

Reprinted from:

Evolution of Shrews

Edited by

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MAMMAL RESEARCH INSTITUTE
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Białowieża
1998

A Classification of the Fossil and Recent Shrews

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Introduction

Shrews have attracted little taxonomic attention for a long time. Things seemed so easy: there are red-toothed shrews (subfamily Soricinae) and there are white-toothed shrews (subfamily Crocidurinae). Moreover, shrews were considered small and primitive mammals, their dentitions all look very similar and they certainly do not show as much evolutionary splendour as rodents do. Reason enough not to pay too much attention to them. As a consequence, taxonomically interested soricidologists have never been many. Shrew systematics has typically been a domain of paleontologists for a long time. But at the same time most paleontologists often displayed the habit of identifying shrew remains in their samples merely as "soricid indet.", or the like. This habit, too, did not stimulate shrew taxonomy.

One of the first published classifications of shrews was that by Simpson (1945). It is shown in Table 1.1. Friant (1947) followed shortly after this, unfortunately only on taxa from the European Quaternary and Recent times. Both were paleontologists.

If one date stands out as a milestone in shrew research, it is the year 1967. In that year, the American paleontologist C.A. Repenning published his *Subfamilies and Genera of the Soricidae*, summarizing the contemporary knowledge on the extinct and living shrews (Table 1.2). Even though some parts of the systematic framework proposed by Repenning (1967) are now considered out-of-date, his synthesis laid the foundation for much of the work reviewed in the present volume, and it triggered an increase in number of publications on fossil shrews and shrew taxonomy.

A few years later, in 1971, the Russian scientist A.A. Gureev published a monograph on shrews. It was issued in Russian and has not had much influence. The lack of influence is not so much caused by the Cyrillic

Table 1.1 Simpson's (1945) classification of shrews. The taxa are arranged in alphabetical order. Authorship of the names of the taxa is as stated in Simpson (1945)

Family Soricidae Gray, 1821
Subfamily Crocidurinae Milne Edwards, 1868–1874, white-toothed shrews
Genus <i>Anourosorex</i> Milne Edwards, 1870
Genus <i>Chimarrigale</i> Anderson, 1877 ¹
Genus <i>Crocidura</i> Wagler, 1832
Genus <i>Diplomesodon</i> Brandt, 1853
Genus <i>Feroculus</i> Kelaart, 1852
Genus <i>Limnoecus</i> Stirton, 1930
Genus <i>Myosorex</i> Gray, 1838
Genus <i>Nectogale</i> Milne Edwards, 1870 ¹
Genus <i>Praesorex</i> Thomas, 1913
Genus <i>Solisorex</i> Thomas, 1924
Genus <i>Suncus</i> Ehrenberg, 1832
Genus <i>Surdisorex</i> Thomas, 1906
Genus <i>Sylvisorex</i> Thomas, 1904
Subfamily Scutisoricinae Allen, 1917, armoured shrews
Genus <i>Scutisorex</i> Thomas, 1913
Subfamily Soricinae Murray, 1866, red-toothed shrews
Genus <i>Blarina</i> Gray, 1838
Genus <i>Blarinella</i> Thomas, 1911
Genus <i>Cryptotis</i> Pomel, 1848
Genus <i>Domnina</i> Cope, 1873
Genus <i>Heterosorex</i> Gaillard, 1915
Genus <i>Microsorex</i> Baird, 1877
Genus <i>Mystipterus</i> Hall, 1930 ²
Genus <i>Necrosorex</i> Filhol, 1889
Genus <i>Neomys</i> Kaup, 1829
Genus <i>Notiosorex</i> Baird, 1877
Genus <i>Saturninia</i> Stehlin, 1940 ³
Genus <i>Sorex</i> Linnaeus, 1758
Genus <i>Soriculus</i> Blyth, 1855

¹ Its teeth are pigmented, in fact, though the pigment is very scarce and usually indiscernible without ultraviolet light (Repenning 1967).

² It is either a bat or a talpid, not a shrew (Repenning 1967).

³ It is a nyctitheriid, not a shrew (Sigé 1976).

Table 1.2 Repenning's (1967) classification of shrews. The taxa are arranged in alphabetical order. Authorship of the names of the taxa is as stated in Repenning (1967)

