempt to combine the evolution of extant and fossil shrews since Repenning (1967) and Jammot (1983). Based on an analysis of molecular data from Asian shrews, Hutterer et al. (2018) presented a time-calibrated phylogeny of shrews that rooted the genera *Myosorex* and *Congosorex* back to 20 to 15 Ma, which is older than proposed in the diagram of Furio et al. (2007). Recently, Koenigswald and Reumer (2020) published a comprehensive study on the tooth enamel structure of shrews, with emphasis on fossil taxa. They also proposed to treat Heterosoricidae and Soricidae as distinct families and to recognize six subfamilies of the Soricidae.

Most recently, Yuan et al. (2024) conducted dated phylogenetic analyses of morphological (217 characters scored from 23 fossil and 44 living taxa) and genetic traits (mitochondrial and six nuclear genes from 28 soricids). While recognizing the Heterosoricidae as outside the Soricidae, they inferred a Paleocene or Eocene soricid origin in North America.

The preceding history of attempts to understand diversity and phylogenetic relationships of the Soricidae reveals three basic questions relevant to the subject of our study. It is not our intent to comprehensively determine the answers to these questions, but rather to contribute to their long-term solutions by investigating the relationships of the new genus described here and to consider the implications of our studies.

1. What is a shrew? The answer is unquestionable for the living fauna, but is not as clear which fossil taxa should be included. There is no fully accepted definition of the family Soricidae, although a majority of neontologists and paleontologists tend to agree with definitions and systems used by Repenning (1967), Engesser (1972, 1975), Jammot (1983), Yates (1984), Hutterer (1993a), and others. However, Simpson (1945), Gromova (1968), and Gureev (1971, 1979) included †*Saturninia*, currently regarded as a member of Nyctitheriidae, in the Family Soricidae. Wang and Li (1990) included the Eocene insectivore †*Ernosorex* Wang and Li, 1990, which may be a plesiosoricid (Hutterer, 1993a), or a member of Changlelestidae Tong and Wang (1993) (Ziegler, 2009a). Likewise, Reumer (1987, 1989), Ziegler (1989), Koenigswald and Reumer (2020), and Yuan et al. (2024) excluded the Heterosoricinae from the Soricidae, where they had been since 1885. When Lopatin (2002) named the new fossil subfamily Soricolestinae Lopatin, 2002, from the Eocene of Mongolia, he proposed to include it in the Soricidae, but there is no trace of an internal pocket (= internal temporal fossa) on the mandible, a character typical of the family. We therefore do not include it in the Soricidae.

2. Which is the sister group of the Soricidae? There is still no general agreement on this. At least seven groups are under discussion: Talpidae G. Fischer (1814) (Gill, 1875; Gregory, 1910), Nyctitheriidae (Stehlin, 1940; Robinson, 1968; Gureev, 1971, 1979; Reumer, 1987, 1989; Ziegler, 2007), Plesiosoricidae (Winge, 1917; Van Valen, 1967; Butler, 1988; Martin and Lim, 2004a; Peigne et al., 2009; Ziegler, 2009a), Heterosoricidae (Viret and Zapfe 1951, if not included as a subfamily of Soricidae: Yuan et al, 2024), Adapisoricidae (= Dormaaliidae) (Van Valen, 1967), Solenodontidae (Gill, 1875; McDowell, 1958; Landry, 1989), and †*Ernosorex* (Wang and Li, 1990), if this fossil is not accepted as a soricid. Recently, the Erinaceidae G. Fischer, 1814, have been added to this list, based on molecular data (Murphy et al., 2001; Douady et al., 2002; Esselstyn et al., 2017; Sato et al., 2019). In our morphological analyses, we include the Nyctitheriidae and Plesiosoricinae as outgroups, as well as the Geolabididae McKenna, 1960, which are thought to be closely related (McKenna, 1960; Lillegraven et al., 1981).

3. What are the sister-group relationships among the genera of Soricidae? The available phylogenies (figs. 2–6) are not congruent and the position of a given genus is often unstable. Some groups, like the extant soricines and a few crocidurines, are fairly well known, but the relationships of many of the rarer genera have never been studied. Some molecular studies show para- or polyphyly of extant genera (e.g., He et al., 2018). Also, the rate of unnatural definitions of fossil genera is at least as problematic.

We have briefly outlined the conflicting theories that form the background of the new discovery reported herein. In the pages to follow, we first name and characterize the new shrew from Nagaland. We then conduct a phylogenetic analysis of morphological and genetic characters of most living and the best-known fossil genera of shrews to determine the sister taxon of the Naga shrew and to place it within its phylogenetic context. This analysis provides a new perspective on the evolution and classification of shrews, which we present at the end of the third section.

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MATERIALS AND METHODS

Specimens studied: This study is principally based on the collections of extant mammals in the Field Museum of Natural History, Chicago (FMNH), which at the time of writing contained all but three genera of extant shrews, and some fossil shrews as well (PM FMNH; appendix 1). Additional specimens were borrowed from the University of Kansas Biodiversity Institute and Natural History Museum (KU), or examined at the American Museum of Natural History (AMNH), Senckenberg-Museum, Frankfurt (SMF), Museum voor Midden-Africa, Tervuren (KMMAT), the University of Michigan Museum of Zoology, Ann Arbor (UMMZ), and Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK). Specimens used in molecular analyses include material curated by FMNH, KU, AMNH, and Lousiana State University Museum of Natural Science (LSUMZ).

Measurements: All quantitative characters were obtained with an electronic caliper graduated to 0.01 mm. Teeth and skulls were also examined under ultraviolet light (50–60 cycles, Mineralight, Ultra-Violet Products Inc., South Pasadena, CA).

Techniques: A scanning electron microscope (AMRAY 1810) was used without coating in Chicago, and a Zeiss Gemini Sigma 300 VP machine in Bonn, for which we sputtered the objects (hair) with gold in a Cressington sputter coater. Additional photographs were made with a Canon EOS 5D Mark IV camera and were processed with the software EOS Utility 3 Version 3.10.20.0 and Adobe Photoshop and Lightroom. Figures 16 and 17 were made with the Visionary Digital Microptics system at the Field Museum.

In the use of technical terms for skull and tooth features we follow mainly Repenning (1967), Butler and Greenwood (1979), Jenkins (1984), and Reumer (1984). Some frequently used terms are explained in figure 7. Tooth measurements were defined by Reumer (1984), however, instead of his

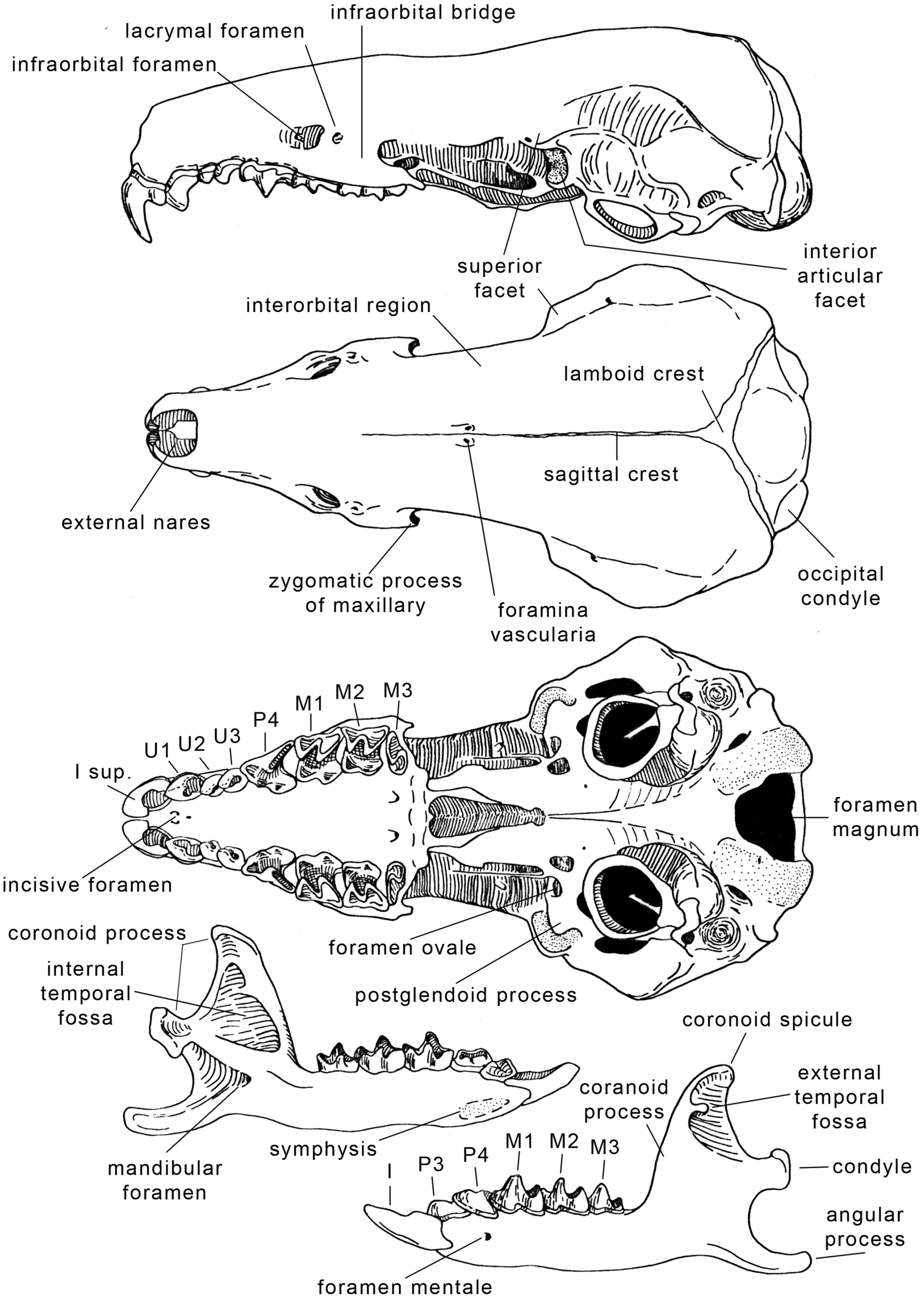


FIG. 7. Sketch of a skull of *Surdisorex polulus* (FMNH 43846), illustrating anatomical features mentioned in the text.

term "antemolar" we use the term "unicuspid" for the series of small single-cusped teeth between the first incisor and the fourth premolar. We use the term "antemolar series" to refer to the unicuspids plus the fourth premolar.

Morphological analyses: The morphological character matrix we assembled from both living and extinct shrews and putative shrews included 45 characters scored for 45 taxa (30 living and 15 extinct; see table 4). Specimens used for scoring character states for extant species are listed in appendix 1; character states for fossil taxa were taken from figures and descriptions in publications listed in tables 1 and 7. The matrix is 89% complete; all missing character states are from fossil taxa. We used the extinct taxa Geolabididae, Nyctitheriidae, and Plesiosoricidae as outgroups. Individual characters varied in the number of states from two to five. Forty-two of the 45 characters are parsimony informative. We used both parsimony analysis and explicitly model-based Bayesian inference. Parsimony analysis was conducted in PAUP* 4.0a, using a heuristic search initiated with a tree generated by stepwise addition. We ordered characters 7, 23, 30, 31, and 40 from 0 <-> 1 <-> … N; all others were unordered. Reversals were allowed. We capped the number of trees retained in memory at 1000. The search employed the tree-bisection-reconnection branch-swapping algorithm with the reconnection limit set to 8. To measure support, we generated 100 bootstrap pseudoreplicates that used full heuristic searches and retained one tree per replicate.

Bayesian analyses were conducted using RevBayes 1.0.12 (Höhna et al., 2016). We divided characters into sets grouped by the number of states and modeled each independently using the Mk model of Lewis (2001), but with the "variant" correction available in RevBayes. The variant flag corrects for the ascertainment bias that derives from scoring only variable characters (Lewis, 2001; Höhna et al., 2016). The Markov chain Monte Carlo analysis consisted of two independent runs of 80,000 generations with the tuning interval set at 200 and the sample frequency set at 10. Initial analyses failed to converge, apparently due to problems modeling Γ-distributed rate variation. We experimentally reduced the upper limit of the uniform distribution from which the α shape parameter was drawn and noted improved performance. Our final analysis used an upper limit to α of 100 (the RevBayes Discrete Morphology tutorial uses 1,000,000) and this yielded apparent convergence. Other priors and settings were as in the RevBayes tutorial. We examined trace plots and effective sample sizes for all parameters in Tracer 1.8. Trees from the two runs were combined into a maximum clade credibility tree. We discarded the first 50% of trees from each run as burnin, leaving 4000 samples in the posterior.

DNA Extraction and Sequencing: We extracted DNA from a clip of skin from the ventral incision of the holotype of the Nagaland specimen by following the Tsai et al. (2020) phenol-chloroform extraction protocol with the minor modifications that we did not grind the skin clip during digestion, and centrifugation was performed with refrigeration. We quantified total genomic DNA in the extract with a Qubit 2.0 fluorometer and recovered about 28.5 ng of DNA.

We used a similar protocol as reported in Esselstyn et al. (2017) to prepare, enrich, and sequence DNA libraries with modifications made to accommodate a degraded sample. We attempted to repair possible age-related DNA damage by treating the sample with PreCR Repair Mix (New England Biolabs, Ipswich, MA) following the manufacturer's instructions. We followed this treatment with a 3x Sera-Mag bead cleanup. DNA libraries were prepared using the Kapa Biosystems Hyper Prep Kit for Illumina platforms with dual indexed iTru adapters (Glenn et al., 2019). Because of the low yield of DNA, we used one half of the manufacturer's recommended reagent volume, diluted the iTru adapters to 1.25nM, increased the library amplification extension time to 1 min, and used 16 amplification cycles. We pooled this library with other degraded samples in an equimolar ratio and enriched it for 5060 ultraconserved element (UCE) loci and 30 exons using a custom probe set manufactured by Mycroarray (Ann Arbor, MI) (Esselstyn et al., 2021). We determined the size distribution of enriched libraries with an Agi-

TABLE 1

Size of *Nagasorex albidens* Compared with the Pliocene *Myosorex robinsoni* of Africa and with Oligocene and Miocene Shrews of Europe and Asia

Based on the length of lower m1–3 (mm).

Species	Length m1–3	N	Reference
†*Carposorex sylviae*	4.18	1	Crochet, 1975
†*Clapasorex bonisi*	2.82	1	Crochet, 1975
†*Clapasorex sigei*	3.09	1	Crochet, 1975
†*Crocidosorex antiquus*	3.48-3.69	2	Crochet, 1975
	3.38-3.54	2	Ziegler, 1989
†*Crocidosorex piveteaui*	3.77	1	Crochet, 1975
†*Crocidosorex thauensis*	3.43	1	Crochet, 1975
†*Dobenflorinia discrepans*	4.10-4.85	16	Doben-Florin, 1964
†*Dobenflorinia* sp.	5.05	1	Ziegler, 1989
†*Miocrocidosorex zazhigini*	4.0	1	Lopatin, 2004a
†*Miosorex desnoyersianus*	3.08-3.38	16	Doben-Florin, 1964; Klietmann et al., 2013
	3.15-3.16	2	Ziegler, 1989
†*Miosorex grivensis*	3.58-3.75	6	Doben-Florin, 1964
	3.26-3.84	8	Jong, 1988
†*Myosorex robinsoni*	3.93	23	Butler and Greenwood, 1979
Nagasorex albidens	3.62	1	This paper
†*Srinitium marteli*	3.25	1	Hugueney, 1976
†*Ulmensia ehrensteinensis*	3.95-4.15	2	Ziegler, 1989

lent Bioanalyzer and removed remaining adapter dimer from pools using a Qiagen GeneRead Size Selection Kit (Venlo, NL). We sequenced the enriched library and unenriched library on an Illumina HiSeq Platform PE150 at Novogene USA (Sacramento, CA).

Bioinformatics: Novogene USA demultiplexed raw reads from BCL files using bcl2fastq 1.8.4 (Illumina, Inc.) and returned FASTQ-formatted files to us. We trimmed low-quality bases and adapter sequences from reads using illumiprocessor ver. 2 (https://github.com/faircloth-lab/illumiprocessor), which incorporates trimmomatic (Bolger et al., 2014). We assembled cleaned reads into contigs using metaSPAdes implemented in MitoFinder (Nurk et al., 2017; Allio et al., 2019).

Phylogenetic Analyses of Mitochondrial DNA: We obtained mitochondrial sequences from the holotype of the Nagaland specimen as by-catch in our effort to sequence UCEs. We extracted mitochondrial sequences using PHYLUCE's phyluce_assembly_match_contigs _to_barcodes command (Faircloth, 2016) and a *Niviventer fulvescens* mitochondrial genome template sequence (NCBI Genbank accession NC_028715). While multiple mitochondrial genes were recovered, we performed subsequent analyses using cytochrome *b* because of its broad availability in published eulipotyphlan datasets. In total, we recovered two fragments of cytochrome *b* from the Nagaland specimen, totaling 976 base pairs out of the 1140 total nucleotide length of the gene.

We added the mitochondrial sequence from the Nagaland specimen to the cytochrome-*b* alignment of Hutterer et al. (2018) and supplemented these initial data with sequences from GenBank (table 5). Ingroup taxa were selected to maximize phylogenetic diversity and represent major groups of shrews, while keeping the dataset fairly small and minimizing missing characters. Sequences were aligned using default settings in Geneious 2 and inspected by eye. No premature stop codons or ambiguous alignment regions were noted. The final mitochondrial alignment contained 33 taxa and 1140 characters. Among the 33 taxa, we included two moles (genus *Talpa* Linnaeus, 1758) and three erinacaeids (genera *Hemiechinus* Fitzinger (1866) and *Hylomys* Müller (1840) as outgroups. Ingroup taxa included representatives of eight soricine, two myosoricine, and 10 crocidurine genera. The alignment was 91.2% complete, with average and minimum sequence lengths of 1043 and 681 nucleotides, respectively (https://doi.org/10.5531/sd.sp.75).

We conducted model-fitting analyses using PartitionFinder 2 (Lanfear et al., 2017), which employs phyml (Guindon et al., 2010) for tree building. We ran PartitionFinder to choose the best model among those available in MrBayes, allowing a maximum partitioning into three subsets corresponding to codon positions 1, 2, and 3. We used the AICc to choose the best modeling strategy, with searches performed using the greedy algorithm and linked branch lengths. The optimal scenario consisted of three partitions with SYM + I + Γ applied to the first codon position and GTR + I + Γ models applied separately to positions 2 and 3.

