

Climate and history of European shrews (family Soricidae)

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Abstract. This paper reviews the history, faunal transformations and migrations of Recent and fossil, especially Plio-Pleistocene, shrews (Soricidae) of Europe on the basis of the climatic requirements of Recent taxa and distributions of Recent and fossil forms. It is concluded that Soricidae are more successful and diversified in warm and humid climates and that the climatic cooling which has taken place since the Villanyian resulted in the extinction or decreased ranges of numerous soricids. This impoverishment of the shrew fauna of Europe during the Plio-Pleistocene progressed from the west toward the east.

Key words: Europe, Mammalia, Soricidae, zoogeography, paleoecology.

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I. INTRODUCTION

The extant Soricidae consists of about 300 species in 23 genera. These are found on all major land areas with the exception of the Arctic islands, the Australian zone and South America, although 3 species today occur in the northernmost part of that continent (that is to say the mountains of Columbia and Venezuela).

According to the latest study of REUMER (1994) the family should be divided into five subfamilies. Two of these (Limnoecinae and Allosoricinae) are extinct, while a third, (Crocidosoricinae), previously thought extinct, is proposed to be represented by the 11 extant South African species of the genus *Myosorex* GRAY, 1838. The two final subfamilies, Crocidurinae and Soricinae, have survived to the present and are both rich in genera and species. With the exception of the North American Limnoecinae all subfamilies have representatives in the fossil or Recent fauna of Europe.

There is a clear difference in climatic requirements between the two living subfamilies of shrews. The subfamily Crocidurinae, or white-toothed shrews, contains mainly tropical forms of the Old World. Their distribution is basically restricted to Africa and south-eastern Asia. In Africa, where they show the greatest diversity and where this subfamily probably originated, as well as in India and Ceylon, the Crocidurinae are the only living

shrews. Species of two genera, *Suncus* EHRENBERG, 1832 and *Crocidura* WAGLER, 1832, which have successfully invaded the Palearctic, are not found north of about 53 latitude and many of them are synanthropic.

The second living subfamily, Soricinae, or shrews with pigmented teeth, occurs in Eurasia, North, Central and northern South America. The boundary between the areas occupied by the subfamilies Crocidurinae and Soricinae coincides to a significant degree with the position of the Miocene Tethys and suggests a high degree of endemism of both subfamilies (REPENNING 1967).

As the subfamily Soricinae evolved in the Holarctic region, their recent representatives, especially the species-rich genus *Sorex* LINNAEUS, 1758 are adapted to colder environments than Crocidurinae. For example, the smallest *Sorex* species, *S. minutissimus* ZIMMERMANN, 1780 can inhabit areas where the minimum winter temperatures are as low as -40°C . Soricinae that inhabit southeastern Asia, such as *Soriculus* BLYTH, 1854, *Blarinella* THOMAS, 1911, *Solisorex* THOMAS, 1924, *Anourosorex* MILNE-EDWARDS, 1870 or *Chimarrogale* ANDERSON, 1877 can live at altitudes of 3000 m above sea level, and some of them are restricted to the mountains (NOWAK 1991). Since they live in cool regions, the Recent Soricinae are characterized by higher metabolic levels and higher average body temperature (ca. 3°C) than Crocidurinae. To satisfy their food requirements they have to be active night and day, whereas the Crocidurinae are mostly nocturnal (VOGEL 1980).

Representatives of the two subfamilies also differ in their preferences concerning humidity, where, generally speaking, the Crocidurinae are adapted to more arid conditions than are Soricinae.

It seems, however, that in the Miocene and especially in the Pliocene, when Soricinae were the dominant shrew group in Europe, they were adapted to milder climates and each cooling event resulted in their extinction or in a decrease in their range (REUMER 1989).

In general, shrews are more successful in warmer climates. This is reflected in their history and in their present latitudinal distribution. As concerns their history, it may be noted that in Europe fossil shrew assemblages of high species diversity are found in periods with a warmer palaeoclimate than are assemblages with only a few species. At present six species live in Finland (all are Soricinae adapted to a cold climate), eight in Poland (six Soricinae and two Crocidurinae adapted to a milder environment), ten in Switzerland (six Soricinae and four Crocidurinae) and up to more than a dozen in African countries (all of them thermophilous Crocidurinae).