Family Soricidae

Subfamily Allosoricinae Fejfar, 1966

Genus *Allosorex* Fejfar, 1966

"*Sorex*" *gracilidens* Viret and Zapfe, 1951

Subfamily Crocidurinae Milne Edwards, 1868–1874

Genus *Crocidura* Wagler, 1832

Genus *Diplomesodon* Brandt, 1853

Genus *Feroculus* Kelaart, 1852

Genus *Miosorex* Kretzoi, 1959

Genus *Myosorex* Gray, 1838

Genus *Paracrocidura* Balsac, 1956

Genus *Praesorex* Thomas, 1913

Genus *Scutisorex* Thomas, 1913

Genus *Solisorex* Thomas, 1924

"*Sorex*" *dehmi* Viret and Zapfe, 1951

"*Sorex*" *pusilliformis* Doben-Florin, 1964

Genus *Soricella* Doben-Florin, 1964

Genus *Suncus* Ehrenberg, 1832

Genus *Surdisorex* Thomas, 1906

Genus *Sylvisorex* Thomas, 1905

Incertae sedis: "*Limnoecus*" *micromorphus* Doben-Florin, 1964

Incertae sedis: "*Sorex*" *collongensis* Mein, 1958

Subfamily Heterosoricinae Viret and Zapfe, 1951

Genus *Domnina* Cope, 1873

Genus *Ingentisorex* Hutchison, 1966

Genus *Paradomnina* Hutchison, 1966

Genus *Trimylus* Roger, 1885

Subfamily Limnoecinae Repenning, 1967

Genus *Angustidens* Repenning, 1967

Genus *Limnoecus* Stirton, 1930

Subfamily Soricinae Fischer von Waldheim, 1817

Tribe Blarinini Stirton, 1930

Genus *Adeloblarina* Repenning, 1967

Genus *Blarina* Gray, 1838

Genus *Blarinoides* Sulimski, 1959

Table 1.2 continued

Genus <i>Cryptotis</i> Pomel, 1848
Genus <i>Paracryptotis</i> Hibbard, 1950
Genus <i>Shikamainosorex</i> Hasegawa, 1957
" <i>Sorex</i> " <i>dehneli</i> Kowalski, 1956
<i>Incertae sedis</i> : genus <i>Peisorex</i> Kowalski and Li, 1963
<i>Incertae sedis</i> : <i>Sorex kretzoi</i> Sulimski, 1962
Tribe Neomyini Repenning, 1967
Genus <i>Amblycoptus</i> Kormos, 1926
Genus <i>Anourosorex</i> Milne-Edwards, 1870
Genus <i>Beremendia</i> Kormos, 1934
Genus <i>Chimarrogale</i> Anderson, 1877
Genus <i>Chodsigoa</i> Kastschenko, 1907
Genus <i>Episoriculus</i> Ellerman and Morrison-Scott, 1951
Genus <i>Hesperosorex</i> Hibbard, 1957
Genus <i>Megasorex</i> Hibbard, 1950
Genus <i>Nectogale</i> Milne-Edwards, 1870
Genus <i>Neomys</i> Kaup, 1829
Genus <i>Nesiotites</i> Bate, 1945
Genus <i>Notiosorex</i> Baird, 1877
Genus <i>Petenyiella</i> Kretzoi, 1956
Genus <i>Soriculus</i> Blyth, 1854
<i>Incertae sedis</i> : genus <i>Deinsdorfia</i> Heller, 1963
Tribe Soricini Fischer von Waldheim, 1817
Genus <i>Alluvisorex</i> Hutchison, 1966
Genus <i>Antesorex</i> Repenning, 1967
Genus <i>Blarinella</i> Thomas, 1911
Genus <i>Crocidosorex</i> Lavocat, 1951
Genus <i>Drepanosorex</i> Kretzoi, 1941
Genus <i>Microsorex</i> Baird, 1877
Genus <i>Petenya</i> Kormos, 1934
Genus <i>Sorex</i> Linnaeus, 1758
<i>Incertae sedis</i> : <i>Sorex hibbardi</i> Sulimski, 1962
<i>Incertae sedis</i> : <i>Sorex stehlini</i> Doben-Florin, 1964
<i>Incertae sedis</i> : genus <i>Zelceina</i> Sulimski, 1962
<i>Soricidae incertae sedis</i>
Genus <i>Podihik</i> Deraniyagala, 1958

lettering of the book, but it is mostly due to the systematic jumble that was produced (Table 1.3). Nevertheless, if shrew classifications are dealt with, seen from a historical perspective, it cannot be overlooked.

Table 1.3 Gureev's (1971) classification of shrews. The taxa are arranged in alphabetical order. Authorship of the names of the taxa is as stated in Gureev (1971)