We analyzed the mitochondrial alignment in both a maximum likelihood and Bayesian framework. For the former, we used RAxML 8.2.12 (Stamatakis, 2014) on the CIPRES portal (Miller et al., 2010). Because RAxML does not support alignment partitioning or the use of a proportion of invariant sites, we analyzed the data unpartitioned with the GTRCAT model of substitution. We estimated support using bootstrap replicates, and applied RaxML's automatic stopping criteria for determining an adequate number of replicates. For our Bayesian analyses, we used MrBayes 3.2.2 (Ronquist et al., 2012), with the models and partitioning scheme resulting from our PartitionFinder analysis. Four independent runs of four Markov-chain Monte Carlo analyses were run for 5 million generations, with samples drawn every 1000 generations. Parameters were unlinked and the "temperature" was set to 0.2. Convergence was supported by the average standard deviation of split frequencies dropping below 0.01 and the average Gelman Rubin statistic equaling 1.0. We discarded the first 25% of trees as burnin. Summaries of both bootstrap support and posterior distributions were generated using the SumTrees utility in DendroPy 5.0.1 (Moreno et al., 2024).

Phylogenetic Analysis of Nuclear DNA: We used PHYLUCE to find Nagaland specimen contigs that matched UCE loci (56) and aligned these with both sequences extracted in silico from genomes in previous work (Esselstyn et al., 2017) and previously published target capture UCE sequences (table 6; SAMN 20991443, LSUMZ 39025; Esselstyn et al., 2021) using MAFFT (Katoh et al., 2005). We trimmed all alignments using Geneious 2 to the length of sequences from the Nagaland specimen to avoid missing data artifacts that can affect analyses of sequences from degraded samples (Hosner et al., 2016). Initial phylogenetic analyses placed the Nagaland specimen outside of shrews, which caused us to suspect the sequences might be contaminated with human DNA. To identify potentially human contaminated sequences, we calculated site-likelihoods for alternative tree topologies with the Nagaland specimen + *Homo sapiens* Linnaeus, 1758, the Nagaland specimen + *Sorex araneus* Linnaeus, 1758, and the Nagaland specimen + *Sorex* + *Condylura cristata* (Linnaeus, 1758) relationships and summed these site-likelihoods by locus following a previously described approach (Esselstyn et al., 2017; Shen et al., 2017). This approach allowed us to identify individual loci that favored the Nagaland specimen + *Homo sapiens* relationship, which would suggest those loci derive from human

DNA. After eliminating likely contaminants, we used only loci that supported the Nagaland specimen as a eulipotyphlan for further analyses.

We aligned the remaining *Nagasorex* UCE loci to sequences from a selection of eulipotyphlan clades using MAFFT and combined these alignments into a concatenated dataset in PHYLUCE (Faircloth, 2016). This alignment was 5172 base pairs long, included 21 UCE loci, and was 99% complete (https://doi.org/10.5531/sd.sp.75). We partitioned this dataset by locus, performed model selection while allowing partitions to have different speeds (Kalyaanamoorthy et al., 2017), and inferred a maximum likelihood tree with 10,000 ultrafast bootstrap replicates (Hoang et al., 2018) and 10,000 SH-Like Test replicates in IQTree 1.6.10 on the CIPRES portal (Miller et al., 2010; Nguyen et al., 2015). We also used the unpartitioned concatenated dataset to generate a maximum likelihood tree using RAxML-HPC2 on the CIPRES portal using the GTR+ Γ model and 100 bootstrap replicates. We then inferred gene trees with 1000 ultrafast bootstrap replicates in IQTree 1.7 beta17 and estimated the species tree using ASTRAL 5.6.3 (Zhang et al., 2018). We examined the number of loci and strength of per locus support for a Nagaland specimen + (Crocidurinae + Myosoricinae) topology over Nagaland specimen + Myosoricinae, Nagaland specimen + Soricidae, and Nagaland specimen + Crocidurinae using the site-likelihood analysis described above.

SYSTEMATIC RESULTS: THE SHREW FROM NAGALAND

Order Eulipotyphla Waddel et al. (1999)

Family Soricidae Fischer, 1814

Nagasorex, new genus

LSID:urn:lsid:zoobank.org:act:2603D0A0-A72F-472B-A3CC-4FF1A9A966E7

Type Species: *Nagasorex albidens*, new species.

Included Species: The type species only.

Etymology: The generic name combines the place of origin (Naga Hills) with the Latin *sorex* (shrew); the gender is masculine. The specific epithet combines the Latin *albus* (white) and *dens* (tooth).

Diagnosis: As for the type and only species.

Nagasorex albidens, new species

Figures 8, 9, 10, 11, 12, 13

LSID:urn:lsid:zoobank.org:act:1ECE5F14-3FCF-49DF-95C7-A7D6C434703A

Holotype: FMNH 76197, skin (fig. 8) and skull (figs. 9–12) of young adult female in good condition, left mandible missing, right mandible present in two parts; collected by Walter N. Koelz on 20 August 1950 at Jakhama (see appendix 2 for notes on type locality), Naga Hills, Nagaland, northeastern India. Collector's measurements (in mm): total length 97; tail 38; hindfoot 12; ear 8. We extracted DNA from a small piece of dry skin and hair, removed from the posterior ventral surface, and obtained a sequence of the mitochondrial cytochrome *b* gene and UCEs (NCBI BioSample SAMN37568052).

Diagnosis: A small dark shrew with narrow tail covered by very short hairs (fig. 8); cross section of guard hairs with H-profile (fig. 13); ear conch small, round and almost naked (fig. 8); skull roof with traces of the foramina vascularia (fig. 9); 34 nonpigmented teeth, tooth formula I 3/1 C 1/1 P 3/2 M 3/3 (figs. 10, 11); p4 with a distinct "myosoricine" Y-pattern (fig. 12B); mandibular articulation with upper and lower facets (fig. 11); plus the unique combination of characters described in the following section.

Description: As indicated by length of m1–m3, *Nagasorex albidens* is a small shrew, similar in size to †*Carposorex* Crochet, 1975, †*Clapasorex* Crochet, 1975, †*Crocidosorex,* and †*Miosorex* (table 1). Externally, *Nagasorex albidens* is indistinct and at first sight may be mistaken as a small *Blarinella* Thomas (1911) or a short-tailed *Episoriculus* Ellerman and Morrison-Scott (1951); however, the conspicuous, small, round,

American Museum of Natural History
Takubama, Naga Hills
VIII ·20.52. W. Koelz ♀
EUM
Walter N. Koelz

of Natural History
CHICAGO NATURAL 76197 HISTORY MUSEUM
~~INDIA,~~ Soricidae
Assam: Takubama; Naga Hills
20 August 1952 Walter N. Koelz

FIG. 8. **A,** Dorsal; **B,** ventral; and **C,** lateral aspects of the holotype skin of *Nagasorex albidens* (FMNH 76197). Total length of specimen is 97 mm. Also shown are photographs of the original field label and subsequent FMNH label.

and almost naked ear conch (rather than hidden in the fur) separates it readily (fig. 8). The general color of the pelage is deep brown, with dark plumbous underparts and reddish-brown tips. The ventral surface of the body is slightly grayer but otherwise has a similar color as the dorsum. The hairs of the dorsum are very soft and about 4 mm in length; the ventral hairs are shorter (3.2 mm) and less dense. The terminal shield of the curly guard hairs shows a complex structure (fig. 13): its cross section forms an H in which the grooves are covered by a number of thin longitudinal crests. Similar structures have been observed in *Feroculus* Kelaart (1852) (Amerasinghe, 1986) and *Myosorex* (Ducommun et al., 1994). The head from nose tip to posterior margin of ear conch comprises more than 30% of the head and body length. The

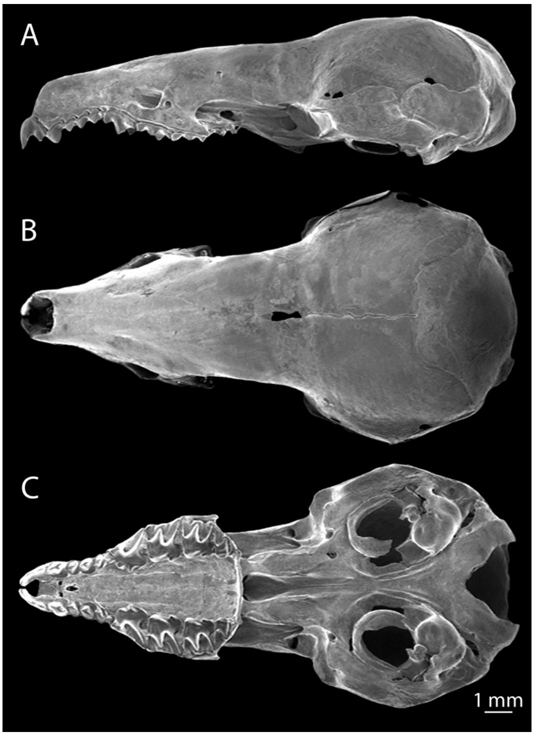


FIG. 9. Cranium in **A,** lateral; **B,** dorsal; and **C,** ventral views of the holotype of *Nagasorex albidens* (FMNH 76197). Greatest length of skull is 18.1 mm. SEM photographs of uncoated skull.

anterior 4 mm of the nose are covered by only a few hairs, indicating a rather fleshy nose in life. There are few facial vibrissae, the longest of which measure 14 mm. The ear conch is small and almost naked, covered by very short hairs. Its rounded shape resembles that of various *Crocidura* species, as figured by Hutterer (1985: fig. 3). Fore and hindfeet are short, as are the claws. The two posterior intertarsal pads are elongated, as in *Suncus megalura* (Jentink (1888)) (Hutterer, 1985: fig. 1); the other pads are not visible on the shrunken feet of the holotype skin. The upper surfaces of the hindfeet are covered by hexagonal scales overlain by stiff hairs that are longer than a scale. The tail is thin and delicate and is covered by very short hairs of approximately 0.5 mm length, giving it the aspect of a naked tail that characterizes most soricine shrews.

Cranium: The skull is fragile, with a large braincase and a slender rostrum (fig. 9). The braincase is hexagonal in dorsal view and domed in lateral view. No occipital crest is present, and the outer surfaces of the parietal and frontal bones are smooth. The interparietal is a well-delimited narrow bone with an undulated anterior border. An opening of irregular shape in the middle of the skull roof we interpret as fused foramina vascularia (fig. 9), usually present as a pair of foramina but sometimes as a single one in soricine and myosoricine shrews. The interorbital region is comparatively wide, and the maxillary region narrow. A maxillary zygomatic process is present but short, its tip rooted between M2 and M3. In side view, the rostrum is low; its length from the tip to the anterior border of P4 is equal to the distance from there to the posterior border of the zygomatic plate. The zygomatic plate is wide, and the lacrimal foramen is positioned near the anterior border of the plate. The palate extends only slightly beyond the posterior border of M3. There is one pair of incisive foramina present between the first upper unicuspids, followed by a single, elongated foramen (fig. 10). The foramina ovale are positioned behind the postglenoid processes.

Mandible: The mandible is weakly constructed, with a narrow coronoid process and a thin angular process (fig. 11). The internal temporal fossa is pocketed. An external temporal fossa is present. No masseteric fossa exists. The ascending ramus is set at an angle of 105° to the main body of the mandible. A coronoid spicule is absent. The condyle is small, its upper and lower facets arranged above one another, with some confluence between them on the lingual side. The facets are not clearly delimited. The mental foramen is below p4. The mandibular foramen is posterior to the midline of the ascending ramus.

Upper teeth: All teeth appear white. There are 10 teeth on each side of the maxilla and premaxilla combined. The first incisor is rather short and rounded, as is its second cusp (figs. 9, 10). Five simple unicuspid teeth are present, the first of which is largest, followed by three unicuspids of about half the size of the first in lateral view, and a fifth unicuspid less than half the size of the preceding three (figs. 9, 10). The fourth premolar is characterized by a large parastyle (fig. 10) and in occlusal view by a protocone strongly projecting in anterior-lingual direction. A hypocone is present and forms a thin lingual crest. Protocone and metacone are clearly separated. First and second upper molars are nearly equal in size. Their protocones form strong crests fully separated from the smaller metacones. The third upper molar is about one third the size of M2 (fig. 10).

Lower teeth: Seven teeth are present on each side (fig. 11). The first lower incisor is short and little pointed: its cutting surface is smooth except for a denticulation at its posterior end. A strong cingulum is present on the lingual side of the incisor. The first two unicuspids are simply built, with a thin cingulum. The p4 is remarkable: the elongated crests of its cutting surface form a Y, with a deep basin running between the two posterior crests to the lingual side of the tooth (fig. 12B). The lower molars are subequal in size; their cinguli are weak but present on both labial and lingual sides. Lower m3 is large with a deep entoconid basin.

Skull Measurements (mm): Condylo-incisive length 18.11; palatal length 7.58; greatest width 8.90; bimaxillary breadth 5.18; interorbital width 4.15; postglenoid width 5.99; upper toothrow length 7.88; lower toothrow length 7.29; height of coronoid process 4.10; height of mandibular ramus at m1 1.25; height × width of condyle 1.23 × 1.00.

Tooth Measurements (mm) (as defined by Reumer, 1984): Upper jaw in labial view: I1 length 1.23 × height 1.02; I2 (= U1) length 0.87; A2 (= U2) length 0.66; A3 (= U3) length 0.60; A4 (= U4) length 0.54; A5 (= U5) length 0.30; P4 length 1.35; M1 length 1.29; Lower jaw in labial view: i1 length 2.37 × height 0.69; m1–3 length 3.62; Upper jaw in occlusal view: P4 length 1.50 × width 1.53; M1 BL 1.29 × AW 1.41 PW 1.68; M2 BL 1.14 × AW 1.62 PW 1.38; M3 length 0.62 × width 0.14; Lower jaw in occlusal view: p4 length 1.12 × width 0.62; m1 length 1.37 × width 0.81; m3 length 1.06 × width 0.56.

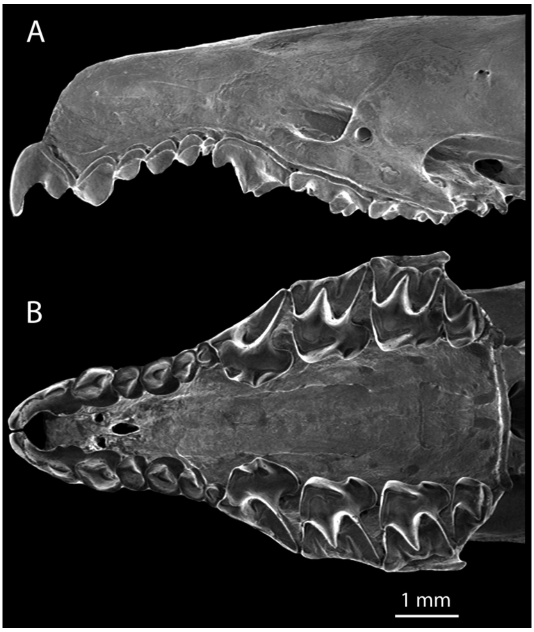


FIG. 10. Enlarged views of the **A,** lateral and **B,** ventral anterior half of the skull of the holotype of *Nagasorex albidens* (FMNH 76197). SEM photographs of uncoated skull. Scale is 1 mm.

Comparisons: Among the living Soricidae, *Nagasorex albidens* seems to have no close relative. From all extant genera, the new genus is distinguished by the number of teeth alone (table 2). In Repenning's key to living and fossil genera (1967: 64), one would run to †*Soricella* Doben-Florin, 1964 (a name preoccupied that we replace with a new name, see below), a genus known only from Miocene deposits of Germany (Doben-Florin, 1964). However, †*Soricella discrepans* Doben-Florin, 1964, and a further undescribed species (Ziegler, 1989) have pigmented teeth, only four unicuspid teeth in the upper jaw, a sharply pointed lower incisor with two denticulations, and they differ in several other characters. Some characters are shared with the extant African genera *Congosorex*, *Myosorex* and *Surdisorex* (these three were

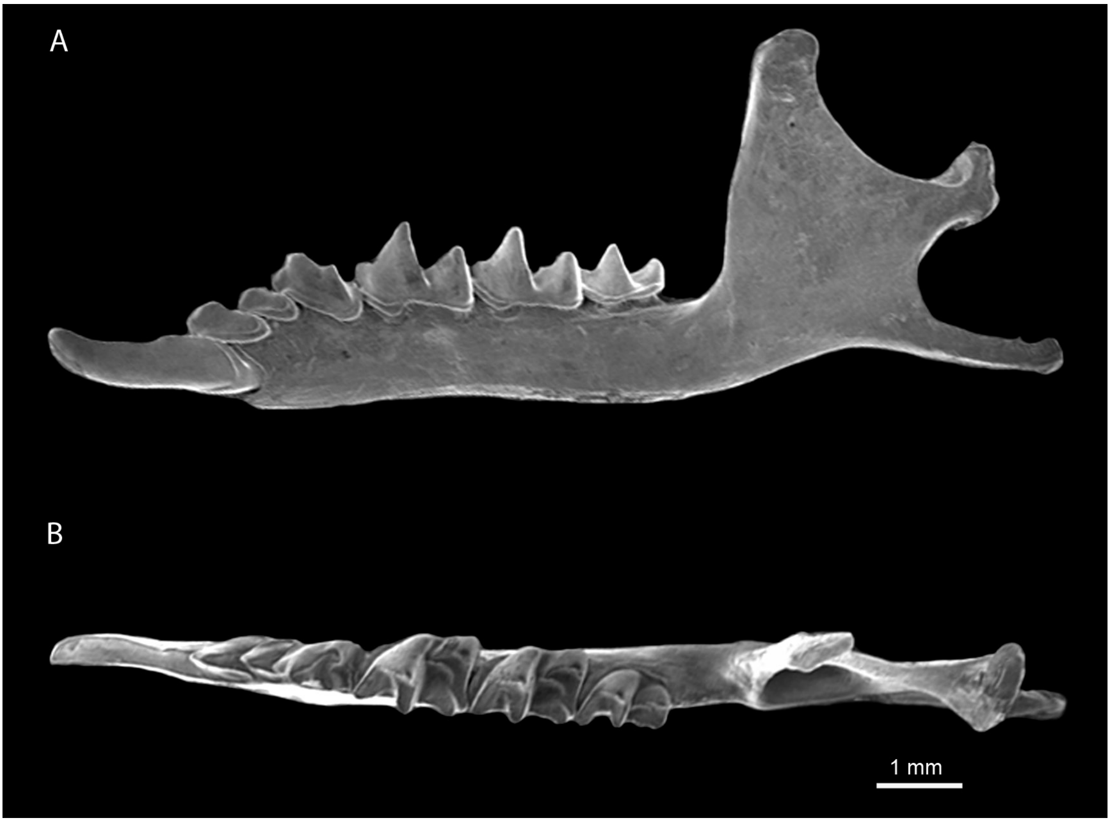


FIG. 11. Left mandible in **A,** lateral and **B,** occlusal views of the holotype of *Nagasorex albidens* (FMNH 76197). SEM photographs of uncoated mandible. Scale is 1 mm.

regarded as full genera by Hutterer, 1993a), particularly the myosoricine (Jammot, 1983) shape of the lower p4. All these genera show a considerable to extreme (*Surdisorex*) adaptation toward subterranean habits.