According to most authors the Soricinae originated in Asia. The oldest shrew known is from the Early Oligocene of Mongolia (REUMER 1994, YANOVSKAYA et al. 1977). Like all primitive Oligocene and Miocene shrews it belonged to the subfamily Crocidosoricinae. REUMER (1989) is of the opinion that representatives of Crocidosoricinae gave rise to all other subfamilies of shrews.

Shrews probably came to Europe at the end of the Early Oligocene, about 33 million years ago. The oldest true shrew known from Europe, *Srinitium marteli* HUGUENEY, 1976, was found in France, in a locality dated to the Middle Oligocene. Not very numerous in the Oligocene, they increase in number during the Early Miocene. A drop in relative

humidity and the following cooling period around the Early-Middle Miocene boundary were probably responsible for a decline in diversity. A second cooling event at the beginning of the Late Miocene and competition from more advanced shrews (subfamilies Allosoricinae and Soricinae), which appeared in the Miocene, were most likely the reason for the almost complete extinction of the small, primitive forms of Crocidossoricinae. They persisted in the Early Pliocene only in some isolated places, for example in Peninsula Gargano in Italy, which in the Tertiary was probably an island (DE GIULI et al. 1987).

II. TRANSFORMATION OF THE SHREW FAUNA IN THE PLIOCENE AND QUATERNARY

In the Early Pliocene of Europe shrews belonging mainly to the subfamily Soricinae become extremely numerous and diversified. This diversity was caused partly by an in-situ radiation, as in the case of some species of *Paenelimnoecus* BAUDELLOT, 1972 or *Blarinella*, which had their ancestors in the Miocene of Europe, and partly by an invasion of newcomers from Asia, for example the genus *Beremendia* KORMOS, 1934. According to most palaeontologists the amelioration of the climate at the beginning of the Pliocene, as well as the availability of empty ecological niches after the extinction of primitive Miocene shrews, could be responsible for this rather unusual diversity (REUMER 1984). For example, the number of species found at the Early Ruscian Polish locality Podlesice reaches 23 (11-12 genera), and at the Late Ruscian Węże 1 and Early Villanyian Rębielice Królewskie 1A sites 15 and 20 (11 genera) respectively (RZEBIK-KOWALSKA 1994). A high number of shrew species was also found in Middle and Late Ruscian localities of Hungary and Slovakia. Fifteen are known at Osztramos 7, twelve at Csarnóta 2 (REUMER 1984) and ten at Ivanovce (FEJFAR 1966). In Western Europe diversity was much lower, however.

At the Ruscian/Villanyian boundary, well documented as an intense cooling episode (REUMER 1985), about half of the shrew taxa (e.g. *Blarinella*, *Zelceina* SULIMSKI, 1962, *Mafia* REUMER, 1984) became very rare in Eastern and extinct in Western Europe. Other genera (e.g. *Paenelimnoecus*, *Sulimskia* REUMER, 1984, *Deinsdorfia* HELLER, 1963) persisted into the Late Pliocene, particularly in Eastern Europe, but they seem to be very rare during that time. In the Late Pliocene (Early Villanyian) of Poland, *Sulimskia* is still present and constitutes about 10% of shrew specimens, whereas in the Pliocene/Pleistocene boundary only about 3% belong to this genus. The same is true for *Deinsdorfia*, which is more abundant in the Ruscian and Early Villanyian (5-14%) than in the Late Villanyian and Pliocene/Pleistocene boundary (3-4%) (RZEBIK-KOWALSKA 1994).

In general, the number of shrew taxa in the Late Villanyian is much lower than in the early part of that period. For example, at the Polish locality Kielniki 3B the number of shrew species was eight (five genera), and in the slightly younger Kadzielnia 1, dated to the Plio/Pleistocene boundary, nine (six genera) (RZEBIK-KOWALSKA 1994). In southwestern Europe diversity was even lower. Plešivec in Slovakia yielded five (FEJFAR & HORÁČEK 1983), Villány 3 in Hungary six (JÁNOSSY 1970) and Mountoussé 5 in France five species (CLOT et al. 1976).