Family Soricidae Gray, 1821

Subfamily Saturniinae Gureev, 1971

Genus *Saturninia* Stehlin, 1940¹

Subfamily Soricinae Murray, 1866

Tribe Anourosoricini Stirton, 1930

Genus *Amblyoptus* Kormos, 1926

Genus *Anourosorex* Milne-Edwards, 1870

Genus *Anourosoricodon* Topacevski, 1965

Tribe Blarinini Stirton, 1930

Subtribe Allosoricina Gureev, 1971

Genus *Allosorex* Fejfar, 1966

Genus *Deinsdorfia* Heller, 1963

Subtribe Beremendina Gureev, 1971

Genus *Beremendia* Kormos, 1930

Genus *Cryptotis* Pomel, 1848

Genus *Hesperosorex* Hibbard, 1957

Genus *Paracryptotis* Hibbard, 1957

Genus *Peisorex* Kowalski and Li-Chuan-Kuei, 1963

Genus *Petenya* Kormos, 1930

Genus *Petenyiella* Kretzoi, 1956

Genus *Shikamainosorex* Hasegawa, 1957

Subtribe Blarinina Stirton, 1930 *sensu stricto*

Genus *Adeloblarina* Repenning, 1967

Genus *Blarina* Gray, 1838

Genus *Blarinoidea* Sulimski, 1959

Subtribe Nectogalina Gureev, 1971

Genus *Chimarrogale* Anderson, 1877

Genus *Nectogale* Milne-Edwards, 1870

Subtribe Soriculina Kretzoi, 1965

Genus *Macroneomys* Fejfar, 1966

Genus *Neomys* Kaup, 1829

Genus *Notiosorex* Baird, 1877

Subgenus *Chodsigoa* Kastschenko, 1905

Table 1.3 continued

	Subgenus <i>Notiosorex</i> Baird, 1877 <i>sensu stricto</i>
	Genus <i>Podihik</i> Deraniyagala, 1958
	Genus <i>Soriculus</i> Blyth, 1854
	Genus <i>Zelceina</i> Sulimski, 1962
Tribe Crocidurini	Stirton, 1930
	Subtribe Crocidurina Stirton, 1930 <i>sensu stricto</i>
	Genus <i>Crocidura</i> Wagler, 1832
	Genus <i>Diplomesodon</i> Brandt, 1852
	Genus <i>Feroculus</i> Kelaart, 1852
	Genus <i>Limnoecus</i> Stirton, 1930
	Genus <i>Paracrocidura</i> Heim de Balsac, 1956
	Genus <i>Praesorex</i> Thomas, 1913
	Genus <i>Scutisorex</i> Thomas, 1913
	Genus <i>Similisorex</i> Stogov and Savinov, 1965
	Genus <i>Solisorex</i> Thomas, 1924
	Genus <i>Suncus</i> Ehrenberg, 1833
	Genus <i>Sylvisorex</i> Thomas, 1904
	Subtribe Myosoricina Kretzoi, 1965
	Genus <i>Myosorex</i> Gray, 1837
	Genus <i>Surdisorex</i> Thomas, 1906
Tribe Heterosoricini	Gureev, 1971
	Genus <i>Heterosorex</i> Gaillard, 1915
	Genus <i>Ingentisorex</i> Hutchison, 1966
	Genus <i>Pseudotrinytus</i> Gureev, 1971
Tribe Oligosoricini	Gureev, 1971
	Genus <i>Alluvisorex</i> Hutchison, 1966
	Genus <i>Amphisorex</i> Filhol, 1884
	Genus <i>Angustidens</i> Repenning, 1967
	Genus <i>Crocidosorex</i> Lavocat, 1951
	Genus <i>Domnina</i> Cope, 1873
	Genus <i>Miosorex</i> Kretzoi, 1959
	Genus <i>Oligosorex</i> Kretzoi, 1959
	Genus <i>Paradomnina</i> Hutchison, 1966
	Genus <i>Soricella</i> Doben-Florin, 1964
Tribe Soricini	Fischer, 1817
	Genus <i>Blarinella</i> Thomas, 1911
	Genus <i>Microsorex</i> Coues, 1877
	Genus <i>Sorex</i> Linnaeus, 1758

¹ It is a nyctitheriid, not a shrew (Sigé 1976).

Nowadays, as a result of continued research, the evolutionary history of shrews is becoming better known. However, many hiatuses still exist in our knowledge, which are not due to an insufficient fossil record but rather to the fact that so few paleontologists work on shrews. One could speak of an insufficiently studied fossil record. It needs to be noted that no general consensus exists about the shrew classification. The delimitations of the family Soricidae, as well as those of some of its subfamilies and of some tribes of the subfamily Soricinae, are still open to discussion. In the face of these disagreements, it is now impossible to provide a classification that would be unanimously accepted. Nevertheless, it is hoped that a synthesis of the recent results presented below will provoke a further discussion and help in updating the knowledge of shrew systematics.

New Approach to Shrew Classification

The present approach to the classification of shrews (Table 1.4) has been developed in a series of studies (Reumer 1984, 1987, 1992, 1994) that attempted to clarify uncertain identifications and to update the shrew classification according to the growing amount of the published data. Following Reumer (1987), the shrews are subdivided into two families, the Heterosoricidae and the Soricidae, principally based on the structurally different articulation of the mandible. This taxonomic arrangement has been adopted by some workers (e.g., Rzebik-Kowalska, this volume), but some others (e.g., Storch et al., this volume) have not accepted it.