Distribution, Habitat Associations, and Conservation: The mountains in which *Nagasorex albidens* was found (fig. 14) are part of the Burmese Arc, a relatively narrow but prominent geological feature that extends from the northeast border of India with Myanmar and China south through eastern India (including Nagaland and Manipur) and western Myanmar (including Chin) to the Andaman and Nicobar Islands (Acharyya, 2007; Krishnan, 1974). The highest point in Nagaland is Mt. Saramati (= Sarameti), at 3826 m, along the border with Myanmar (fig. 15). The climate of the Nagaland is monsoonal, with rains from the southwest beginning in February, peaking in July, and declining to October. Temperatures slightly below freezing often are reached in December and January in the lowlands, and through much of the year above 1800 m (Choudhury, 2006; Stracey, 1967). Vegetation in Nagaland is highly varied, depending on elevation, exposure, and rain-shadow effects. Of all the northeastern Indian mountains, the vegetation of Nagaland is the most similar to that of the Himalayan region, primarily because Nagaland has the highest peaks of the Burmese Arc (Deb, 1960; Rao, 1974). In moist areas of Nagaland from 900 m to a maximum of 1500 m (where *Nagasorex albidens* was likely to have been collected; appendix 2), there is a transition from

TABLE 2

Extant and Fossil Genera of Shrews (Soricidae) for which the Tooth Number Is Known

(Hutterer, 2005b, plus Repenning, 1967, Rabeder 1982, Klietmann et al., 2013, Hutterer et al., 2018, Moya-Costa et al., 2019)

Tooth Number	Extant Genera	Extinct Genera
38	---	†*Lusorex*
36	---	†*Crocidosorex*, †*Oligosorex*
34	*Nagasorex*	†*Domnina*, †*Lartetium*, †*Miosorex*, †*Pseudotrimylus*
32	*Blarina, Blarinella, Myosorex, Sorex*	†*Blarinoides*, †*Dobenflorinia*, †*Lartetium*, †*Paenepetenyia*
30	*Congosorex, Cryptotis, Episoriculus, Feroculus, Neomys, Palawanosorex, Ruwenzorisorex, Scutisorex, Soriculus, Suncus, Sylvisorex*	†*Asoriculus*, †*Beremendia*, †*Cokia*, †*Dinosorex*, †*Nesiotites*, †*Paenesorex*, †*Paracryptotis*, †*Petenyia*, †*Shikamainosorex*, †*Zelceina*
28	*Chimarrogale, Chodsigoa, Crocidura, Crossogale, Megasorex, Nectogale, Notiosorex, Paracrocidura, Solisorex, Surdisorex*	†*Dimylosorex*, †*Ingentisorex*, †*Dolinasorex*
26	*Anourosorex, Diplomesodon*	†*Paranourosorex*
24	---	†*Amblycoptus*
22	---	†*Kordosia*

tropical wet evergreen forest (characterized by *Ficus*, *Cinnamomum*, *Musa*, and *Terminalia*) to montane wet temperate forests (characterized by *Castanopsis*, *Acer*, and *Quercus*; Gupta, 1976; MacKinnon and MacKinnon, 1986; Tamma et al., 2016; Wikramanayake et al., 2002).

Associated with the nearly continuous high-elevation habitat, the mammal fauna of Nagaland and adjacent states is similar to that of the southeastern Himalayan Front (Dilger, 1952; Moore, 1960; Kurup, 1974; Mani, 1974; Tamma et al., 2016; Wikramanayake et al., 2002; Jenkins, 2013; Choudhury, 2013). Although little research has been published about the small mammals of Nagaland and adjacent states, the holotype of *Nagasorex albidens* is part of a large collection of small mammals made in northeastern India by Walter N. Koelz, the collector of the holotype of the new species. These specimens were collected from August 1948 to March 1955 in the current states of Nagaland, Manipur, and Meghalaya. Specimens were deposited at the FMNH and UMMZ. With the exception of a few uses of the collection for monographic studies of systematics (e.g., Moore and Tate, 1965; Musser, 1981, 1987; Musser and Newcomb, 1983), this collection has remained unused and unknown.

Based on the Koelz collection in FMNH and a summary of published records (Jenkins, 2013), eight species of the Soricidae are currently known from Nagaland and Manipur (table 3). *Nagasorex albidens* and *Anourosorex assamensis* Anderson (1875) appear to be local endemics of the Nagaland region. One species, *Suncus murinus* (Linnaeus, 1758), is a commensal widespread in Asia and northern Africa (Hutterer, 2005a). The others are widespread in northeastern India and the Himalayan front (*Chimarrogale himalayica* (Gray (1842)) and *Soriculus nigrescens* (Gray, 1842), and a few more widely distributed (members of the *Crocidura attenuata* group, *C. fuliginosa* group, and *Suncus etruscus* group; Hutterer, 2005a; Jenkins, 2013; Choudhury, 2013).

Natural habitats in Nagaland have been extensively converted to anthropogenic uses,

FIG. 12. Occlusal views of the **A,** fourth upper premolar and **B,** fourth lower premolar and adjacent teeth of the holotype of *Nagasorex albidens* (FMNH 76197). In B, note the groove running down from the posterior rim of the enamel surface toward the lingual side of the mandible. SEM photographs of uncoated skull. Each scale is 1 mm.

and medium to large mammals are heavily hunted (Choudhury, 2006; Dorji et al., 2018; Joshi et al., 2019). Although we have no direct information about the current conservation status of *Nagasorex albidens*, we note that there are parks or wildlife reserves in all of the states of northeastern India (IUCN, 1992) as well as some community-based protected areas (e.g., Chase and Singh, 2012; Joshi et al., 2019). In the vicinity of the type locality of *N. albidens* are two reserves, one (Intanki Sanctuary: 20,202 ha, declared in 1975) in southern Nagaland that is near Mt. Japvo, and one (Sirui National Park: 4,130 ha, declared in 1982) in northeastern Manipur. The largest park in the mountainous portion of the general region is Namdapha National Park (198,524 ha) in southern Arunachal Pradesh (IUCN, 1992). It is possible that *N. albidens* occurs in one or more of these parks, but surveys are needed to determine whether this is so and whether the populations are stable. We suggest that *N. albidens* should be sought not only in Nagaland but throughout the high mountains of northeastern India and consider it possible that it might occur in northern Myanmar and southern China, and perhaps along the eastern Himalayan front as well. We especially recommend thorough sampling in the moderate and high-elevation areas that produces voucher specimens of small mammals for morphological studies and tissue samples for genetic studies. These areas are often especially poorly represented in current collections, and specimens are necessary for definitive study of the diversity and phylogenetic relationships and for determining conservation priorities for the many little-known species.

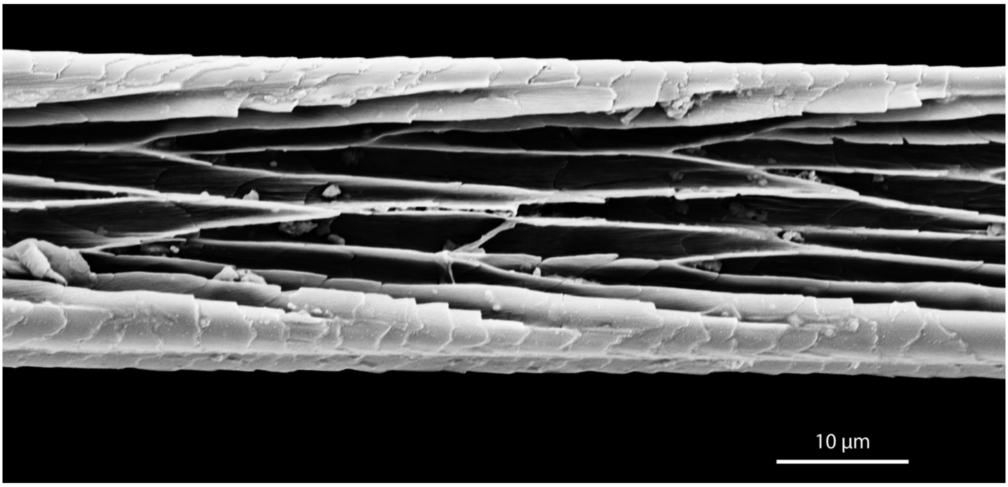


FIG. 13. Detail of the shield segment of a curly guard hair taken from the dorsal pelage of *Nagasorex albidens* (FMNH 76197). A lateral ridge filled with thin longitudinal crests is visible. SEM photograph of gold-coated hair.

RELATIONSHIPS OF *NAGASOREX* TO OTHER SORICIDS

In the following sections we first present a phylogenetic analysis of extant and selected fossil genera of shrews based on morphological characters described below and summarized in table 4. For the extant genera, we were able to take all characters directly from specimens, but for the fossil taxa we had mostly to rely on descriptions and figures given in the literature (see Materials and Methods). The sources used are cited in the following classification, if not mentioned otherwise. Character states for all genera are listed in table 4. We then present phylogenetic analyses of most extant genera using cytochrome *b* and ultraconserved elements (UCEs) as part of our effort to place *Nagasorex* into a phylogenetic context.

Description of Morphological Characters

A. External

1. Color of animal: **0,** uniformly dark or gray (e.g., *Nagasorex*, *Cryptotis* Pomel (1848); **1,** slight to strong contrast between dorsum and venter (e.g., most *Crocidura*, *Neomys* Kaup (1829), *Sorex*); **2,** variable color pattern (*Diplomesodon* Brandt, 1852).

2. Tail bristles: **0,** tail fully or to some extent covered by scattered long bristles (*Crocidura*, *Paracrocidura*, etc.); **1,** tail without scattered long bristles (*Sorex*, *Sylvisorex*, etc.); **2,** undersurface of tail with row of stiff bristles (*Neomys*); **3,** tail with dorsal, lateral and ventral keels (*Nectogale*).

3. External ear: **0,** ear conch well developed, antitragus forming an ear pocket (most shrews); **1,** ear conch strongly reduced, completely or nearly hidden in fur (e.g., *Blarina* Gray (1838), *Cryptotis*, *Neomys, Surdisorex*); **2,** ear conch absent (*Nectogale*).

4. Digits of fore and hindfoot: **0,** not fringed (general pattern); **1,** fringed with rows of long and stiff hairs (*Diplomesodon*, *Neomys*, *Chimarrogale*, *Nectogale*; variable but uncommon in *Sorex*).

5. Claws on fore foot: **0,** short or slightly elongated (nearly all genera, e.g., *Crocidura*); **1,** more than twice as long as in hindfoot (*Surdisorex*, *Ferocolus*, *Solisorex* Thomas (1924)).

6. Cross section through awn hair: **0,** smooth or with tiled notches; **1,** groove with irregular notches; **2,** groove with central ridge (Vogel and Köpchen, 1978; Hutterer and Hürter, 1981).

TABLE 3

Shrews (Soricidae) from Nagaland and Manipur, Northeastern India

X = Koelz collection in FMNH; 1 = Jenkins (2013). Species indicated by an asterisk are endemic to Nagaland and Manipur (see Hutterer, 2005; Jenkins, 2013).

Taxon	Jakhama	Nagaland	Manipur
*Anourosorex assamensis**		1	X
Chimarrogale himalayica		1	
Crocidura attenuata group		1	
Crocidura fuliginosa group	X	X	X
Nagasorex albidens*	X	X	
Soriculus nigrescens			1
Suncus etruscus group			X
Suncus murinus		1	X

B. Skull (see fig. 7 for location of most features)

7. Zygomatic arch: **0,** complete; **1,** well developed but incomplete; **2,** rudimentary or absent.

8. Squamosal zygomatic process: **0,** present; **1,** absent.

9. Maxillary zygomatic process: **0,** present; **1,** absent.

10. Root of maxillary part of zygomatic process: **0,** between M1 and M2; **1,** between M2 and M3.

11. Zygomatic plate: **0,** narrow, about the length of M1 or less; **1,** wide, considerably wider than length of M1.

12. Position of lacrimal foramen: **0,** central to the zygomatic plate; **1,** clearly asymmetrical, near to anterior border of bony plate.

13. Supraorbital process: **0,** absent; **1,** present. When present, it is a small and inconspicuous bump.

14. Foramina vascularia (naso-frontal foramina, Landry, 1957): **0,** present and widely separated; **1,** significantly separated on both sides of dorsal suture; **2,** close, sometimes in contact or fused; **3,** always absent.

15. Interparietal bone: **0,** large parietal bone present, posterior suture fused but still visible; **1,** small parietal bone traceable, sutures fused; **2,** not traceable.

16. Position of foramen ovale: **0,** behind the postglenoid process; **1,** on ventral side, partially or fully integrated in postglenoid process.

17. Outer surface of parietal and frontal bone: **0,** smooth; **1,** covered by low and inconspicuous rugosae; **2,** covered by high prominent rugosae (fig. 16).

C. Mandible

18. Internal temporal fossa of the mandible: **0,** shallow; **1,** pocketed.

19. External temporal fossa: **0,** absent; **1,** present.

20. Coronoid spicule: **0,** absent; **1,** small, inconspicuous; **2,** short ridge in upper part of external temporal fossa; **3,** long, forming a crest dividing the external temporal fossa almost in half. See Choate (1969).

21. Masseteric fossa: **0,** present; **1,** present, divided in superior and inferior fossa by a ridge; **2,** absent.

22. Angular process: **0,** short and stout; **1,** short and pointed; **2,** long and slender.

23. Condyle: **0,** a simple horizontal facet; **1,** slightly oblique, with some degree of differentiation; **2,** condyle differentiated into an upper and lower facet with little or no contact, both shifted horizontally so that almost no overlap exists; **3,**

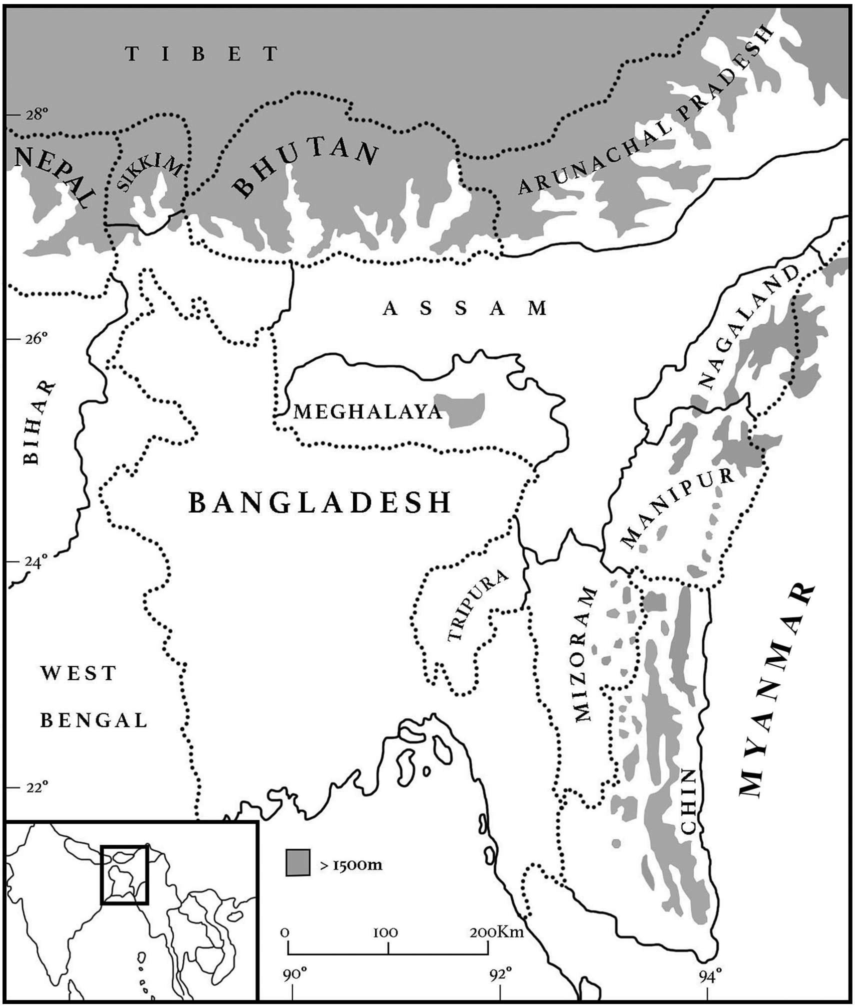


FIG. 14. Map of northeastern India showing the location of Nagaland.

upper and lower facets arranged above one another, with some confluency between both on lingual side; **4,** upper and lower facets arranged one above another, with no confluency between both.

24. Mental foramina: **0,** two are present; **1,** one, anterior to p4; **2,** one, below p4; **3,** one, below m1; **4,** one, below m2.

25. Postsymphysial foramen: **0,** absent; **1,** occasionally present; **2,** always present.

26. Position of mandibular foramen: **0,** near midline of ascending ramus; **1,** posterior to midline.

27. Postmandibular foramen: **0,** absent or not traceable; **1,** present, confluent or nearly so with mandibular foramen; **2,** present, widely separated from mandibular foramen.

D. Teeth in general

28. Pigmentation: **0,** teeth white, without traces of pigmentation; **1,** teeth at least partially pigmented, visible as red by the eye, or visible under ultraviolet light. See Repenning (1967) and McKenna (1960).

TABLE 4

Data Matrix Used for the Phylogenetic Analysis

Characters 1–7 (external) and 8–45 (cranial); See text for character descriptions.