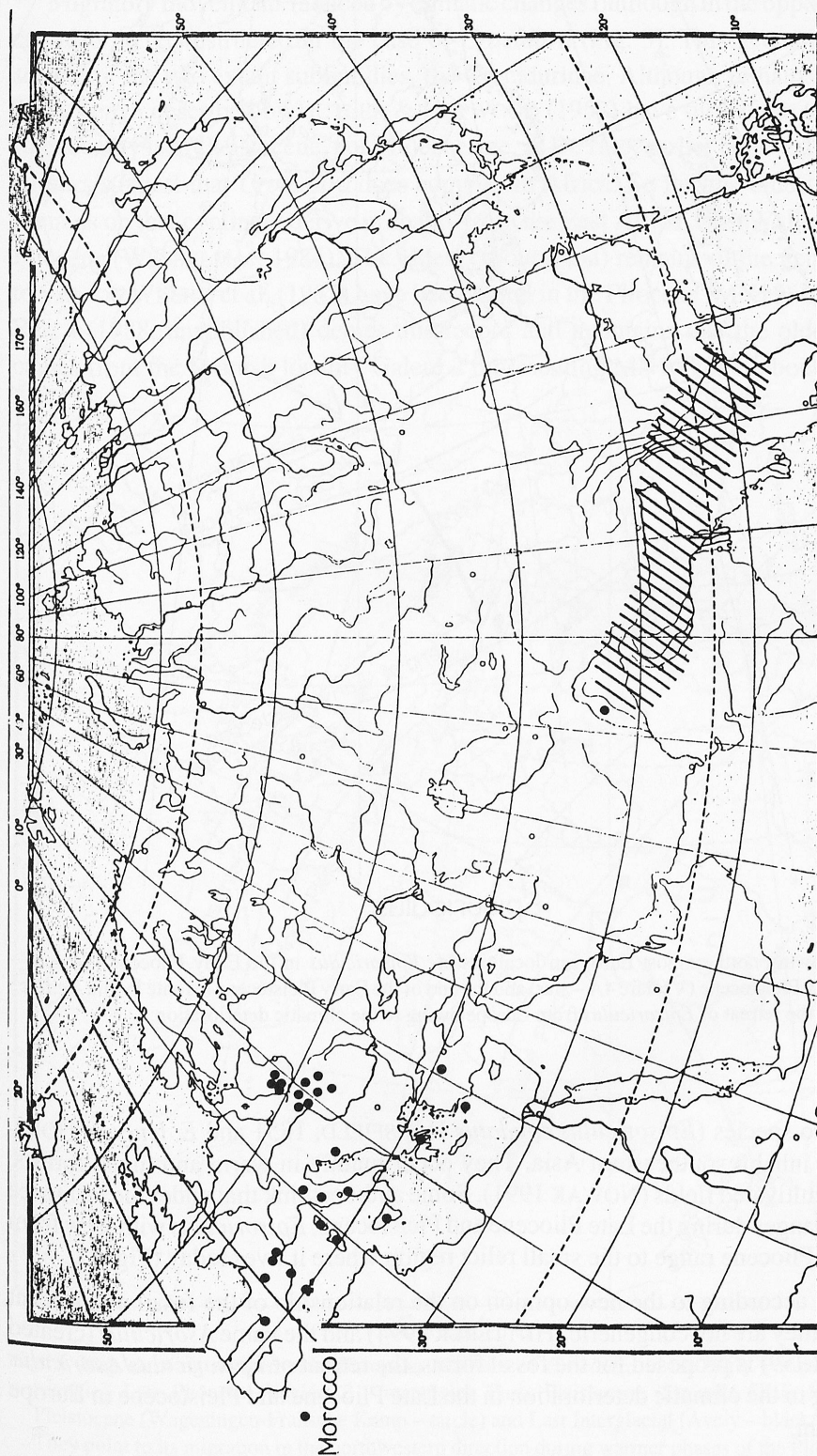
The influence of climatic change on shrew distribution is clearly visible during the Pleistocene. Three examples are particularly well documented.