In a recent taxonomic treatment of the living shrews, Hutterer (1993) regarded them, his Soricinae, as a sister group of the heterosoricids (his Heterosoricinae) and subdivided them into the two tribes: Soricini and Crocidurini. Consequently, the extinct subfamilies Crocidosoricinae, Limnoecinae, and Allosoricinae ought to be lowered to the rank of tribes as well. In turn, the soricine tribes as recognized by Repenning (1967) and other authors ought to be given the rank of subtribes. If this procedure were meticulously followed, the outcome would be exactly the same as that proposed in the present classification except that all suprageneric taxa would have a lower rank (Table 1.5). It is then entered a semantic rather than a taxonomic discussion.

Another reason to prefer the two-family concept as adopted here is that it comes closest to Repenning's (1967) influential classification (Table 1.5). Since Repenning's scheme has generally been accepted for the last 30 years, it seems to be less upsetting to adopt the two-family concept rather than the single-family-with-two-subfamilies concept of Hutterer (1993).

A preferred and increasingly utilized means of defining taxa is with reference to common ancestry (de Queiroz and Gauthier 1990; Sundberg

Table 1.4 Present approach to the classification of shrews. Extinct taxa are indicated by “†”

Family Heterosoricidae Viret and Zapfe, 1951 (†)
Genus <i>Dinosorex</i> Engesser, 1972 (†)
Genus <i>Domnina</i> Cope, 1873 (†)
Genus <i>Gobisorex</i> Sulimski, 1970 (†)
Genus <i>Heterosorex</i> Gaillard, 1915 (†)
Genus <i>Ingentisorex</i> Hutchison, 1966 (†)
Genus <i>Mongolosorex</i> Qiu, 1995 (†)
Genus <i>Paradomnina</i> Hutchison, 1966 (†)
Genus <i>Pseudotrinytus</i> Gureev, 1971 (†)
Genus <i>Quercysorex</i> Engesser, 1975 (†)
Genus <i>Wilsonosorex</i> Martin, 1978 (†)
Family Soricidae Fischer, 1817
Subfamily Allosoricinae Fejfar, 1966 (†)
Genus <i>Allosorex</i> Fejfar, 1966 (†)
Genus <i>Paenelimnoecus</i> Baudelot, 1972 (†)
Subfamily Crocidosoricinae Reumer, 1987 (†)
Genus <i>Carposorex</i> Crochet, 1975 (†)
Genus <i>Clapasorex</i> Crochet, 1975 (†)
Genus <i>Crocidosorex</i> Lavocat, 1952 (†)
Genus <i>Florinia</i> Ziegler, 1989 (†)
Genus <i>Lartetium</i> Ziegler, 1989 (†)
“ <i>Limnoecus</i> ” <i>truyolsi</i> Gibert, 1975 (†)
Genus <i>Miosorex</i> Kretzoi, 1959 (†)
“ <i>Oligosorex</i> ” <i>bruijni</i> Gibert, 1975 (†)
“ <i>Sorex</i> ” <i>collongensis</i> Mein, 1958 (†)
“ <i>Sorex</i> ” <i>gracilidens</i> Viret and Zapfe, 1951 (†)
Genus <i>Soricella</i> Doben-Florin, 1964 (†)
Genus <i>Srinitium</i> Hugueney, 1976 (†)
Genus <i>Ulmensia</i> Ziegler, 1989 (†)
Subfamily Crocidurinae Milne-Edwards, 1872
Genus <i>Congosorex</i> Heim de Balsac and Lamotte, 1956
Genus <i>Crocidura</i> Wagler, 1832
Genus <i>Diplomesodon</i> Brandt, 1852
Genus <i>Feroculus</i> Kelaart, 1852
Genus <i>Myosorex</i> Gray, 1838
Genus <i>Paracrocidura</i> Heim de Balsac, 1956
Genus <i>Ruvenzorisorex</i> Hutterer, 1986