Taxon	05	10	15	20	25	30	35	40	45
†Geolabididae	?????	?1?01	10???	?000?	0000?	10000	10010	00000	0?000
†Nyctitheriidae	?????	?????	?????	??000	00000	00000	000?0	0?000	00000
†Plesiosoricidae	?????	?0000	0????	?0000	00000	0000?	00??0	0?000	00001
†*Heterosorex*	?????	?1000	000??	00000	01242	00?12	30212	00001	01000
†*Domnina*	?????	?2001	0000?	00000	11132	00112	20?02	00001	0?000
Anourosorex	01100	22000	11112	01113	21431	02014	40011	20102	01211
Blarina	01000	22001	11122	10112	22430	01111	40011	20101	01210
Blarinella	01000	22101	11121	00112	22430	01111	40001	20010	01210
Chimarrogale	12100	22011	11021	10112	22430	00113	40110	20100	00210
Chodsigoa	01000	22101	11120	10113	22430	01113	40110	20010	00210
Congosorex	01000	12111	01020	00111	22320	00013	30010	20000	20100
Crocidura	10000	02100	01032	00111	22330	00013	40000	01000	20000
Crossogale	12100	22011	11021	10112	22430	00113	40110	20100	00210
Cryptotis	01000	22101	11121	10112	22430	01112	40010	20010	00210
Diplomesodon	20000	02110	01032	00111	22330	00014	40000	31000	20000
Episoriculus	01000	22101	11121	10111	22430	10112	40020	20010	00210
Feroculus	00001	12101	01031	00111	22320	00012	40000	00100	20000
Megasorex	01000	02111	11111	10113	21430	02013	40001	21011	00200
Myosorex	01000	12101	01020	00111	22320	00012	30010	20000	20100
Nagasorex	01000	12101	01020	00111	22320	00011	30000	20000	20110
Nectogale	13210	22101	11121	10111	22430	10113	40000	20010	00210
Neomys	12000	22101	11120	10113	22430	10112	40000	20010	00210
Notiosorex	11000	02111	11111	10113	21430	10113	40000	20010	00210
Palawanosorex	01000	02111	01022	10111	22230	10012	40000	10000	20110
Parablarinella	01000	22101	11121	00112	22430	01111	40001	20010	01210
Paracrocidura	00000	02111	01031	00111	22320	00113	40001	21000	10120
Pseudosoriculus	01000	22101	11121	10111	22430	10112	40020	20010	00210
Ruwenzorisorex	01000	12101	01031	00111	22320	00112	40000	00100	20000
Scutisorex	01000	02111	01032	02111	02320	10012	40010	00000	20120

TABLE 4 *continued*

Taxon	0	1	1	2	2	3	3	4	4
	5	0	5	0	5	0	5	0	5
Solisorex	01001	02110	11032	00111	21331	00013	40000	11100	20000
Sorex	11000	22101	01021	00112	22431	11111	40120	20010	00210
Soriculus	01000	22101	11121	10113	22430	11112	40110	20010	00210
Suncus	00000	02111	01032	00111	22330	00012	40000	10000	20000
Surdisorex	01101	12101	11021	00111	22320	00013	40010	20000	20110
Sylvisorex	00000	02101	01030	00111	22320	01012	40001	20000	20100
†*Crocidosorex*	?????	?2??1	00???	?0111	22320	0?111	20000	21000	20100
†*Clapasorex*	?????	?2?01	0002?	?011?	2?320	??011	200?0	?1000	20120
†*Miosorex*	?????	?2??1	000??	?0111	22320	01011	30000	21000	20100
†*Paenelimnoecus*	?????	?2???	?????	??111	22330	1211?	200?0	110?0	20010
†*Limnoecus*	?????	?????	?????	??111	22330	0011?	40???	?????	?0310
†*Dobenflorinia*	?????	?2??1	000??	??111	22320	00112	30000	21000	20000
†*Paranourosorex*	?????	?2?01	11???	0?113	2043?	00113	40001	20102	01001
†*Allosorex*	?????	?????	?????	??112	2?430	0001?	402??	??10?	?1211
†*Amblycoptus*	?????	?2?01	00???	0?113	21430	00013	41011	20102	01001
†*Beremendia*	?????	?2?01	1????	?0112	20431	0?112	40100	10001	00210

29. Number of functional lower incisors per mandible: **0,** more than one; **1,** one only. See Green (1977) for †*Plesiosorex* Pomel, 1848, and Cantuel and Didier (1950) for *Neomys*.

30. Number of unicuspids (excluding incisor) in upper jaw: **0,** more than six; **1,** six; **2,** five; **3,** four; **4,** three.

31. Number of unicuspids (excluding incisor) in lower jaw: **0,** more than five; **1,** five; **2,** four; **3,** three; **4,** two.

32. Number of upper and lower molars in one quadrant: **0,** three; **1,** two.

E. Upper dentition

Upper molars of some rarely illustrated shrews are shown in figure 17; see also table 4.

33. Anterior tip of incisor: **0,** unicuspid; **1,** with traces of second cusplet; **2,** strongly bifid.

34. Unicuspid teeth: **0,** simple construction, weak or heavy cingulum; **1,** with additional lingual-posterior cusplets; **2,** main crest with additional lingual loph.

35. Fourth lower premolar in occlusal view (fig. 18): **0,** shape irregular, talonid elongated and its posterior border slightly or strongly emarginated; **1,** shape less irregular, more squarish or trapezoidal, talonid not elongated lingually and its posterior border very little emarginated; **2,** shape nearly triangular or trapezoidal, posterior border straight.

36. Protocone of P4: **0,** cusp on lingual side of talonid; **1,** shifted to anterio-lingual side; **2,** strongly projecting in anterio-lingual direction; **3,** absent.

37. Hypocone of P4: **0,** present; **1,** absent.

38. Degree of heterodonty between M1 and M2: **0,** molars nearly equal in size; **1,** molars different in size.

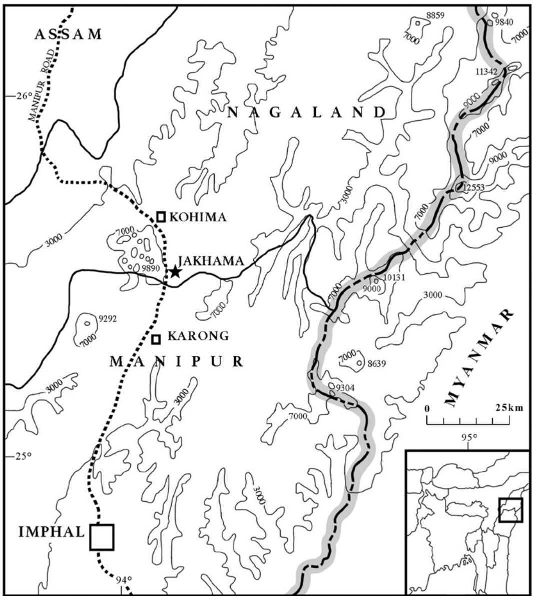


FIG. 15. Map of area around Kohima and Jakhama, Nagaland, showing place names mentioned in the text. Contours of 3000, 7000, 9000, and 12,000 ft show the locations of highlands.

39. Labial outline of M1 and M2: **0,** labial outline irregularly bent; **1,** labial outline almost parallel.

40. Shape of M1: **0,** irregular with anterior and/or posterior emarginations; **1,** squarish to rectangular; **2,** saddle shaped with deep labial emargination (fig. 17, table 4).

41. Condition of protocone: **0,** fully or partially connected by ridge with basis of metacone, sometimes also connected with hypocone, if present; **1,** connected with hypocone by ridge, forming a single crest; **2,** two separate cusps, hypocone usually reduced, sometimes absent.

F. Lower dentition

42. First incisor length: **0,** length moderate, shorter than molar series; **1,** very long, longer than molar series.

43. Structure of lower p4: **0,** tooth with central cusp, either simple or with small posterior cusplets, abrasion platform semitriangular and more or less symmetrical; **1,** tooth with elongated crests with a basin; **2,** lingual cutting blade widely or completely lacking; **3,** single crest, symmetrical or nearly so.

44. Posterior basin of p4: **0,** absent, indistinct or strictly in posterior direction; **1,** deep, running to lingual side; **2,** deep, running to labial side.

45. Size of m1: **0,** nearly equal to m2; **1,** strongly elongated, about twice as long as m2.

Autapomorphic characters not used in analysis:

Tail length: **0,** length medium or long, always longer than hindfoot; **1,** tail shorter than hindfoot, reduced to stump (*Anourosorex* Milne-Edwards (1872)).

Eye opening: **0,** present (most shrews); **1,** absent (*Nectogale*, see Hutterer 1993b).

Pads on fore and hindfeet: **0,** not specialized; **1,** forming adhesive disk organs (*Nectogale*).

Vertebrate column: **0,** not or little modified from general plan; **1,** lumbar vertebrae strongly modified and increased in number (*Scutisorex* Thomas, (1913)).

Occipital crest: **0,** absent or moderately developed; **1,** expanded posteriorly, forming a bony plate (*Scutisorex*).

Incisive foramen: **0,** present by pairs, followed by a single foramen or another small pair more posteriorly; **1,** only one large foramen present (*Anourosorex*).

Determination of Outgroups

Recent molecular phylogenetic studies have supported the Eulipotyphla hypothesis, which places hedgehogs and gymnures (Erinaceidae) as the sister group to shrews, with talpids sister to all other living eulipotyphlans (Murphy et al., 2001; Douady et al., 2002; Esselstyn et al., 2017). For the molecular analyses, we therefore included hedgehogs and moles as outgroups.

All moles are characterized by a unique double shoulder joint (Reed, 1951) and a highly specialized skull. According to Reed (1951) they may have evolved from a soricidlike ancestor, possibly in the Eocene. Because of these mor-

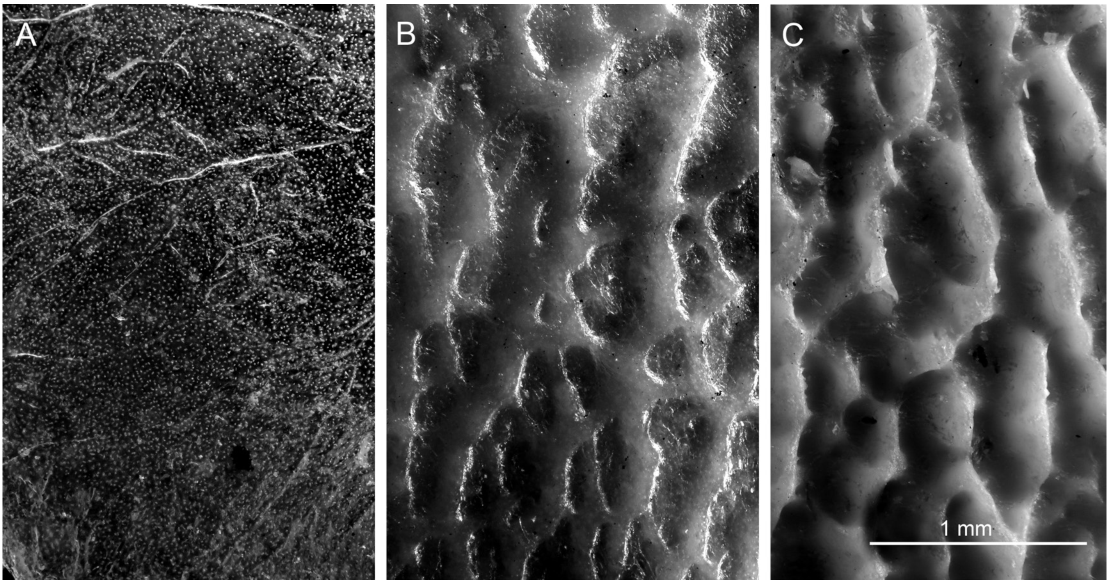


FIG. 16. Details of the fine structure of the dorsal roof of the braincase in *Sylvisorex morio* (A, FMNH 42622), *Anourosorex squamipes* (B, FMNH 45812), and *Scutisorex somereni* (C, FMNH 16180). Scale is 1 mm.

phological specializations, we chose instead to use the fossil taxa Geolabididae, Nyctitheriidae, and Plesiosoricidae as outgroups, with character states as shown in table 4, for morphological analyses (figs. 19, 20).

Morphological Analyses

The purposes of our phylogenetic analyses are: first, to determine the relationships of *Nagasorex albidens* in a broad phylogenetic context of soricids; and second, given the evidence that *Nagasorex* is morphologically distinct from all other living genera, to consider more broadly the higher-level relationships within the family. Our intent is not to conduct an exhaustive review of soricid phylogeny; this would require inclusion of a large number of fossil taxa, a number that is growing yearly but often based on fragmentary material (see the provisional classification of living and extinct Soricidae, below). Rather, we wish to investigate the general adequacy of past classification systems, to introduce an explicitly defined set of characters, and to introduce an explicit set of phylogenetic hypotheses, all of which will help to guide future research. In our analyses, we have included a representative set of the best-known fossil taxa from most of the higher-order groupings (mostly tribes) that have been named.

To determine the effects of such differences, we have analyzed our data with and without characters based on soft anatomy. Many classifications have been based on only a few or even a single character; we have included all seemingly relevant characters in our analyses, including those that have been emphasized in various past analyses. Some characters used by previous authors turned out to be undefinable; we have not included them.

Our maximum parsimony search with five characters ordered found 32 equally parsimonious trees with a length of 213 steps. The consensus of these trees (strict or majority rule) places *Nagasorex* as the sister to all other living shrews, but bootstrap support for this relationship was absent (fig. 19). Our parsimony analyses that did not order any characters (not shown) found many slightly shorter trees (2023 trees of length

TABLE 5

Voucher Specimens and Corresponding GenBank Accession Numbers of Mitochondrial DNA Sequences Used to Estimate the Cytochrome B Gene Tree

Species	Voucher Specimen	Cytochrome B NCBI Accession
Anourosorex squamipes		KY652321
Blarina hylophaga	TTU 100821	AY546681
Chodsigoa parva		KX765545
Congosorex phillipsorum	FMNH 177682	MG973425
Crocidura batakorum	KU 165320	FJ813968
Crocidura miya	WHT6826	EU122216
Crocidura negrina	KU 165108	FJ813962
Crocidura orii	SO-03misc8 (Institute of Low Temperature Science, Hokkaido University)	AB175087
Crocidura quasielongata	FMNH 218550	KY771708
Crocidura suaveolens	CS4	MF988047
Diplomesodon pulchellum	MVZ 179157	MG973433
Episoriculus caudatus	HA 7122 (Museum of Botanic Garden, Hokkaido University)	AB175115
Feroculus feroculus	WHT6827	JQ433898
Hemiechinus auritus	ZMMU S-176502	KF783138
Hylomys megalotis	ZIN98502	KF783147
Hylomys suillus	KIZ0611095	HQ857524
Megasorex gigas	LACM 055131	AB175150
Myosorex zinki	FMNH 174124	JX193702
Nagasorex albidens	FMNH 76197	SAMN37568052
Neomys fodiens	IZEA7453	AB175071
Palawanosorex muscorum	FMNH 195240	MG973430
Parablarinella griselda	AMNH 101610	AB175144
Paracrocidura schoutedeni	FMNH 167721	MG973434
Ruwenzorisorex suncoides	FMNH 148939	MG973431
Scutisorex thori	FMNH 219669	KF110765
Solisorex pearsoni	WHT6810	JQ433899
Sorex palustris	UWBM 79809	EU856457
Sorex satunini		*GU827402*
Suncus etruscus		JN556043
Suncus murinus		JF784171
Sylvisorex granti	FMNH 209792	KF876413
Talpa levantis	T10299, Zoological Museum, Lomomosov Moscow State University	FN640572
Talpa occidentalis	T011.06.15.04	KU189712

TABLE 6

Voucher Specimens and Corresponding GenBank Accession Numbers of Short–read DNA Sequences Used to Estimate the UCE Trees

Species	Voucher Specimen	NCBI Accession
Canis lupus		GCA_000331495.1
Condylura cristata		GCA_000260355.1
Congosorex phillipsorum	FMNH 177682	SAMN08535804
Crocidura tenebrosa	LSUMZ 39025	SAMN20991443
Erinaceus europaeus		GCA_000296755.1
Myosorex geata	FMNH 158299	SAMN08535816
Nagasorex albidens	FMNH 76197	SAMN37568052
Parablarinella griselda	AMNH 274263	SAMN08535803
Scapanus townsendii	LSUMZ 31414	SAMN07542997
Scutisorex thori	FMNH 219669	SAMN08535823
Sorex araneus		GCA_000181275.2
Suncus murinus	KU 164724	SAMN08535825

= 210), but these analyses placed *Nagasorex* as the sister to a clade of extinct shrews (†*Dobenflorinia* new name, †*Miosorex*, †*Crocidosorex* and †*Clapasorex*), though again, the relationship lacked statistical support. Our Bayesian phylogenetic analysis of morphology appeared to converge, as evidenced by the trace plots and large effective sample sizes (>500 for all parameters). Support values across the tree were generally low, but the maximum clade credibility tree places *Nagasorex* as the sister to the same extinct group of shrews (fig. 20) as our unordered parsimony analysis. In the Bayesian and unordered parsimony inferences, *Nagasorex* + fossils are sister to the Myosoricinae, here represented by *Surdisorex*, *Congosorex* and *Myosorex*.

Genetic Analyses

Mitochondrial tree: Our ML and Bayesian analyses of cytochrome *b* (fig. 21; table 5) from 22 living soricid genera (table 6) produced similar results. Both topologies placed *Nagasorex* as sister to the Crocidurinae with strong support. The monophyly of Crocidurinae, *Nagasorex* + Crocidurinae, Myosoricinae, and Myosoricinae + *Nagasorex* + Crocidurinae were all moderately to strongly supported by ML and Bayesian approaches. We note that these analyses show *Diplomesodon* and *Paracrocidura* as embedded within *Crocidura*, indicating the potential need for a taxonomic revision. In addition, Soricidae was paraphyletic, with *Anourosorex* placed as the sister to Erinaceidae + other Soricidae. However, the placement of *Anourosorex* was not well supported and probably represents a symptom of saturation in our alignment.

Ultraconserved Elements: Our UCE analyses failed to provide confident inference regarding *Nagasorex*'s relationships to other shrews. Our partitioned IQTree maximum likelihood tree did not produce SH-like test or ultrafast bootstrap support for relationships among

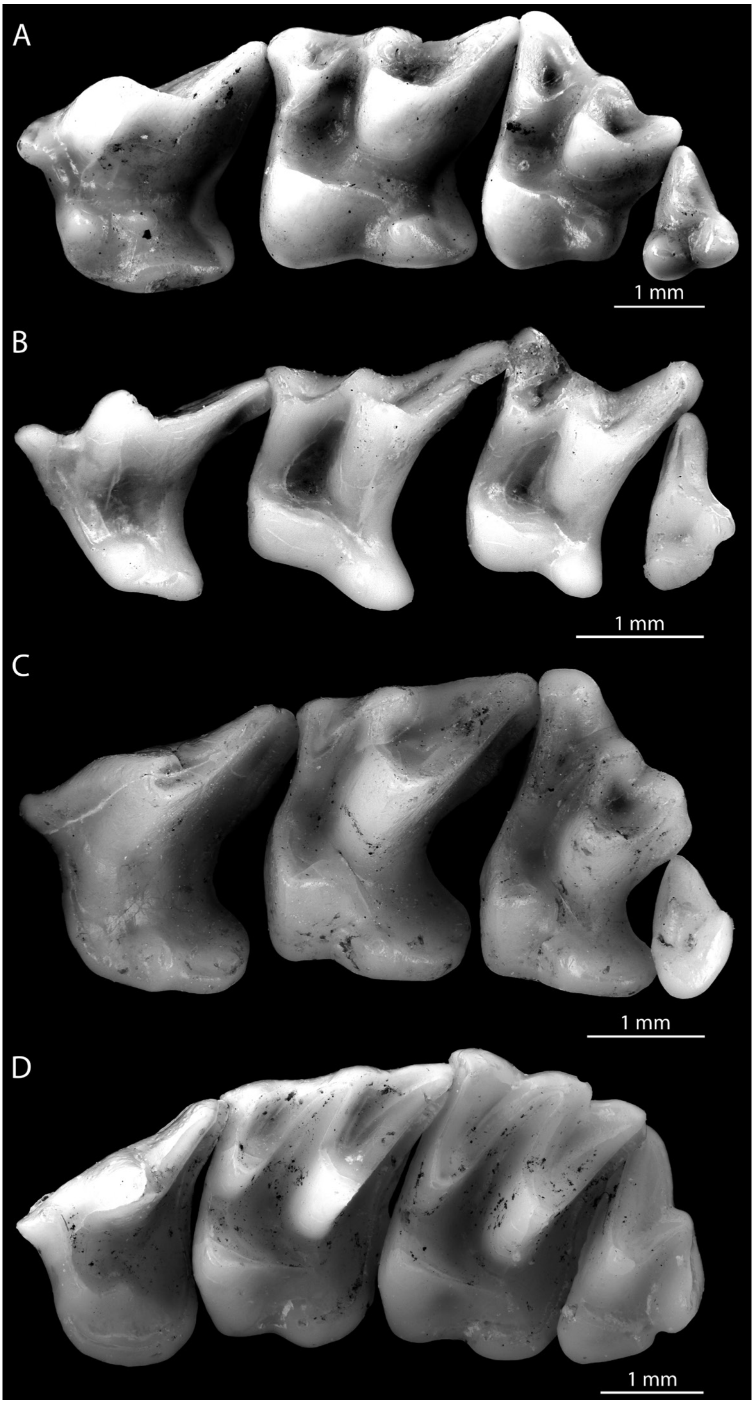


FIG. 17. Upper molariform teeth of four uncommon genera and species of shrews. **A,** *Solisorex pearsoni* (FMNH 108990); **B,** *Feroculus feroculus* (FMNH 99453); **C,** *Ruwenzorisorex suncoides* (FMNH 148268); **D,** *Paracrocidura maxima* (FMNH 157411). Each scale is 1 mm.