The first concerns representatives of the genus *Episoriculus* (Soricinae). In the Pliocene and Early Pleistocene, different species of this genus, associated with rather warm and above all moist climates, lived in many European countries. They were found from Spain in the west (CRUSAFONT et al. 1969, JAMMOT 1977) through France (CLOT et al. 1976, JAMMOT 1977), Italy (PASA 1947, BERZI et al. 1967, ESU & KOTSAKIS 1979), Croatia (MALEZ & RABEDER 1984), Poland (RZEBIK-KOWALSKA 1981), Austria (MAIS & RABEDER 1977a), former Czechoslovakia (FEJFAR 1966, FEJFAR & HORÁČEK 1983), Hungary (REUMER 1984), Bulgaria (TERZEA & JURCSÁK 1969), Greece (BRUIJN et al. 1970, VAN DE WEERD et al. 1982, REUMER et al., 1985) to Turkey in the east (SEN 1977, ENGESSER 1980) (Fig. 1).

Climatic conditions favorable to this genus probably existed farther east and south as well, since KOTLIA (1991) has recently described *Episoriculus* ELLERMAN and MORRISON-SCOTT, 1951 from the Late Pliocene of northwestern India (Karewas, Kashmir) and I described a new species from Morocco, at a locality (Irhoud-Ocre) dated to the Pliocene/Pleistocene boundary (RZEBIK-KOWALSKA 1988) (Fig. 1). This is the first and so far only record of Soricinae in Africa. As mentioned above, shrews with pigmented teeth do not occur on this continent today, and their fossil remains have not previously been found in Africa. They probably reached Morocco from Eastern Europe along the southern coast of the Mediterranean Sea, as at that time direct migration from Spain was hardly possible. How long this form persisted in North Africa and what its range was is not clear.

Episoriculus was thus very common and wide-spread in the Early Ruscinian (in the Polish locality Podlesice it constituted 28%, and in the Hungarian sites, Osztramos 1 and Osztramos 9, 17 and 48 % of the total number of shrew specimens respectively). Later, probably due to climatic deterioration, it withdrew southwards on the European continent. From the Late Ruscinian onwards, it becomes very rare north of the Carpathian Basin. In Polish Late Ruscinian and Villanyian localities (Weże 1, Rębielice Królewskie 1A, 2, Kielniki 3B) it constitutes only about 0.2 to 4 % of the shrew fauna, whereas on the southern side of Carpathians, in Hungary, there were still localities, such as Csarnóta 2, where about 38 % of shrew remains belong to *Episoriculus* (REUMER 1984, RZEBIK-KOWALSKA 1994). After the Pliocene the genus disappeared from Poland, but was still present in the Early Pleistocene of Slovakia (Včeláre 4A/5; FEJFAR & HORÁČEK 1983) and Romania (Betfia X; TERZEA & JURCSÁK 1969). Later it survived only in southern Europe. At the end of the Early Pleistocene (? Middle Biharian) it was present in Italy (Cava Sud, Monte Peglia; PASA 1947, VAN DER MEULEN 1973) and in Croatia (Podumci 1; MALEZ & RABEDER 1984) (Fig. 2).

According to some authors (REUMER 1984) very close relatives or direct descendants of *Episoriculus* belonging to the genus *Nesiotites* BATE, 1944 were living from the Late Pliocene to the Holocene on Corsica, Sardinia, Sicily (pers. comm., M. SARÀ) and the Balearic Islands. According to the author of the present paper the dental morphology of *Nesiotites* seems to be much closer to that of *Neomys* KAUP, 1829 than *Episoriculus* (RZEBIK-KOWALSKA 1988).



Episoriculus and Nesiotites

Fig. 1. Map showing the recent (hatched) and Pliocene to Holocene (circles) distribution of *Episoriculus* and *Nesiotites*.