Table 1.4 continued

	Genus <i>Scutisorex</i> Thomas, 1913
	Genus <i>Solisorex</i> Thomas, 1924
	Genus <i>Suncus</i> Ehrenberg, 1832
	Genus <i>Surdisorex</i> Thomas, 1906
	Genus <i>Sylvisorex</i> Thomas, 1904
Subfamily	Limnoecinae Repenning, 1967 (†)
	Genus <i>Angustidens</i> Repenning, 1967 (†)
	Genus <i>Limnoecus</i> Stirton, 1930 (†)
Subfamily	Soricinae Fischer, 1817
Tribe	Anourosoricini Anderson, 1879
	Genus <i>Amblyoptus</i> Kormos, 1926 (†)
	Genus <i>Anouroneomys</i> Hutchison and Bown, 1980 (†)
	Genus <i>Anourosorex</i> Milne-Edwards, 1872
	Genus <i>Anourosoricodon</i> Topachevsky, 1966 (†)
	Genus <i>Crusafontina</i> Gibert, 1974 (†)
	Genus <i>Kordosia</i> Mészáros, 1997 (†)
	Genus <i>Paranourosorex</i> Rzebik-Kowalska, 1975 (†)
Tribe	Beremendiini Reumer, 1984 (†)
	Genus <i>Beremendia</i> Kormos, 1934 (†)
	Genus <i>Lunanosorex</i> Jin and Kawamura, 1996 (†)
	Genus <i>Peisorex</i> Kowalski and Li, 1963 (†)
Tribe	Blarinellini (new)
	Genus <i>Alloblarinella</i> Storch, 1995 (†)
	Genus <i>Alluvisorex</i> Hutchison, 1966 (†)
	Genus <i>Anchiblarinella</i> Hibbard and Jammot, 1971 (†)
	Genus <i>Blarinella</i> Thomas, 1911
	Genus <i>Cokia</i> Storch, 1995 (†)
	Genus <i>Hemisorex</i> Baudelot, 1967 (†)
	Genus <i>Paenepetenya</i> Storch, 1995 (†)
	Genus <i>Parydrosorex</i> Wilson, 1968 (†)
	Genus <i>Petenya</i> Kormos, 1934 (†)
Tribe	Blarinini Kretzoi, 1965
	Genus <i>Adeloblarina</i> Repenning, 1967 (†)
	Genus <i>Blarina</i> Gray, 1838
	Genus <i>Blarinoidea</i> Sulimski, 1959 (†)
	Genus <i>Cryptotis</i> Pomel, 1848
	Genus <i>Mafia</i> Reumer, 1984 (†)
	Genus <i>Paracryptotis</i> Hibbard, 1950 (†)

Table 1.4 continued

	Genus <i>Shikamainosorex</i> Hasegawa, 1957 (†)
	Genus <i>Sulimskia</i> Reumer, 1984 (†)
	<i>Incertae sedis</i> : genus <i>Tregosorex</i> Hibbard and Jammot, 1971 (†)
Tribe	Neomyini Matschie, 1909
	Genus <i>Asoriculus</i> Kretzoi, 1959 (†)
	Genus <i>Chimarroale</i> Anderson, 1877
	Genus <i>Macroneomys</i> Fejfar, 1966 (†)
	Genus <i>Nectogale</i> Milne-Edwards, 1870
	Genus <i>Neomys</i> Kaup, 1829
	Genus <i>Neomysorex</i> Rzebik-Kowalska, 1981 (†)
	Genus <i>Nesiotites</i> Bate, 1945 (†)
	Genus <i>Soriculus</i> Blyth, 1854, including among others:
	Subgenus <i>Chodsigoa</i> Kastschenko, 1907
	Subgenus <i>Episoriculus</i> Ellerman and Morrison-Scott, 1951
Tribe	Notiosoricini Reumer, 1984
	Genus <i>Beckiasorex</i> Dalquest, 1972 (†)
	Genus <i>Hesperosorex</i> Hibbard, 1957 (†)
	Genus <i>Megasorex</i> Hibbard, 1950
	Genus <i>Notiosorex</i> Coues, 1877
Tribe	Soricini Fischer, 1817
	Genus <i>Antesorex</i> Repenning, 1967 (†)
	Genus <i>Deinsdorfia</i> Heller, 1963 (†)
	Genus <i>Dimylosorex</i> Rabeder, 1972 (†)
	Genus <i>Planisorex</i> Hibbard, 1972 (†)
	Genus <i>Sorex</i> Linnaeus, 1758, including among others:
	Subgenus <i>Drepanosorex</i> Kretzoi, 1941 (†)
	Subgenus <i>Microsorex</i> Baird, 1877
	Genus <i>Zelceina</i> Sulimski, 1962 (†)

and Pleijel 1994). A convention that is rapidly gaining acceptance seeks to stabilize widely used names by restricting them to genealogical entities bounded by extant taxa. Accordingly, the family name Soricidae is restricted to the most recent common ancestor of the living shrews and all of its descendants. The monophyly of the so-defined Soricidae is supported by the two synapomorphies: the absence of the zygomatic arches and the presence of the pocketed internal temporal fossa. Because the plesiomorphic states of these characters are present in the heterosoricids, that is, the zygomatic arches are present and the internal temporal fossa is missing or very shallow

Table 1.5 Summary of the presently available shrew classifications. Classification A is based on the framework presented by Repenning (1967), in which the Heterosoricidae are a subfamily next to the other subfamilies of shrews. Classification B is based on the suggestions by Hutterer (1993), in which the Heterosoricidae are a subfamily within the Soricidae and a sister taxon of all other shrews. Classification C is a classification preferred by the present author, in which the Heterosoricidae are a sister taxon to the Soricidae

Classification A

Family Soricidae

- Subfamily Allosoricinae
- Subfamily Crocidosoricinae
- Subfamily Crocidurinae
- Subfamily Heterosoricinae
- Subfamily Limnoecinae
- Subfamily Soricinae
- Seven tribes (Neomyini, Soricini, etc.)