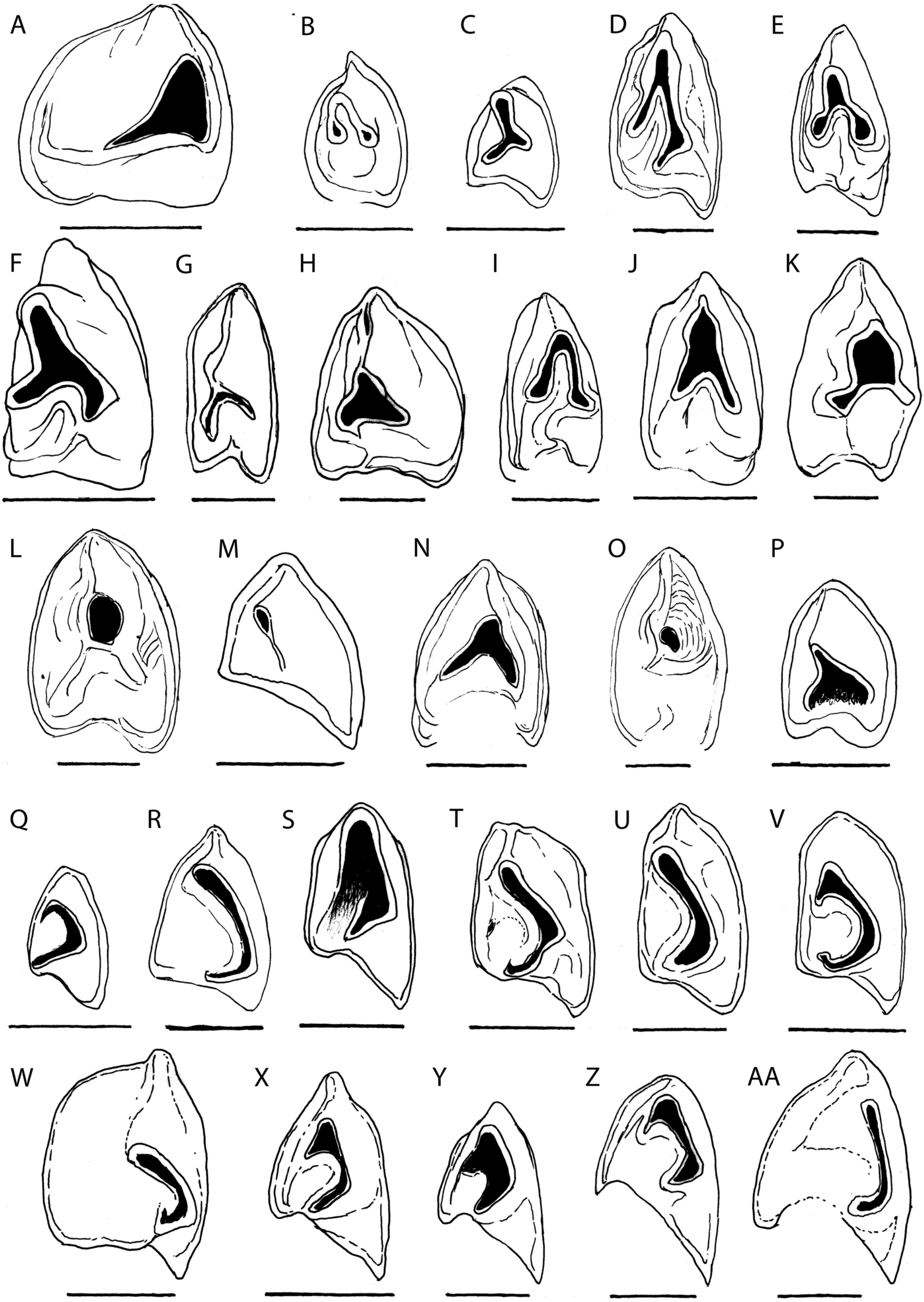
Nagasorex, soricines, or crocidurines + myosorines (fig. 22). The unpartitioned concatenated RAxML tree also did not produce support for relationships among these groups (fig. 23). Our ASTRAL tree resulted in bootstrap support for a *Nagasorex* + crocidurines + myosoricines clade (BS: 99), but failed to resolve relationships among these three groups (support for Crocidurinae + Myosoricinae was only 62; fig. 24). Loci were nearly evenly divided in their support for the three possible topologies we tested in the per locus site-likelihood analysis (fig. 25).

DISCUSSION

Our morphological and molecular phylogenetic analyses necessarily differ in the taxa included (especially for fossil vs. extant taxa), but there is sufficient overlap to develop an integrated perspective. We prefer this approach over the possibility of conducting a combined analysis, which we feel would merely obscure the sources of uncertainty that operate in the analyses we described above. Our morphological analyses suggest that the new genus *Nagasorex* groups close to some extinct genera (†*Clapasorex*, †*Crocidosorex*, †*Dobenflorinia* new name, †*Miosorex*) and the extant *Congosorex*, *Myosorex*, and *Surdisorex* (fig. 20). In the mitochondrial genetic tree (considering only extant genera for which genetic results are available), it holds a position between Myosoricinae and Crocidurinae, sister to the latter (fig. 21). Results from inferences based on UCEs from available extant taxa placed *Nagasorex* variably as the sister to all living shrews (fig. 22) or to Crocidurinae + Myosoricinae (figs. 23, 24). However, in nearly all cases, the inferred relationships lacked statistically meaningful support. In the morphology of the p4 (figs. 12B, 18F), *Nagasorex* is also most similar to the myosoricine genera *Congosorex*, *Myosorex*, and *Surdisorex* (fig. 18B–E), and to some extinct genera of †Geolabididae, †Nycteritheriidae and †Plesiosoricidae, but not to †*Domnina* Cope (1873) or †*Heterosorex* (table 4), particularly in the long branch of the upside-down Y enamel.

Nagasorex is unique among the extant shrew genera in having 34 upper teeth; only a few fossil genera have more (†*Lusorex* Storch and Qiu, 2004, has 38; †*Crocidosorex* and †*Oligosorex* Kretzoi (1959b) have 36). The extinct †*Domnina*, †*Lartetium* Ziegler, 1989, †*Miosorex*, and †*Pseudotrimylus* Gureev, 1971, also have 34 teeth. Among extant Myosoricines, *Myosorex* has 32, *Congosorex* 30, and *Surdisorex* 28; many extant and extinct soricines and crocidurines have 32 or fewer; table 2). Thus, *Nagasorex* is distinctive among living soricids in having a large number of upper teeth, and resembles several fossil genera in this respect. However, the phylogenetic signal of a high number of teeth is fairly weak, given the extent of variation within the subfamilies.

The earliest geological occurrence of Soricidae genera, including also the possible most recent common ancestor of the Soricidae (table 7) and the relative crown ages based on the phylogeny shown in figure 20, is presented in table 5. One of the oldest soricid clades included †*Heterosorex* and †*Domnina* (both Oligocene), which occurred coevally with the †Geolabidid ae+†Nyctitheriidae+†Plesiosoricidae. For the next eight extant genera that follow in the tree, including *Nagasorex* (fig. 20), we lack any geological age data, except for *Myosorex* (which appeared in the Miocene). These are followed by three extinct genera of Miocene age (†*Clapasorex,* †*Dobenflorinia,* †*Miosorex*) and one of Oligocene age (†*Crocidosorex*). The following genera (*Scutisorex* to †*Limnoecus*) are of Miocene to Pleistocene age, as are most clades of red-toothed shrews (*Pseudosoriculus* to †*Amblycoptus* Kormos (1926)) (fig. 20, table 5). With the exception of †*Crocidosorex* (Oligocene), all genera in this phylogenetic tree (fig. 20) are in a seemingly consistent temporal sequence; in other words, the more basal a genus is in our phylogeny, the older are the first fossil records. In the most comprehensive phylogenetic analysis of extinct and extant shrews, Yuan et al. (2024) estimated an Eocene-Paleocene origin for Soricidae and their separate Heterosoricidae.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In table 8 we list some coeval and sympatric records from the early Oligocene to late Miocene of Heterosoricinae and Soricinae from the northern hemispheres (North America, Europe, and Asia). It is shown that species from each subfamily occurred at the same time in the same areas. We take this, along with the accordance of most diagnostic characters (figs. 19, 20), as consistent with inclusion of the Heterosoricinae in the family Soricidae, as done previously by Rzebik-Kowalska (1994, 2005, and Storch and Qiu (2004). The only principle difference between the Heterosoricinae and the Soricinae is the presence of a shallow internal pocket on the mandibular ramus in the Heterosoricinae, in contrast to a deep internal pocket in the latter.

We may never know the correct phylogenetic relationships of all the fossil taxa because they often are based on very few teeth or bone fragments that do not allow a proper assignment. Complete preservations of the skeleton such as in the case of *Lusorex* Storch and Qiu, 2004, are extremely rare. Luckily, *Nagasorex* was collected alive in Nagaland and its phylogenetic position could be analyzed morphologically and genetically. While we recognize the uncertainty regarding the phylogenetic position of *Nagasorex*, we believe that placing it in the Myosoricinae best reflects our overall results. Clearly, further study and testing of this hypothesis is needed; we especially recommend development and analysis of UCEs from an expanded set of soricids, along with efforts to find and provide detailed description of more fossil shrews.

A Provisional Classification of Living and Extinct Soricidae

Below we present a classification of the shrews in the light of our results. Several taxa at the subfamily and tribal level recognized in many paleontological studies have been listed here as synonyms. Our proposed classification is based on the results of our morphological and genetic studies.

Order Eulipotyphla Waddel, Okada, and Hasegawa, 1999: 1–5

Family Soricidae G. Fischer, 1814: x

Subfamily †Heterosoricinae Viret and Zapfe, 1951: 419

Tribe †Heterosoricini Viret and Zapfe, 1951: 419

†*Belgicasorex* Smith and Van den Hoek Ostende (2006). Type species †*Belgicasorex ramboeri* Smith and Van den Hoek Ostende, 2006. Lowermost Oligocene, Belgium. One sp.

†*Dinosorex* Engesser, 1972. Type species †*Sorex sansaniensis* Lartet (1851). Six spp. Lower Miocene to Upper Oligocene of Eurasia. See Engesser (1975), Ziegler (1989), Van den Hoek Ostende (1995), Rzebik-Kowalska and Topachevsky (1997), Rabeder (1998), and Prieto et al. (2010).

†*Heterosorex* Gaillard, 1915. Type species †*Heterosorex delphinensis* Gaillard, 1915. Upper

FIG. 18. Comparison of the shape of the lower right p4 in shrews in **A,** a Heterosoricine shrew, *Domnina gradata* (PM FMNH P15320), and of 26 (of 30) extant genera of shrews. **B,** *Congosorex verheyeni* (FMNH 227536); **C,** *Congosorex philippsorum* (FMNH 177683); **D,** *Surdisorex polulus* (FMNH 43846); **E,** *Myosorex blarina* (FMNH 144209); **F,** *Nagasorex albidens* (FMNH 76197); **G,** *Feroculus feroculus* (FMNH 99453); **H,** *Ruwenzorisorex suncoides* (FMNH 148268); **I,** *Paracrocidura maxima* (FMNH 157411); **J,** *Sylvisorex morio* (FMNH 42622); **K,** *Scutisorex somereni* (FMNH 43860); **L,** *Suncus murinus* (FMNH 56391); **M,** *Diplomesodon pulchellum* (ZFMK 1999.0911); **N,** *Crocidura leucodon* (FMNH 66217); **O,** *Solisorex pearsoni* (FMNH 108990); **P,** *Palawanosorex muscorum* (FMNH 195236); **Q,** *Episoriculus caudatus* (FMNH 94145); **R,** *Nectogale sikhimensis* (FMNH 37013); **S,** *Neomys fodiens* (FMNH 66264); **T,** *Chodsigoa smithii* (FMNH 39614); **U,** *Soriculus nigrescens* (FMNH 114162); **V,** *Sorex araneus* (FMNH 63839); **W,** *Chimarrogale himalayica* (FMNH 38997); **X,** *Cryptotis parva* (FMNH 134396); **Y,** *Blarinella quadraticauda* (FMNH 37030); **Z,** *Blarina brevicauda* (FMNH 20314); **AA,** *Anourosorex squamipes* (FMNH 76252). Scales are 1 mm.

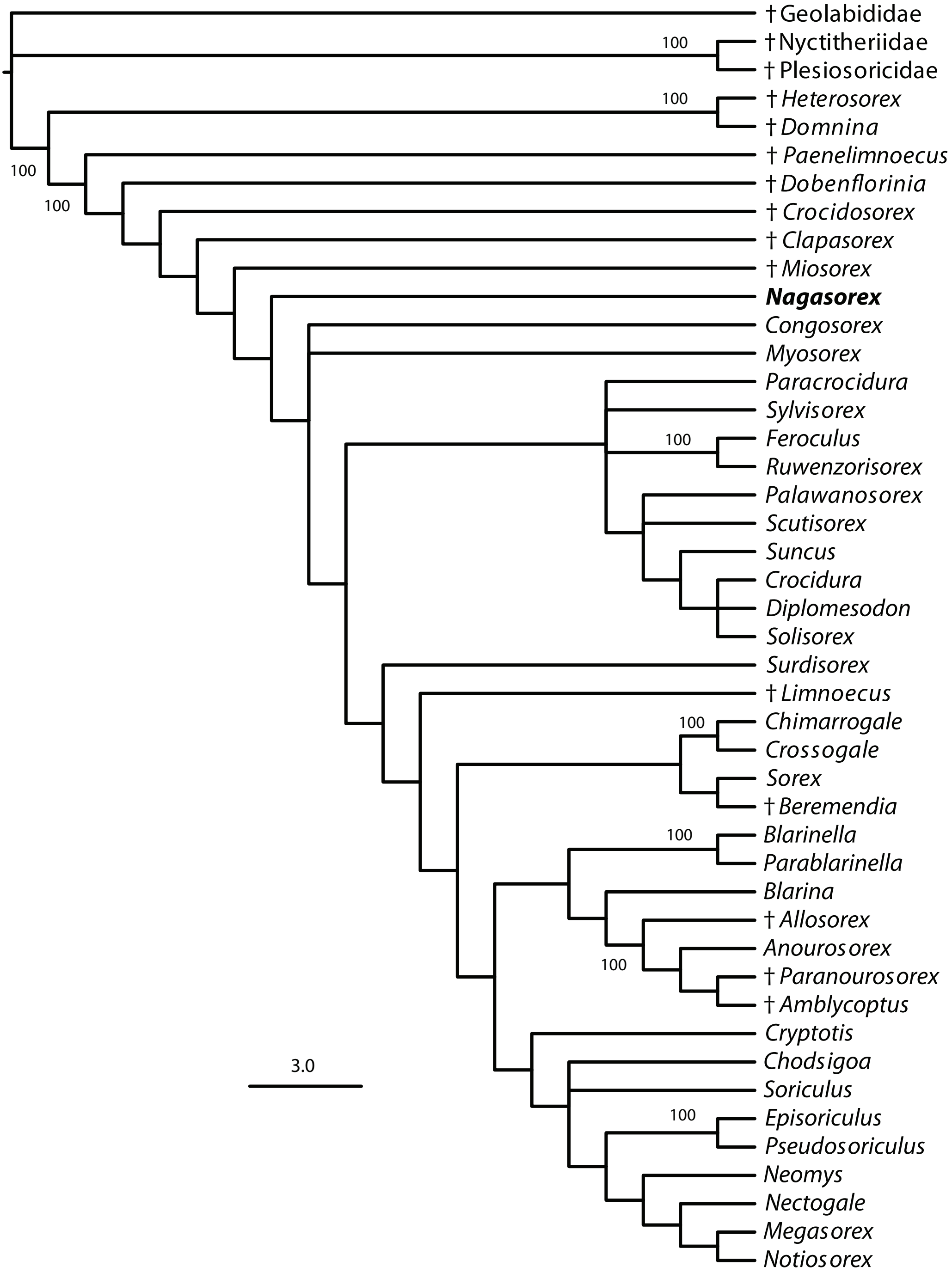

FIG. 19. Majority-rule consensus of 32 equally parsimonious trees resulting from our maximum parsimony analysis using a heuristic search of 45 morphological characters (see table 4) in which five characters were ordered. Bootstrap support values ≥50 are shown.