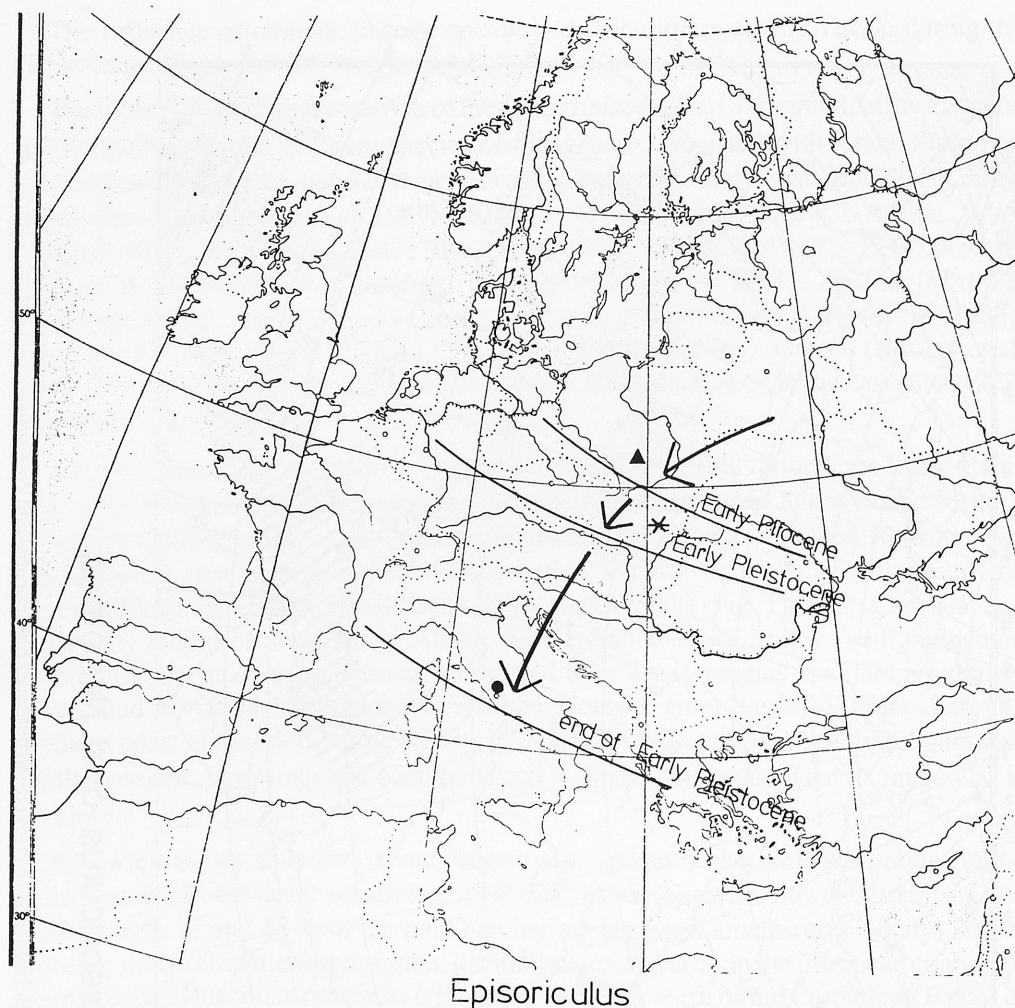


Fig. 2. Map showing northernmost European localities of *Episoriculus* in the Early Pliocene (Weże 1 – triangle), Early Pleistocene (Včeláre 4A – star) and the end of the Early Pleistocene (Monte Peglia – circle). They point to the retreat of *Episoriculus* from Europe owing to the climatic deterioration.

Today, two species (*Episoriculus caudatus* HORSFIELD, 1851 and *E. leucops* HORSFIELD, 1855) inhabit southeastern Asia. They occur mainly in warm and moist forests, thickets and cultivated fields (NOWAK 1991). Some authors think that under the influence of climatic changes during the Late Pliocene and Pleistocene, *Episoriculus* withdrew from its enormous Pliocene range to the small relict region where it lives today (Fig. 1).

Although, according to the new opinion on the relationship of the fossil and Recent *Episoriculus* they are not congeneric (HUTTERER 1994) and the name *Asoriculus* (created by KRETZOI 1959) is proposed for the fossil forms, the retreat of *Episoriculus*/*Asoriculus* shrews owing to the climatic deterioration in the Late Pliocene and Pleistocene in Europe is quite evident.