Classification B

Family Soricidae

- Subfamily Heterosoricinae
- Subfamily Soricinae
 - Tribe Allosoricini
 - Tribe Crocidosoricini
 - Tribe Crocidurini
 - Tribe Limnoecini
 - Tribe Soricini
- Seven subtribes (Neomyina, Soricina, etc.)

Classification C

Family Heterosoricidae

Family Soricidae

- Subfamily Allosoricinae
 - Subfamily Crocidosoricinae
 - Subfamily Crocidurinae
 - Subfamily Limnoecinae
 - Subfamily Soricinae
 - Seven tribes (Neomyini, Soricini, etc.)
-

but never pocketed, this group must be excluded from the so-defined Soricidae.

Family Heterosoricidae

The representatives of this family are medium-sized to very large insectivorans diagnosed by a combination of the following features (Repenning

1967; Reumer 1987): zygomatic arches of skull present; internal temporal fossa of mandible lacking or very shallow and never pocketed; masseteric fossa of mandible well developed; ventral condyle of mandible offset medially much farther than in the soricids and at an approximately right angle to a vertical axis of the horizontal ramus; mental foramen situated below the middle of M_1 to below the anterior root of M_2 and usually associated with a depressed area on the lateral face of mandible or with a groove running anterodorsad from the foramen to the region of P_4 , or both; small foramen of unknown function present on the medial face of mandible near the ventral margin below M_1 or M_2 ; tooth pigment present; P^4 and M^1 with no emargination of the posterior basal outline and no posterior projection of the hypoconal flange; P_4 with a triangular cusp, little or no posterior sulcus on the cusp, and the transversely broadened or even doubled root in most species; M_1 low-cusped, with a reentrant between the protoconid and hypoconid opened at the level of the cingulum; M_3 with a double-cusped or crescentic talonid when present.

The heterosoricids include the following genera: *Dinosorex*, *Domnina*, *Gobisorex*, *Heterosorex*, *Ingentisorex*, *Mongolosorex*, *Paradomnina*, *Pseudotrimylus*, *Quercysorex*, and *Wilsonosorex*. Following suggestions of Engesser (1975, 1979), who thoroughly revised the family, the genus *Trimylus* Roger, 1885 is suppressed in this listing. In an earlier paper (Reumer 1994), I listed the genus *Gobisorex* among the crocidosoricines. I have recently been able to study the holotype and the paratype of its type species *Gobisorex kingae* Sulimski, 1970, which proved the heterosoricid status of the genus.

Family Soricidae

The members of this family are very small to very large insectivorans, but usually of small size, distinguished by a combination of the following characters (Reumer 1987): zygomatic arches of skull absent (synapomorphy); internal temporal fossa of mandible deeply pocketed (synapomorphy); mandibular condyle separated dorsoventrally; upper and lower anterior dentition reduced and limited to a single large incisor and two to five small antemolars; P^4 molarized; P_4 not molarized.

The soricids consist of the five subfamilies: Allosoricinae, Crocidosoricinae, Crocidurinae, Limnoecinae, and Soricinae.

Subfamily Allosoricinae

The allosoricines are characterized by the following distinctive traits (Reumer 1984): mandibular condyle with a short interarticular area and a triangular upper facet; upper incisor fissident or not; entoconid and entoconid crest vestigial or completely absent, so that the hypolophid is

ended in the entostylid (synapomorphy); metaconid low and close to the protoconid; parolophid long and nearly parallel to the longitudinal axis of the dentary, resembling a carnassial blade, particularly in M_1 .

This subfamily contains the two genera: *Allosorex* and *Paenelimnoecus*. The taxonomic position of *Paenelimnoecus* is a point of scientific disagreement. The inclusion of this genus in the Allosoricinae is followed here after Reumer (1992), but Storch (1995) and Storch et al. (this volume) referred to it as Soricinae *incertae sedis*.

Subfamily Crocidosoricinae

The following features diagnose the crocidosoricines (Reumer 1987): mandibular condyle small, with its articular facets slightly separated; upper incisor never fissident; lower incisor small and cuspluate, with a slightly developed posterior extension of its buccal face or without it; possession of two or, more frequently, three to five lower antemolars; P_4 shaped like a tetrahedron, with a posterior groove or sulcus that may be only weakly defined and a V-shaped wear surface if worn.

The Crocidosoricinae incorporate the genera *Carposorex*, *Clapasorex*, *Crocidosorex*, *Florinia* (including "*Sorex*" *stehlini* Doben-Florin, 1964), *Lartetium* (including "*Sorex*" *dehmi* Viret and Zapfe, 1951), *Miosorex* (including "*Sorex*" *pusilliformis* Doben-Florin, 1964), *Soricella*, *Srinitium*, and *Ulmensia*, as well as "*Limnoecus*" *truyolsi*, "*Oligosorex*" *bruijni*, "*Sorex*" *collongensis*, and "*Sorex*" *gracilidens*.