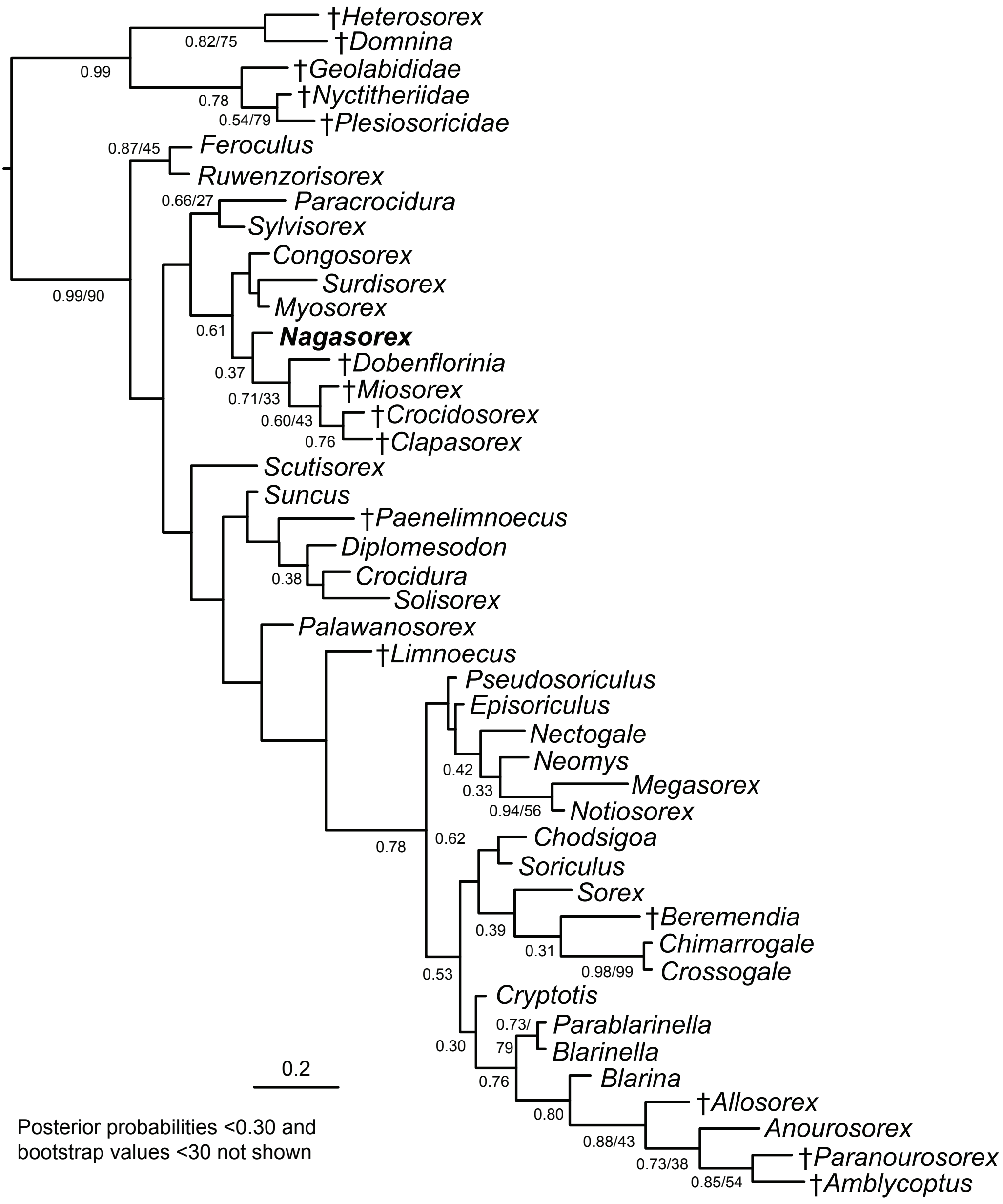

FIG. 20. A phylogeny of living and extinct shrews, inferred from 45 unordered morphological characters (table 4) in a Bayesian context. Numbers at nodes are posterior probabilities, followed by bootstrap support from a parsimony analysis.

TABLE 7

Earliest Geological Occurrence Documented by the Fossil Record and Geographical Distribution of the Taxa (fig. 20)

For extant taxa without any fossil record the current distribution is indicated.

Taxon	Earliest Geological Record (Ma)	Area of Ocurrence	Selected References
†*Geolabididae*	Lower Eocene	Nearctic, Palearctic	Bown and Schankler (1982); Mahboubi et al. (1984)
†*Nyctitheriidae*	Paleocene, 65 Ma	Nearctic, Palearctic	Archibald et al. (1987)
†*Plesiosoricidae*	Eocene to Miocene	Nearctic, Palearctic, Asia	Ziegler (2009b); Oshima et al. (2017)
†*Heterosorex*	Oligocene	Nearctic, Palearctic	Mawby (1960); Storch and Qiu (1991)
†*Domnina*	Oligocene/Eocene	Nearctic	Simpson (1941); Krishtalka and Setoguchi (1977)
†*Paenelimnoecus*	Middle Miocene	Eurasia	Engesser (1980)
†*Dobenflorinia*	Upper Oligocene	Europe	Mörs (1996)
†*Crocidosorex*	Upper Oligocene	Palearctic	Storch (1988)
†*Clapasorex*	Lower Miocene	Palearctic	Crochet (1975)
†*Miosorex*	Miocene	Palearctic	Rzebik–Kowalska (1994)
Nagasorex	[?]	NE India	This paper
Congosorex	[?]	C. Africa	Hutterer et al. (2002)
Myosorex	Upper Miocene	Africa	Robinson and Black (1974); Butler and Greenwood (1979); Pickford and Mein (1988)
Paracrocidura	[?]	C. Africa	Hutterer (1986a)
Sylvisorex	Pliocene	Africa	Butler and Greenwood (1979)
Ferocolus	[?]	Sri Lanka, India	Meegaskumbura et al. (2014)
Ruwenzorisorex	[?]	C. Africa	Hutterer (1986b)
Palawanosorex	[?]	S. Asia	Hutterer et al. (2018)
Scutisorex	Holocene	C. Africa	Van Neer (1989)
Suncus	Miocene, Pliocene	Palearctic, Africa	Wesselmann (1984); Butler and Greenwood (1979); Pickford and Mein (1988); Mein and Pickford (2006)
Crocidura	Miocene, Pliocene	Palearctic, Africa	Wesselman (1984); Mein and Pickford (2006); Conroy et al. (1992)
Diplomesodon	Early Pleistocene	Asia, Africa?	Repenning (1965)
Solisorex	[?]	Sri Lanka	Meegaskumbura et al. (2014)
Surdisorex	[?]	E. Africa	Kerbis et al. (2009)
†*Limnoecus*	Middle Miocene	Nearctic	Hutchison and Lindsay (1974)

TABLE 7 *continued*

Taxon	**Earliest Geological Record (Ma)**	**Area of Ocurrence**	**Selected References**
Chimarrogale	Pliocene	Asia	Qiu and Storch (2005)
Crossogale	[?]	S. Asia	Abramov et al. (2017b)
Sorex	Upper Miocene	Nearctic, Palearctic	Storch (1995)
†*Beremendia*	Pliocene	Palearctic, Asia	Zazhigin and Voyta (2019)
Blarinella	Upper Miocene	Asia	Storch and Qiu (1991)
Parablarinella	[?]	[Asia]	Bannikova et al. (2019)
Blarina	Pliocene	Nearctic	Jones et al. (1984)
†*Allosorex*	Miocene	Palearctic	Mörs et al. (2000)
Anourosorex	Upper Miocene	Asia	Storch and Qiu (1991)
†*Paranourosorex*	Upper Miocene	Palearctic	Storch and Zazhigin (1996)
†*Amblycoptus*	Upper Miocene	Palearctic	Engesser (1980)
Cryptotis	Pleistocene	Nearctic	Woodman and Croft (2005)
Chodsigoa	Pleistocene	Asia	Chen et al. (2017)
Soriculus	[?]	Asia	Kotlia and Sanwal (2005)
Episoriculus	Pliocene	Asia	Abramov et al. (2017a)
Pseudosoriculus	[?]	Asia	Abramov et al. (2017a)
Neomys	Pliocene	Palearctic	Engesser (1980)
Nectogale	[?]	SE. Asia	Fan et al. (2022)
Megasorex	[?]	Mexico	Woodman et al. (2016)
Notiosorex	Miocene, 6.7 Ma	Nearctic	Carraway (2010)

TABLE 8

Contemporaneous Records of Heterosoricinae and Soricinae

Heterosoricinae	Soricinae	Age	Area	Reference
†*Heterosorex*	†*Dobenflorinia*	Upper Oligocene	Germany	Mörs (1996)
†*Heterosorex*	†*Crocidosorex*	Upper Oligocene	Germany	Storch (1988)
†*Quercysorex*	†*Crocidosorex*, †*Srinitium*, †*Ulmensia*	Upper Oligocene	Germany	Ziegler (1998a)
†Heterosoricidae	†*Srinitium*, †*Oligosorex*, ?†*Crocidosorex*	Upper Oligocene	Bosnia, Herzegovina	Van der Sar et al. (2017)
†*Pseudotrimylys*	†*Antesorex*	Lower Miocene	Colorado	Wilson (1960)
†*Heterosorex*	†*Paenelimnoecus*	Middle Miocene	Switzerland, Turkey	Engesser (1972, 1980)
†*Dinosorex*	†*Miosorex*, †*Petenyia*, †*Alloblarinella*, †*Paenesorex*, †*Deinsdorfia*, †*Paenelimnoecus*	Middle Miocene, MN7+8	Germany	Ziegler (2003)
†*Dinosorex*	†*Anourosoricodon*, ?†*Asoriculus*	MN9	Ukraine	Rzebik-Kowalska and Topachevsky (1997)
†*Heterosorex*, †*Dinosorex*	†*Miosorex*, †*Florinia*	Miocene, MN5	Austria, Germany	Ziegler and Fahlbusch (1986); Ziegler (1989, 2000); Rabeder (1998)
†*Heterosorex*	†*Allosorex*	Miocene, MN5–6	Germany	Ziegler and Mörs (2000)
†*Heterosorex*	*Anourosorex*	Late Miocene	China	Storch and Qiu (1991)
†*Heterosorex*	†*Dobenflorinia*, †*Paenelimnoecus*, †*Miosorex*, †*Lartetium*, †*Florinia*	Lower Miocene, MN 3–4	Germany	Klietmann et al. (2014); Ziegler (1998b)
†*Heterosorex*, †*Dinosorex*	†*Miosorex*, †*Limnoecus*	Early Miocene, MN4b	Germany	Ziegler and Fahlbusch (1986)

Oligocene to Middle Miocene of Eurasia. Five spp. See Wilson (1963), Doben-Florin (1964), Engesser (1975), Doukas (1986), Ziegler (1989), and Storch and Qiu (1991).

†*Lusorex* Storch and Qiu, 2004. Type species †*Lusorex taishanensis* Storch and Qiu, 2004. Miocene, China. One sp.

†*Mongolosorex* Qiu (1996). Type species †*Mongolosorex qiui* Qiu (1996). Early to middle Miocene, Nei Mongol, China. One sp.

†*Pseudotrimylus* Gureev, 1971. Type species †*Trimylus schlosseri* Roger (1885) = †*Sorex sansaniensis* Lartet, 1851. Eocene, Oligocene, Lower Miocene, North America, and Europe. Synonym: †*Trimylus* Roger (1885) (preoccupied). Seven spp. (Repenning, 1967; Martin and Lim, 2004b)

†*Wilsonosorex* Martin (1978). Type species: †*Wilsonosorex conulatus* Martin (1978). Miocene, North America. Two spp.

Tribe Domnini Jammot, 1983: 271

†*Domnina* Cope, 1873. Type species †*Domnina gradata* Cope, 1873. Middle Oligocene of Cedar Creek, Logan County, Colorado. Eocene to Lower Miocene, North America. Four spp. Includes †*Miothen* Cope, 1873, and †*Protosorex* Scott (1895). See Patterson and McGrew (1937), Macdonald (1963), Repenning (1967), Hutchison (1972), and Yuan et al. (2024).

†*Gobisorex* Sulimski (1970). Type species †*Gobisorex kingae* Sulimski, 1970. Oligocene, Northern Gobi Desert, Mongolia, China, Kazakhstan. Two spp. New material in the AMNH col-

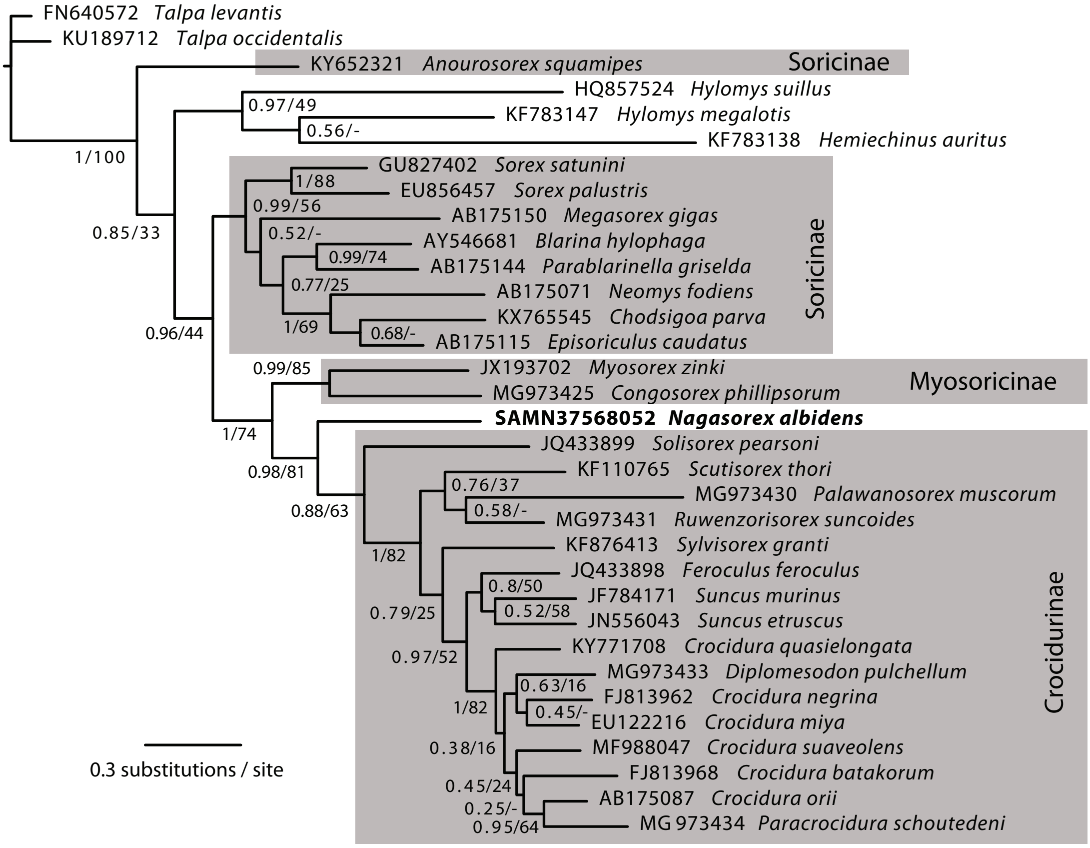

FIG. 21. A maximum-clade-credibility mitochondrial gene tree estimated from the DNA sequences of the cytochrome-*b* gene. The topology and branch lengths are from a Bayesian analysis completed in MrBayes. Numbers at nodes are posterior probabilities followed by bootstrap support from a maximum likelihood analysis completed in RAxML. Tips are labeled with GenBank accession numbers and scientific names. Associated voucher numbers are presented in table 5.

lected by the American-Mongolian Expeditions indicates that the genus is close to *Quercysorex* (R.H., unpubl.); see also Ziegler et al. (2007).

†*Ingentisorex* Hutchison (1966). Type species †*Ingentisorex tumidiens* Hutchison, 1966. Late Miocene, Oregon. One sp.

†*Paradomnina* Hutchison (1966). Type species †*Paradomnina relictus* Hutchison, 1966. Late Miocene, Oregon. One sp.

†*Quercysorex* Engesser, 1972. Type species †*Amphisorex primaevus* Filhol (1884) (†*Amphisorex* Filhol, 1884 non *Amphisorex* Duvernoy (1835)). Oligocene of Europe. Five spp. (Ziegler, 1998a, 1998b).

Subfamily Myosoricinae Kretzoi, 1965: 124

(Myosoricini Kretzoi, 1965: 124; Myosoricina: Gureev, 1971: 122, 1979: 372, Jammot, 1983: 271; Oligosoricini Gureev, 1971: 66 (sensu Lopatin, 2004a); Crocidosoricinae Reumer, 1987: 190; Myosoricinae: Hutterer, 2005a: 263)

? †*Aralosorex* Lopatin, 2004b. Type species *Aralosorex kalini* Lopatin, 2004b. Oligocene of Kazakhstan. One sp.

†*Clapasorex* Crochet, 1975. Type species †*Clapasorex sigei* Crochet, 1975. Upper Oligocene to Lower Miocene of France and Spain. Four spp. (see Van den Hoek Ostende, 2003).

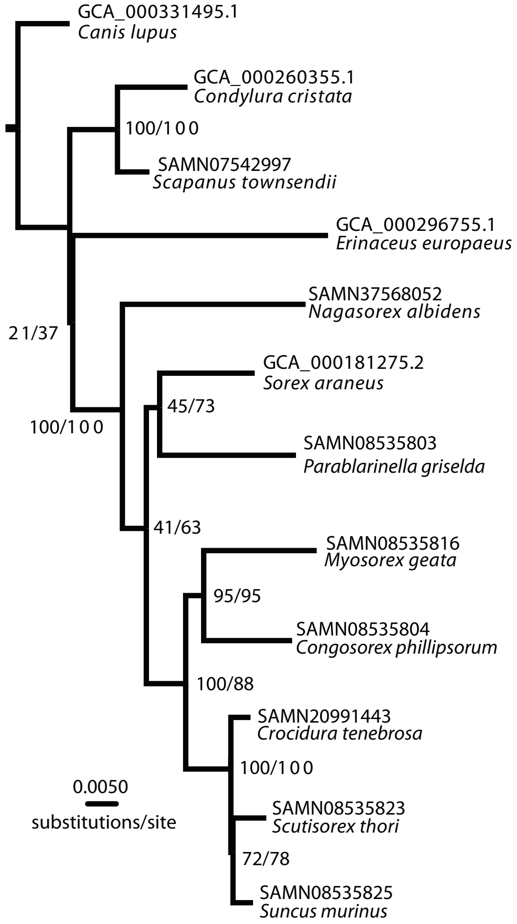

FIG. 22. A concatenated UCE tree estimated from per locus partitioning and model testing in IQTree followed by a maximum likelihood analysis conducted using IQTree. Numbers at nodes are SH-like test values, followed by ultrafast bootstrap approximation support values. See table 6 for museum catalog numbers of voucher specimens identified here by NCBI BioSample and GenBank genome assembly numbers.

Congosorex Heim de Balsac and Lamotte, 1956. Type species: *Congosorex polli* (Heim de Balsac and Lamotte, 1956). Congo Basin, Africa. Three spp. (Hutterer et al., 2002; Stanley et al., 2005).

†*Crocidosorex* Lavocat, 1951. Type species †*Crocidosorex piveteaui* Lavocat, 1951. Upper Oligocene to Miocene of Europe and China; see Reumer (1987) and Storch (1988). One sp.

†***Dobenflorinia***, new name for †*Soricella* Doben-Florin, 1964, preoccupied by *Soricella* Clay and Meinertzhagen (1937: 276) (Mallophaga). Type species †*Soricella discrepans* Doben-Florin, 1964. Miocene, Europe. Two spp. (MN 2–4). LSID:urn:lsid:zoobank.org:act:440EEC48-BA9E-4480-831F-F4565E6BE0E3

†*Meingensorex* Hugueney and Maridet, (2011). Type species †*Sorex ambiguus* Pomel (1853). Allier, France, marine stage MN2a. One sp.