Subfamily Crocidurinae

The members of this subfamily are characterized by the following features (Repenning 1967): articular facets of the mandibular condyle separated but not widely, articulation surfaces usually united either along the lingual side of the condyle with a lateral interarticular depression or across most of the interarticular surface; mental foramen located below the anterior root of M_1 ; dental formula 1.2–4.1.3 / 1.1–2.1.3; tooth pigment absent; P_4 single- or, in *Surdisorex*, double-rooted, with a triangular cusp and a sulcus down the posterior face of the cusp, and with its buccal cingulum that does not overhang or only slightly overhangs over the root or roots and their alveoli.

Following Hutterer (1993), the crocidurines consist of the 12 genera: *Congosorex*, *Crocidura* (including *Praesorex* Thomas, 1913), *Diplomesodon*, *Feroculus*, *Myosorex*, *Paracrocidura*, *Ruwenzorisorex*, *Scutisorex*, *Solisorex*, *Suncus* (including *Podihik* Deraniyagala, 1958), *Surdisorex*, and *Sylvisorex*. All of them are represented in the living fauna.

This subfamily is in need of revision (Reumer 1987, 1994; Hutterer 1993). Its monophyletic status has recently been questioned by Hutterer (1993). The genus *Myosorex* appeared to be equidistant from the living

crocidurines and soricines in the isozyme studies by Maddalena and Bronner (1992).

Subfamily Limnoecinae

The representatives of this subfamily are distinguished by a combination of the following characters (Repenning 1967): articular facets of the mandibular condyle as in the crocidurines; mental foramen positioned below the trigonid of M_1 ; teeth pigmented heavily in the earliest form but only at tips of cusps in later forms; lower dental formula 1.1?–2.1.3; P_4 single-rooted, with little or no lingual segment or posterolingual ridge of the primitive triangular cusp, with the buccal segment and posterobuccal crest of the primitive triangular cusp, both forming a lingually shifted longitudinal ridge, without the buccal shearing blade, with a little-developed posterolingual basin or without it, and with its buccal cingulum that moderately overhangs over the root and its alveolus (but never as extreme as in most soricines); M_1 with its protoconid and metaconid very close to each other and with a strong entoconid and a low entoconid crest; M_3 lacking the double-cusped talonid in the earliest form and an appreciable talonid basin lost through an emphasis of the metalophid by late Miocene time, becoming very nearly a simple trenchant heel like that in living crocidurines and more trenchant than in late Miocene crocidurines.

The limnoecines were exclusively North American in distribution. They include the two genera: *Angustidens* and *Limnoecus*.

Subfamily Soricinae

A combination of the following distinctive features characterizes the soricines (Repenning 1967): articular facets of the mandibular condyle little separated to extremely separated in most living genera and joined along the lateral side of the condyle rather than along its medial side as in crocidurines and limnoecines, with a medial emargination of the interarticular area; mental foramen in many genera situated farther back than in contemporary crocidurines and limnoecines; dental formula 1.2–5.1.2–3 / 1.1.1.2–3; teeth without pigment or, more frequently, pigmented; P_4 single- or, in *Antesorex*, double-rooted, with no lingual segment of the primitive triangular cusp, with the buccal segment and posterobuccal crest of the primitive triangular cusp retained as the buccal shearing blade (in more advanced forms this blade is continuous with an elevated posterior cingulum which forms an L-shaped crest enclosing the posterolingual basin that has evolved from the posterior sulcus between the crests of the primitive triangular cusp), with a greatly reduced posterolingual crest or without the crest, with its cingulum overhanging the root and the lateral surface of mandible below the postero-

buccal corner of P_4 in most genera more than in contemporary forms of other soricid subfamilies.

The Soricinae are subdivided into the seven tribes: Anourosoricini, Beremendiini, Blarinellini (new), Blarinini, Neomyini, Notiosoricini, and Soricini.

Tribe Anourosoricini — The following features are diagnostic of the Anourosoricini (Reumer 1984): internal temporal fossa narrow and small; interarticular area of the mandibular condyle reduced to a narrow ridge; teeth not pigmented and bulbous (synapomorphies); upper incisor not fissident; M^1 with a well-developed parastyle; M^3 reduced or absent (synapomorphy); lower incisor acuspulate; M_3 reduced or absent (synapomorphy).

The Anourosoricini comprise the seven genera: *Amblycoptus*, *Anouro-neomys*, *Anourosorex*, *Anourosoricodon*, *Crusafontina*, *Kordosia*, and *Paranourosorex*.

Tribe Beremendiini — The representatives of this tribe are distinguished by the possession of the following traits (Reumer 1984): mandibular condyle with a broad interarticular area and an anteriorly placed lower facet; teeth heavily pigmented; upper incisor strongly fissident; lower incisor acuspulate; entoconid crests present.

The Beremendiini include the three genera: *Beremendia*, *Lunanosorex*, and *Peisorex*. The last genus is attributed to this tribe after Storch et al. (this volume).

Tribe Blarinellini (new) — This new tribe, whose type genus is *Blarinella* Thomas, 1911, is diagnosed by a combination of the following characters: horizontal ramus of mandible short and high, making the lower dentition compressed anteroposteriorly and giving the lophs and lophids a compressed W-shaped appearance; mandibular condyle large, with a broad interarticular area; coronoid spicule of mandible well developed; teeth heavily pigmented; upper incisor protruding but not fissident; upper molariform teeth with a reduced posterior emargination, showing a tendency to develop a continuous endoloph; occlusal surface of M^1 nearly square; lower molars with the entoconid close to the metaconid so that the entoconid crest is short and high; M_3 with a reduced talonid.

The nine genera are included in this tribe: *Alloblarinella*, *Alluvisorex*, *Anchiblarinella*, *Blarinella*, *Cokia*, *Hemisorex*, *Paenepetenya*, *Parydrosorex*, and *Petenya*.

Tribe Blarinini — The following distinctive features are characteristic of the Blarinini (Reumer 1984): internal temporal fossa of moderate size; mandibular condyle with its articular facets separated and a broad interarticular area, with the lower facet placed closer to the anterior and the

lingual than in the Soricini; teeth pigmented; upper incisor not fissident; lower molars lacking the entoconid crest (synapomorphy).

The Blarinini comprise the genera *Adeloblarina*, *Blarina*, *Blarinoides*, *Cryptotis*, *Mafia* (including "*Sorex*" *dehneli* Kowalski, 1956), *Paracryptotis*, *Shikamainosorex*, *Sulimskia* (including "*Sorex*" *kretzoi* Sulimski, 1962), and presumably also *Tregosorex*, which is placed within this tribe as *incertae sedis*. Although the original diagnosis of *Tregosorex* contradicts its assignment to the Blarinini ("In M_1 and M_2 the entoconid is joined to the metaconid and not separated by a groove"; Hibbard and Jammot 1971: p. 377), the detailed original illustration of the holotype of its type species *Tregosorex holmani* Hibbard and Jammot, 1971 published by these authors as text-fig. 1 does not show any trace of an entoconid crest. The lingual offset of the lower articular facet also hints at a member of the Blarinini. If the entoconid crests were indeed present in *Tregosorex*, it might belong to the Blarinellini.

Tribe Neomyini — A combination of the following characters diagnoses this tribe (Reumer 1984): mandibular condyle with its articular facets strongly separated, with a narrow interarticular area that is present only at the lateral side, and with the lower facet elongated lingually and offset from the lower sigmoid notch at its buccal side; teeth lightly pigmented; upper incisor fissident; lower incisor never tricuspluate; M_1 and M_2 with entoconid crests.

The following eight genera are attributed to the Neomyini: *Asoriculus*, *Chimarrogale*, *Macroneomys*, *Nectogale*, *Neomys*, *Neomysorex*, *Nesiotites*, and *Soriculus*. Following Hutterer (1993), *Chodsigoa* and *Episoriculus* are regarded as subgenera of the genus *Soriculus*.

Tribe Notiosoricini — The members of this tribe are characterized by the possession of the following features (Reumer 1984): internal temporal fossa narrow; mandibular condyle with its interarticular area broad, and with its upper facet oval or triangular and its lower facet oval and broad and clearly separated from the lower sigmoid notch by a groove due to a medial displacement; teeth pigmented; upper incisor not fissident; M_1 and M_2 with low entoconid crests.

The Notiosoricini are exclusively North American in distribution. They include the four genera: *Beckiasorex*, *Hesperosorex*, *Megasorex*, and *Notiosorex*.

Tribe Soricini — The following characters are diagnostic of this tribe (Reumer 1984): internal temporal fossa large and triangular; mandibular condyle with its articular facets little to moderately separated and with a relatively broad interarticular area; teeth pigmented; upper incisor fissident or not; M_1 and M_2 with entoconid crests.

The Soricini, which are likely polyphyletic in origin, contain the six genera: *Antesorex*, *Deinsdorfia* (including *Sorex hibbardi* Sulimski, 1962), *Dimylosorex*, *Planisorex*, *Sorex*, and *Zelceina*. *Drepanosorex* and *Microsorex* are considered subgenera within the genus *Sorex*.

Acknowledgements

Barbara Rzebik-Kowalska, Gerhard Storch, and Mieczysław Wolsan are thanked for their helpful suggestions that improved the manuscript. Thanks also to Rainer Hutterer, Barbara Rzebik-Kowalska, and Gerhard Storch for discussions about shrew classifications. Mieczysław Wolsan allowed me to study the type material of *Gobisorex kingae* in order to establish its taxonomic status; Adam Nadachowski kindly handed over the material to me during a meeting in France.

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