†*Miocrocidosorex* Lopatin, 2004a. Type species †*Miocrocidosorex zazhigini* Lopatin, 2004a. Kazakhstan, Miocene. One sp.

†*Miosorex* Kretzoi, 1959a. Type species *Sorex pusillus* var. *grivensis* Depéret (1892). Miocene (MN 3–4) to Pliocene of Europe. Two spp. See Rzebik-Kowalska (1994).

Myosorex Gray, 1838. Type species *Sorex varius* Smuts (1832). Miocene to Holocene of Africa, Pliocene of Europe and N. Africa; Recent, Africa south of the Sahara. Includes the extinct species *Myosorex meini* Jammot (1977), *Myosorex robinsoni* Meester (1955), and 19 extant species. See Wesselmann (1984), and Taylor et al. (2013).

Nagasorex Hutterer, Swanson, Esselstyn and Heaney, 2025. Type species *Nagasorex albidens* Hutterer, Swanson, Esselstyn and Heaney, 2025. Nagaland, India. Extant, one sp.

? †*Oligosorex* Kretzoi, 1959b. Type species †*Sorex antiquus* Pomel, 1853. Oligocene to Miocene of Europe. Two to three spp. (Van den Hoek Ostende, 2001).

Surdisorex Thomas, 1906. Type species *Surdisorex norae* Thomas, 1906. Africa. Three spp. Recent; see Kerbis Peterhans et al. (2009).

? †*Taatsiinia* Ziegler, Dahlmann, and Storch, 2007. Type species †*Taatsiinia hoeckorum* Ziegler, Dahlmann, and Storch, 2007. Oligocene, Valley of the Lakes, Mongolia. One sp.

? †*Tavoonyia* Ziegler, Dahlmann, and Storch, 2007. Type species †*Tavoonyia altaica* Ziegler, Dahlmann, and Storch, 2007. Oligocene, Valley of the Lakes, Mongolia. One sp.

Subfamily Crocidurinae Milne-Edwards, 1872: 256

(Crocidurinae Milne-Edwards, 1872: 256; Scutisoricinae Allen, 1917: 781; Crocidurini Kretzoi, 1965: 123; Amblycoptini Kretzoi 1965: 125; Scutisoricini Kretzoi, 1965: 125; Paenelimnoecini Fejfar, Storch, and Tobien, 2006: 110)

Crocidura Wagler, 1832. Type species *Sorex leucodon* Hermann (1780). Pliocene to Recent, Old World. Includes *Praesorex* Thomas, 1913b, *Afrosorex* Hutterer (1996). About 183 extant and numerous fossil species.

Diplomesodon Brandt (1852). Type species *Sorex pulchellus* Brandt, 1852. Recent, Asia. One sp. plus a problematic fossil record from the Pleistocene of southern Africa (Repenning, 1965).

Feroculus Kelaart, 1852. Type species *Sorex feroculus* Kelaart, 1852. Recent, Sri Lanka and S. India. One to two spp. (see Meegaskumbura et al., 2014).

Palawanosorex Hutterer, Balete, Giarla, Heaney, and Esselstyn, 2018. Type species *Palawanosorex muscorum* Hutterer, Balete, Giarlia, Heaney, and Esselstyn, 2018. Two spp., recent, Palawan and Borneo (Nations et al., 2022).

†*Paenelimnoecus* Baudelot (1972). Type species *Paenelimnoecus crouzeli* Baudelot, 1972. Miocene of Sansan, France. Six spp. Miocene to Pliocene of Europe, Asia Minor and China (Cai, 1987). See also Doben-Florin (1964), Rzebik-Kowalska (1990b, 1991), Storch (1995), Jin and Kawamura (1997), Pipik and Sabol (2005), and Van den Hoek et al., (2009) for a discussion of distinctive characters and the inclusion into a separate tribe or subfamily. Includes *Prolimnoecus* Savage and Russel (1983: 239) (lapsus).

Paracrocidura Heim de Balsac, 1956. Type species *Paracrocidura schoutedeni* Heim de Balsac, 1956. Recent, C. Africa. Three spp. (Hutterer, 1986b).

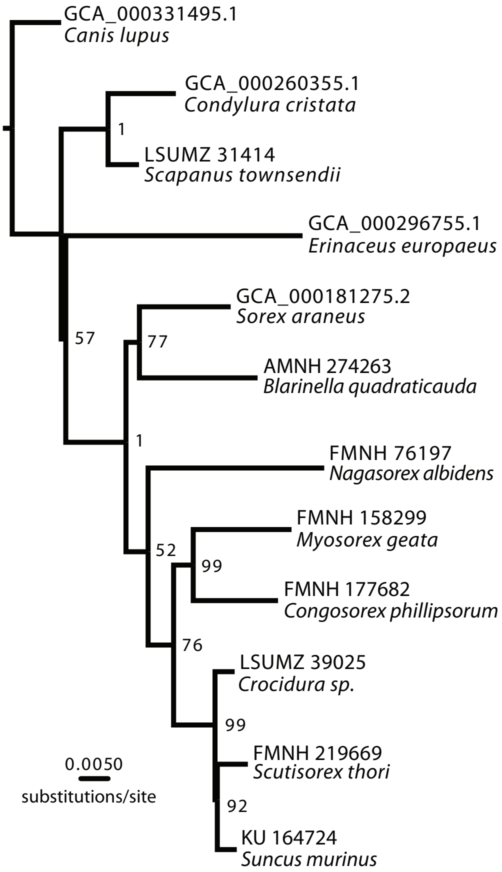

FIG. 23. A concatenated UCE tree estimated from a maximum likelihood analysis conducted using RAxML. Numbers at nodes are ML bootstrap support values. See table 6 for museum catalog numbers of voucher specimens identified here by NCBI BioSample and GenBank genome assembly numbers.

Ruwenzorisorex Hutterer, 1986a. Type species *Sylvisorex suncoides* Osgood, 1936. Recent, C. Africa. One sp. (Hutterer, 1986a).

Scutisorex Thomas, 1913b. Type species *Sylvisorex somereni* Thomas, 1910. Recent, C. Africa. Two to three spp. (Stanley et al., 2013). See also Ahmed and Klima (1978) and Smith and Angielczyk (2020, 2022).

Solisorex Thomas, 1924. Type species *Solisorex pearsoni* Thomas, 1924. Recent, Sri Lanka. One sp. (see Meegaskumbura et al., 2014).

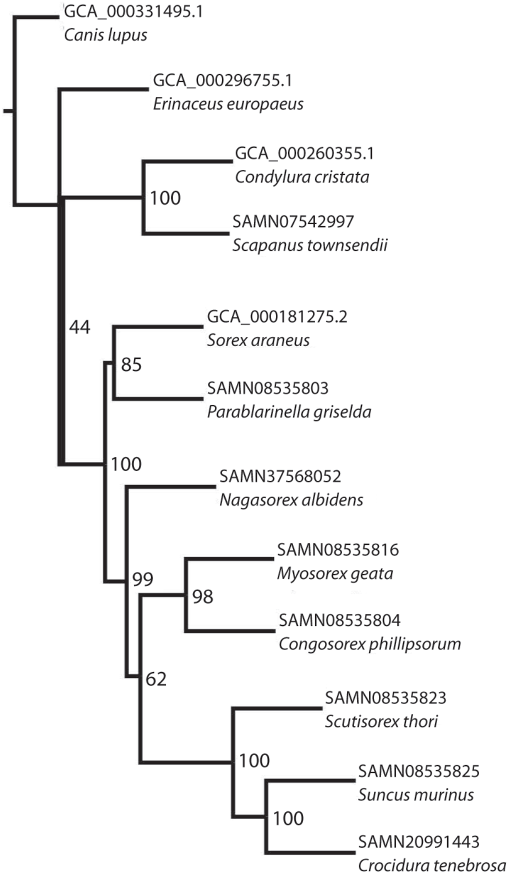

FIG. 24. A species tree estimated with ASTRAL from unrooted gene trees inferred using maximum likelihood implemented in IQTree. Numbers at nodes are bootstrap support values. See table 6 for museum catalog numbers of voucher specimens identified here by NCBI BioSample and GenBank genome assembly numbers.

Suncus Ehrenberg (1832). Type species *Suncus sacer* Ehrenberg, 1832. Pliocene to Recent, Africa, Europe, Asia. Ca. 19 extant and three extinct spp. Includes *Podihik* Deraniyagala (1958).

Sylvisorex Thomas, 1904. Type species *Crocidura morio* Gray (1862). Pliocene to Recent, Africa. About 15 extant spp. (Hutterer and Montermann, 2009: Hutterer et al., 2009), and two fossil spp. (Butler and Greenwood, 1979).

Subfamily Soricinae Fischer, 1814: x

(Soricinorum Fischer, 1814: 143, 1817: 372; Anourosoricinae Anderson, 1878: 159; Nectogalinae Anderson, 1878: 149; Neomyinae Matschie (1909: 9); Amblycoptinae Kormos, 1926: 370, 391; Amblycoptini Kretzoi, 1965: 125; Blarinini Kretzoi, 1965: 124; Soriculini Kretzoi, 1965: 123; Soricini Kretzoi, 1965: 122; Allosoricinae Fejfar, 1966: 223; Limnoecinae Repenning, 1967: 24; Beremendina Gureev, 1971: 190; Beremendiini Reumer, 1984: 101; Notiosoricini Reumer, 1984: 18).

†*Adeloblarina* Repenning, 1967. Type species †*Adeloblarina berklandi* Repenning, 1967. Late Miocene of the United States. One sp.

†*Alloblarinella* Storch, 1995. Type species †*Alloblarinella sinica* Storch, 1995. Late Miocene of Inner Mongolia, China, and Europe. Two spp.

†*Allosorex* Fejfar, 1966. Type species †*Allosorex stenodus* Fejfar, 1966. Late Pliocene of Europe. One sp.

†*Alluvisorex* Hutchison, 1966. Type species †*Alluvisorex arcadentes* Hutchison, 1966. Upper Miocene, United States. Two spp.

†*Amblycoptus* Kormos, 1926. Type species †*Amblycoptus oligodon* Kormos, 1926. Miocene to Pliocene of Europe, Turkey, and Ukraine. Two spp. See Rzebik-Kowalska (1975), and Mészáros (1999).

†*Anchiblarinella* Hibbard and Jammot (1971). Type species †*Anchiblarinella wakeeneyensis* Hibbard and Jammot, 1971. Miocene of Kansas, United States. One sp.

†*Angustidens* Repenning, 1967. Type species †*Sorex vireti* Wilson, 1960. Early Miocene of Colorado (USA) and Pliocene of Germany (Europe). Two spp. (Mayr and Fahlbusch, 1975).

Anourosorex Milne-Edwards, 1872. Type species *Anourosorex squamipes* Milne-Edwards, 1872. Upper Miocene to Recent, Asia and (extinct) Europe. Four extant and two extinct spp. See Schlosser (1924), Bachmayer and Wilson (1970), Qiu et al., (1984), Zheng (1985), Storch and Qiu (1991), and Hutterer (2005a).

†*Anourosoricidon* Topachevsky (1965). Type species †*Anourosoricidon pidoplitschkovi* Topach-

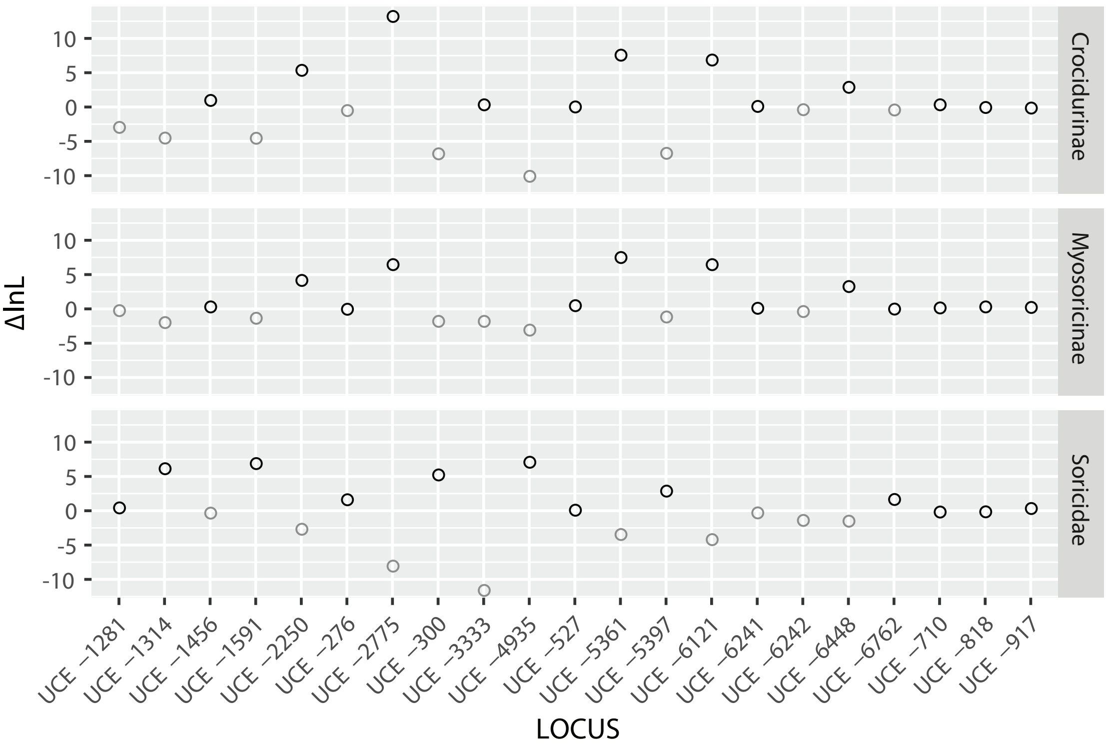

FIG. 25. Delta log likelihoods for each UCE locus used in our phylogenetic analyses. Comparisons show the hypothesis favored by our ASTRAL and RAxML analyses of UCEs, with *Nagasorex* sister to Crocidurinae + Myosoricinae against alternative hypotheses where *Nagasorex* is sister to Crocidurinae (upper panel), Myosoricinae (middle), or Soricidae (lower). Positive values (black) indicate the locus supports *Nagasorex* as sister to Crocidurinae + Myosoricinae, while negative values (gray) indicate support for the alternative hypothesis.

evsky, 1965. Middle Pliocene, Ukraine. One sp. See Bown (1980).

†*Antesorex* Repenning, 1967. Type species †*Antesorex compressus* (Wilson, 1960). Lower Miocene of the Pawnee Creek Formation, Logan County, Colorado, and Dawes County, Nebraska. Two spp., see Korth and Evander (2016).

†*Arctisorex* Hutchison and Harington (2002). Type species †*Arctisorex polaris* Hutchison and Harington, 2002. Pliocene, Canada. One sp.

†*Asoriculus* Kretzoi, 1959a. Type species †*Crocidura gibberodon* Petényi (1864). Quaternary to Pleistocene of Europe, Turkey, and Ukraine. Six spp. See Hutterer (1994b), Fanfani and Masini (1998), Masini and Sarà (1998), and Rofes and Cuenca-Bescos (2006).

†*Beckiasorex* Dalquest, 1972. Type species †*Beckiasorex hibbardi* Dalquest, 1972. Pliocene of North America. One sp.

†*Beremendia* Kormos (1934). Type species †*Crossopus fissidens* Petényi, 1864. Pliocene and Pleistocene of Europe and Asia. See Rzebik-Kowalska (1976). Three spp. Includes †*Similisorex* Stogov and Savinov (1965), Miocene, Asia, and †*Nectogalinia* Gureev, 1979 (Zahzigin and Voyta, 2019). See also Jin et al. (2009) and Furió et al. (2010).

Blarina Gray, 1838. Type species *Sorex talpoides* Gapper (1830). Pliocene to Recent. North America. Four recent, three fossil spp.

Blarinella Thomas (1911). Type species *Blarinella quadraticauda* Milne-Edwards, 1872. Upper Miocene to Recent. Two extant spp. (Jiang et al., 2003), and extinct sp. from China (Qiu et al., 1984; Storch and Qiu, 1991) to Europe (Rzebik-Kowalska, 1989).

†*Blarinoides* Sulimski (1959). Type species †*Blarinoides mariae* Sulimski, 1959. Late Miocene to Pliocene and Quaternary of Europe. Two spp. See Rzebik-Kowalska (1976) and Minwer-Barakat et al. (2007).

†*Builstynia* Ziegler, Dahlmann, and Storch, 2007. Type species *Builstynia fontana* Ziegler, Dahlmann, and Storch, 2007. Miocene, Valley of the Lakes, Mongolia. One sp.

Chimarrogale Anderson, 1877. Type species *Crossopus himalayanus* Gray, 1842. Kashmir to Japan (Hutterer, 2005a), and Quaternary of Asia. Four extant spp. See Vogel and Besancon (1979), Qiu et al. (1984), Yuan et al. (2013) and Abramov et al. (2017b).

Chodsigoa Kastschenko (1907). Type species *Soriculus hypsibius* De Winton (1899). Pleistocene and Recent of eastern Asia. Ten extant spp.; see Lunde et al. (2003), and Chen et al. (2017, 2022).

†*Cokia* Storch, 1995. Type species †*Cokia kowalskae* Storch, 1995. Pliocene and Miocene of Poland and Inner Mongolia, China. Two spp.

†*Cretasorex* Nessov and Gureev, 1981. Type species †*Cretasorex arkhangelskyi* Nessov and Gureev, 1981. Uzbekistan, possibly Miocene; see Lopatin and Tesakov (2004). One sp. A mandibular fragment, consisting of the posterior portion of the ramus and the condyle, is reported by the authors to be taken from Cretaceous sediments. However, the condyle (Nessov and Gureev, 1981: 1003) shows morphology that so far is only known from Oligocene and younger shrews.

Crossogale Thomas (1921). Type species: *Crossogale sumatrana* Thomas, 1921. Two spp. (Abramov et al., 2017b).

†*Crusafontina* Gibert i Clols (1975). Type species: †*Crusafontina endemica* Gibert i Clols, 1975. Includes *Anouroneomys* Hutchison and Bown, in Bown, 1980 (Storch and Qiu, 1991). Seven spp. Europe, Turkey, Nebraska, Oregon, Miocene. See also Gibert i Clols (1976), Bown (1980), Jong (1988), Mészáros (1998), Van Dam (2004), and Prieto and Van Dam (2012).

Cryptotis Pomel, 1848. Type species *Sorex parvus* Say (1822). Middle Pliocene to Recent. North, Central, and South America. 53 extant and three fossil spp. (Woodman, 2015, 2018; Woodman and Timm, 1992, 1993, 1999, 2017).

†*Darocasorex* Van Dam, 2010. Type species †*Darocasorex vandermeuleni* Van Dam, 2010. Spain, ca. 11.5 Ma. One sp. (Van Dam, 2010).

†*Deinsdorfia* Heller (1963). Type species †*Deinsdorfia franconia* Heller, 1963. Miocene to Pleistocene of Europe. Two spp. (see Crochet, 1986; Rzebik-Kowalska, 1990a; Doukas et al., 1995; and Furió and Mein, 2008).

†*Dimylosorex* Rabeder (1972). Type species †*Dimylosorex tholodus* Rabeder, 1972. Pleistocene of Europe. Two spp. (Rabeder, 1982).

†*Dolinasorex* Rofes and Cuenca-Bescós, 2009. Type species †*Dolinasorex glyphodon* Rofes and Cuenca-Bescós, 2009. Lower Pleistocene, Spain. One sp. See Rofes and Cuenca-Bescós (2009) and Moya-Costa et al. (2019).

†*Drepanosorex* Kretzoi, 1941. Type species †*Drepanosorex tasnadaii* Kretzoi, 1941. Pleistocene of Gombasek, Slowakia (= *Sorex savini* Hinton (1911). Four spp. Pleistocene to Quaternary of Europe; see Reumer (1985).

Episoriculus Ellerman and Morrison-Scott, 1951. Type species *Sorex caudatus* Horsfield (1851). Seven Recent and two fossil spp. Includes *Indosuncus* Sahni and Khare (1976). Kashmir, India. Late Cenozoic. The genus and species *Indosuncus bhatiai* Sahni and Khare, 1976 were based on only three lower molars that do not allow a clear diagnosis. Kotlia (1991) questionably included the genus in *Episoriculus*. See Abramov et al. (2017a) for the extant species.

†*Hemisorex* Baudelot (1967). Type species †*Hemisorex robustus* Baudelot, 1967. Miocene of Sansan, France and Europe. One sp. See also Ziegler (1989).

†*Hesperosorex* Hibbard (1957). Type species †*Hesperosorex lovei* Hibbard, 1957. Miocene of Wyoming and Oregon, U.S.A. (Repenning, 1967). One sp.

†*Kordosia* Mészáros (1997). Type species †*Amblycoptus topali* Jánossy (1972). Late Miocene, Europe. Two spp.

†*Limnoecus* Stirton (1930). Type species †*Limnoecus tricuspis* Stirton, 1930. Miocene to Middle Pliocene, western United States, and Austria (Europe). One sp. See Rabeder (1970).

†*Lunanosorex* Jin and Kawamura, 1996. Type species †*Lunanosorex lii* Jin and Kawamura, 1996. Pliocene of China. One sp. See Jin et al. (2007).

†*Macdonaldius* Kretzoi (2000: 208) (syn. †*Stirtonisorex* Hutterer (2003)); for †*Stirtonia* Gureev, 1979: 372 (type species: †*Limnoecus niobrarensis* Macdonald (1947: 123), Soricidae, Miocene sediments of Niobrara River, Nebraska), not †*Stirtonia* Hershkovitz (1970: 6) (type species: †*Humunculus tatacoensis* Stirton (1951), Primates. Late Miocene of Colombia, Quebrada Tatacoa, upper Río Magdalena Valley); the genus name is masculine in gender. James (1963) who compared the type specimens of both taxa concluded that †*L. niobrarensis* Macdonald, 1947 was a synonym of †*L. tricuspis* Stirton, 1930. A different view was held by Gureev (1979) who realized that the two species were not closely related, and who placed *L. niobrarensis* in a new genus *Stirtonia* Gureev, 1979. From the descriptions of both taxa given by Stirton (1930), Macdonald (1947) and James (1963) we are inclined to concur with Gureev (1979). However, the name proposed by him in honor of the North American palaeontologist R.A. Stirton is not available but preoccupied by †*Stirtonia* Hershkovitz, 1970, a genus of fossil primate.

†*Macroneomys* Fejfar, 1966. Type species †*Macroneomys brachygnathus* Fejfar, 1966. Pliocene and Pleistocene of Europe. One sp. See Rzebik-Kowalska (1991), Maul and Rzebik-Kowalska (1998), and Harrison et al. (2006).

†*Mafia* Reumer, 1984. Type species †*Mafia csarnotensis* Reumer, 1984. Pliocene, Europe. One sp. See Rzebik-Kowalska (1990b).

Megasorex Hibbard (1950). Type species: *Notiosorex gigas* Merriam (1897). Mexico, Recent. One sp. (Woodman et al., 2016).

Nectogale Milne-Edwards, 1870. Type species: *Nectogale elegans* Milne-Edwards, 1870. Asia, Nepal to China. Recent. Two spp. (Fan et al., 2022).

Neomys Kaup, 1829. Type species: *Sorex daubentonii* Erxleben (1777). Pleistocene to Recent. Four extant and two to three fossil spp. Palaearctic Region. Includes *Hydrosorex* Duvernoy, 1835. See Rzebik-Kowalska (1991) and Krystufek et al. (2000).

†*Neomysorex* Rzebik-Kowalska (1981). Type species †*Sorex alpinoides* Kowalski (1956). Pliocene of Europe. One sp.

†*Nesiotites* Bate, 1945. Type species †*Nesiotites hidalgo* Bate, 1945. Pliocene to Pleistocene, Spain, and Italy. Four to five spp. (Pons-Monjo et al., 2012; Rofes et al., 2012; Furió and Pons-Monjo, 2013).

Notiosorex Coues, 1877. Type species *Sorex* (*Notiosorex*) *crawfordi* Coues, 1877. Pliocene to Recent. North America south to Mexico. Four extant + four fossil spp. (Choate, 1969; Lindsay and Jacobs, 1985; Carraway, 2010; Carraway and Timm, 2000).

†*Paenepetenyia* Storch, 1995. Type species †*Paenepetenyia zhudingi* Storch, 1995. Late Miocene of Inner Mongolia, China. One sp.

Parablarinella Bannikova et al., 2019 (Syn. *Pantherina* He et al., 2018; name preoccupied). Type species *Blarinella griselda* Thomas (1912). China, extant. One sp.

†*Paracryptotis* Hibbard, 1950. Type species †*Paracryptotis rex* Hibbard, 1950. Pliocene and Miocene of North America. Two spp.

†*Paranourosorex* Rzebik-Kowalska, 1975. Type species †*Paranourosorex gigas* Rzebik-Kowalska, 1975. Pliocene of Podlesice, Poland. Four spp. Late Miocene to Pleistocene of Eurasia (Rzebik-Kowalska, 1975, Harrison and Rzebik-Kowalska, 1991; Storch and Zazhigin, 1996).

†*Parasoriculus* Qiu and Storch, 2000. Type species †*Parasoriculus tongi* Qiu and Storch, 2000. Miocene Marine stage MN14, Inner Mongolia, China. One sp.

†*Parydrosorex* Wilson (1968). Type species: †*Parydrosorex concisus* Wilson, 1968. Pliocene,

Ogallala Formation, Kansas. One sp. Hibbard and Jammot (1971) considered this a synonym of *Peteniya* Kormos, 1934.

†*Peisorex* Kowalski and Li (1963). Type species †*Peisorex pohaiensis* Kowalski and Li, 1963. Middle Pleistocene of China. One sp.

†*Petenyia* Kormos, 1934. Type species †*Petenyia hungarica* Kormos, 1934. Pliocene and Pleistocene of Europe. Four spp. See Rzebik-Kowalska (1989).

†*Planisorex* Hibbard (1972). Type species †*Sorex dixonensis* Hibbard (1956). Early Pleistocene of North America. One sp.

†*Plioblarinella* Koenigswald and Reumer, 2020: 130. Type species †*Petenyia dubia* Bachmayer and Wilson, 1970. Late Miocene, Marine stage MN10, Austria. One sp.

Pseudosoriculus Abramov, Bannikova, Chernetskaya, Lebedev, and Rozhnov, 2017a. Type species *Soriculus fumidus* Thomas, 1913a. Taiwan, Recent. One sp.

†*Shikamainosorex* Hasegawa (1957). Type species †*Shikamainosorex densicingulata* Hasegawa, 1957. Middle Pleistocene, Japan. 1 sp. (Rzebik-Kowalska and Hasegawa, 1976).

Sorex Linnaeus, 1758. Type species *Sorex araneus* Linnaeus, 1758. Upper Miocene to Recent. Europe, Asia, North America (Qiu et al., 1984; Rzebik-Kowalska, 1991, 1994). Includes *Microsorex* Coues, 1877, *Allopachyura* Kormos, 1934, *Drepanosorex* Kretzoi, 1941, *Petenyiella* Kretzoi (1956) (Storch and Qiu, 1991). Numerous extinct and 86 recent spp.

Soriculus Blyth (1854). Type species *Corsira nigrescens* Gray, 1842. Recent in Asia. One extant and one Pleistocene sp. (Qiu et al., 1984; Hoffmann, 1986; Motokawa and Lin, 2005; Kotlia and Sanwal, 2005).

†*Sulimskia* Reumer, 1984. Type species †*Sorex kretzoi* Sulimski, 1962. Pliocene of Europe and China (Rzebik-Kowalska, 1990b; Qiu and Storch, 2000). Two spp.

†*Tregosorex* Hibbard and Jammot, 1971. Type species †*Tregosorex holmani* Hibbard and Jammot, 1971. Pliocene of North America. One sp.

†*Viretia* Hugueney, Mein, and Maridet, 2012. Type species †*Sorex gracilidens* Viret and Zapfe, 1952. Slovakia, Czech Republic, Austria, France. Middle Miocene. One sp.

†*Zelceina* Sulimski (1962). Type species †*Neomys soriculoides* Sulimski, 1959. Miocene of China to Late Pliocene of Poland. One sp.

Tribe Allocation Undetermined

†*Carposorex* Crochet, 1975. Type species †*Carposorex sylviae* Crochet, 1975. Europe, Lower Miocene. Two spp. (Hugueney et al., 2012).

†*Florinia* Ziegler, 1989. Type species †*Sorex stehlini* Doben-Florin, 1964: 61. Miocene (MN 3–4) of Europe. Two sp. Ziegler (1989) refered the genus to Crocidosoricinae.

†*Lartetium* Ziegler, 1989. Type species †*Sorex prevostianus* Lartet, 1851. Miocene (MN 5–6) of Europe, Anatolia, and North Africa. Four spp. (Van den Hoek Ostende, 2001; Hugueney et al., 2015).

†*Srinitium* Hugueney, 1976. Type species †*Srinitium marteli* Hugueney, 1976. France, Middle to Late Oligocene of Europe. Two spp.

†*Shargainosorex* Zazhigin and Voyta (2018). Type species †*Shargainosorex angustirostris* Zazhigin and Voyta, 2018. Miocene, Shargain Gobi, Mongolia. One sp.

†*Suevosorex* Ziegler (2009b). Type species †*Suevosorex ehrensteinensis* Ziegler, 2009a. Ehrenstein 12, Germany, Early Oligocene, MN12. One sp.

†*Taatsinia* Ziegler, Dahlmann, and Storch, 2007. Type species †*Taatsinia hoeckorum* Ziegler, Dahlmann, and Storch, 2007. Early Oligocene of Mongolia, 33.9–28.4 Ma. 1 sp.

†*Tavoonyia* Ziegler, Dahlmann, and Storch, 2007. Type species †*Tavoonyia altaica* Ziegler, Dahlmann, and Storch, 2007. Late Oligocene of Mongolia. One sp.

†*Turiasorex* Van Dam, Van den Hoek Ostende, and Reumer (2011). Type species †*Turiasorex pierremeini* van Dam, Van den Hoek Ostende, and Reumer, 2011. Spain, 13–10 Ma. One sp.

†*Ulmensia* Ziegler, 1989. Type species †*Ulmensia ehrensteinensis* Ziegler, 1989. Germany, Upper Oligocene. Two spp. Crocidosoricinae according to Ziegler (1989).

Doubtful Taxa and Genera Excluded from the Soricidae

†*Ceutholestes dolosus* Rose and Gingerich (1987) (? Nyctitheriidae). The species has two lower incisors with distinct lobes.

†*Ernosorex* Wang and Li, 1990. Type and only species: †*Ernosorex jilinensis* Wang and Li, 1990. China, Jilin, Eocene. This interesting fossil belongs to the Changlelestidae, a possible sister taxon of Soricidae (Ziegler, 2009b).

†*Siwalikosorex* Sahni and Khare, 1976. Type and only species: †*Siwalikosorex prasadi* Sahni and Khare, 1976. Pakistan, Siwalik sediments. The single tooth figured does not represent a member of the Soricidae, although the authors claim that it is "closely allied to †*Blarina adamsi*, †*Notiosorex jacksoni*, †*Sorex rexroadensis*, from the Upper Pliocene of Kansas" (Sahni and Khare, 1976: 115). We compared the drawing of the tooth with various Asian insectivores (*Hylomys*, *Podogymnura*) and small carnivores, but none had a similar third lower molar. Carroll (1988) included the genus in Soricidae, but we do not agree with this classification.

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APPENDIX 1

Specimens Examined and Figured

The following specimens are figured in this paper. They also were used for scoring morphological characters listed in table 4. In addition, three specimens were used for scoring morphological characters but are not shown in figures; these are listed below.

Anourosorex squamipes FMNH 76252 (fig. 18AA), 45812 (fig. 17A); *Blarina brevicauda* FMNH 20314 (fig. 18Z); *Blarinella quadraticauda* FMNH 37030 (fig. 18Y); *Chimarrogale himalayica* FMNH 389971 (fig. 18W); *Chodsigoa smithii* FMNH 39614 (fig. 18T), 33284; *Congosorex philippsorum* FMNH 177683 (fig. 18C); *Congosorex verheyeni* FMNH 227536 (fig. 18B); *Crocidura leucodon* FMNH 66217 (fig. 18N); *Crossogale phaeura* FMNH 49270; *Cryptotis parvus* FMNH 134396 (fig. 18X); *Diplomesodon pulchellum* ZFMK 1999.0911 (fig. 18M); †*Domnina gradata* PM FMNH P15320 (fig. 18A), Oligocene, Brule Fm.; *Episoriculus caudatus* FMNH 94145 (fig. 18Q); *Feroculus feroculus* FMNH 99453 (fig. 16B, 18G); *Megasorex gigas* KU 98879; *Myosorex blarina* FMNH 144209 (fig. 18E); *Nagasorex albidens* FMNH 76197 (figs. 8–13, 18F); *Neomys fodiens* FMNH 66264 (fig. 18S); *Nectogale sikhimensis* FMNH 114165 (fig. 18R); *Palawanosorex muscorum* FMNH 195236 (fig. 18P); *Paracrocidura maxima* FMNH 157411 (fig. 16D, 18I), 26245; *Ruwenzorisorex suncoides* FMNH 148268 (fig. 16C, 18H), 148939; *Scutisorex somereni* FMNH 43860 (fig. 18K), 160180 (fig. 17C); *Solisorex pearsoni* FMNH 108990 (fig. 16A, 18O); *Sorex araneus* FMNH 63839 (fig. 18V); *Soriculus nigrescens* FMNH 114162 (fig. 18U); *Suncus murinus* FMNH 56391 (fig. 18L); *Surdisorex polulus* FMNH 43846 (fig. 7, 18D); *Sylvisorex lunaris* FMNH 26266; *Sylvisorex morio* FMNH 42622 (fig. 17A, 18J).

Specimens examined for morphological characters but not used in figures: *Notiosorex crawfordi* KU 75184; *Parablarinella griselda* AMNH 60449; *Pseudosoriculus fumidus* USNM 332803, 332804, 332805, 332808, 332809, 332810, 332811, 332812.

APPENDIX 2

Notes on the Type Locality and its Habitat

To the best of our knowledge, “Takubama,” the locality name that appears on the specimen label (fig. 8), appears in systematic literature only with reference to the Koelz collection, beginning with Koelz (1954). All mammal specimens from the Koelz collection are listed in the catalogs of the FMNH and UMMZ as “Takubama,” without variant spellings. Neither Koelz (1954) nor other publications by Koelz mentioned the location of this town, beyond stating that it lies in Nagaland. When we began our search for the town on maps, our only clue was the latitude and longitude given by Moore and Tate (1965) in their gazetteer of localities for squirrels; they listed it as 25°50′N, 94°28′E, without comment.

Examination of maps (including the relevant Operational Navigation Chart; Defense Mapping Agency, St. Louis, revised 1978) and gazetteers (including the Board of Geographic Names) failed to produce any evidence of a place called Takubama in Nagaland or adjacent states, with no place name at the latitude and longitude given by Moore and Tate (1965) that resembled "Takubama." We conclude that the coordinates given by Moore and Tate (1965) are not correct.

In the course of examining specimens collected by Koelz and his collaborator Rupchand, we noted that the spelling "Jakubama" was common on original specimen labels, and a few were labelled "Jakuhama" (the original handwritten labels remain on the specimens; the handwriting often is not clear; see fig. 8). We then encountered a map in Hartwig (1979) that showed a village called "Jakhama" south of Kohima, along the Manipur Road at 25°35′N, 94°8′E. With the assistance of J. Fooden, we next examined the published records of the 1971 Census of India. This census showed no town or village in Nagaland called "Takubama," but listed "Jakhama" as the principal village of an administrative division in the Kohima district, at the same location as the town shown by Hartwig (1979). Finally, we examined topographic maps from the U.S. Army Map Service (series U502, scale 1: 250,000) for India, which shows a town called "Zhakhama" at the same place as "Jakhama." Given (1) our inability to find a town with similar spelling elsewhere in Nagaland and (2) the likely accessibility of the village along the Manipur Road to Koelz and Rupchand, we conclude that the place shown in figure 15 at 25°35′N, 95°8′E is very likely to be the locality visited by Koelz and Rupchand, and that the preferred spelling is "Jakhama."

Topographic maps delineated in feet (fig. 15) show the elevation at Jakhama as about 5450 ft (= 1650 m), on the slope of a steep incline that leads up to Mt. Japvo, the highest peak of which lies 7 km west of Jakhama, and down to the upper reaches of the Zulla River. At 9890 ft (= 2995 m), Mt. Japvo is the highest mountain in Nagaland that is not along the crest of the ridge that follows the Burmese border (fig. 15). It is clear from Koelz (1954; see also Sinopoli, 2013) that many specimens were purchased from local people, and that the localities on specimen labels referred to the village where they were based. We conclude that the holotype of *Nagasorex albidens* could have come from any elevation as low as about 1200 m to as high as nearly 3000 m, all of which lie within 7 km of Jakhama, but probably from 1500 m to 2000 m, near the village of Jakhama.

Based on the description of vegetation given above, the predominant natural vegetation in the vicinity of Jakhama should be montane wet temperate forest, grading into tropical wet evergreen forest below about 1500 m and into subalpine forest above 2500 m. Heavy human disturbance, especially burning, would promote development of subtropical pine forest, as well as a wide range of second growth scrub and nonnative grasses.