Migratory movements induced by climatic changes (although in the opposite direction) can also be reconstructed in the case of *Crocidura* (Fig. 3). This genus belongs to the second of the two extant subfamilies, the Crocidurinae. Although remains of *Crocidura* from Kenya described by BUTLER & HOPWOOD (1957) have turned out to be misdated (the locality is of Pleistocene, not Miocene age, as BUTLER earlier believed [1985]) many authors suggest that *Crocidura* does come from Africa. So far, the oldest (about 3 ma) remains on that continent derive probably from the East Africa, Omo Valley, dated to the Pliocene (WESSELMAN 1984). The oldest (about 4 ma) remains of the genus, according to VAN DE WEERD et al. (1982) have been found in the Pliocene (MN15) on Rhodos, but ROCA (1988, unpublished) denies this record and maintains that the oldest *Crocidura* comes from the Spanish locality Galere 2 representing MN16 zone (about 3 ma). From

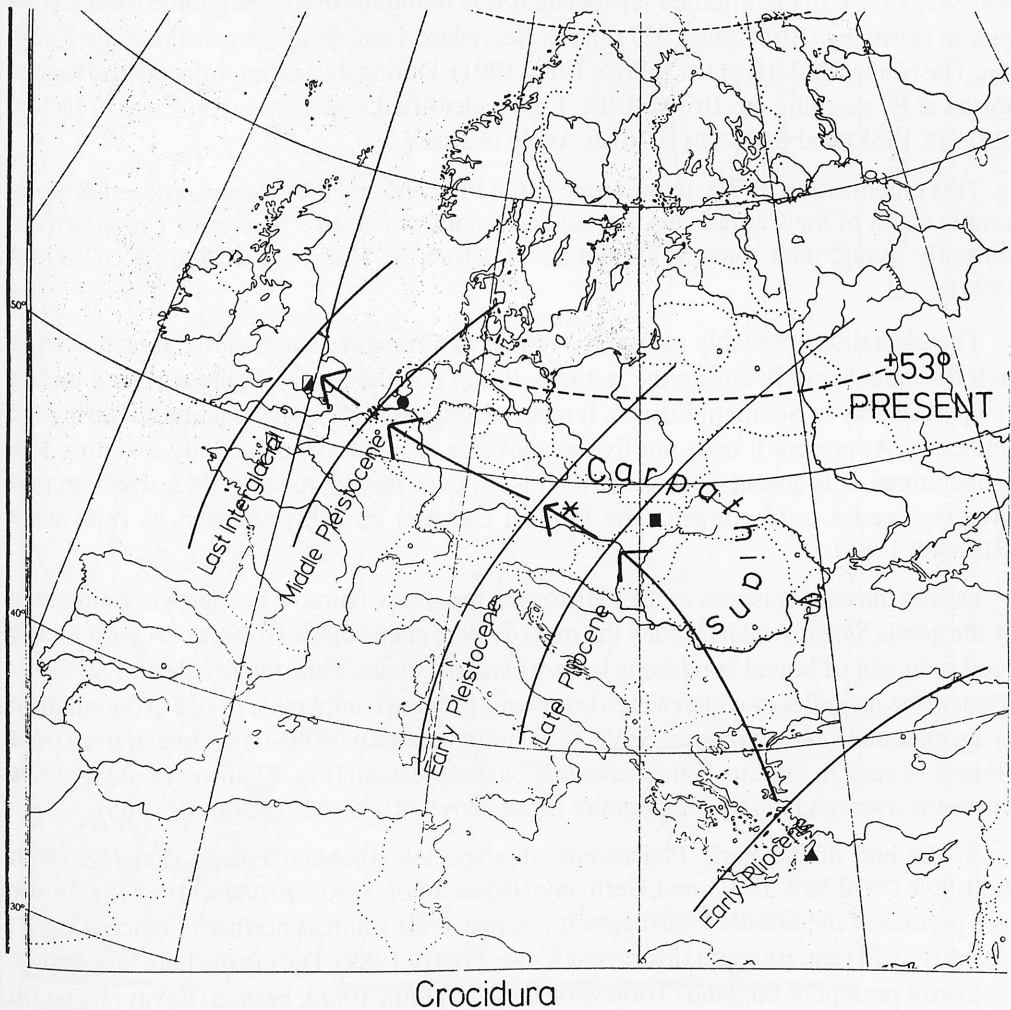


Fig. 3. Map showing northernmost European localities of *Crocidura* in the Early Pliocene (Apolakkia – triangle), Late Pliocene (Včeláre 3 – rectangle), Early Pleistocene (Stránská Skála 1 – star), Middle Pleistocene (Wageningen-Fransche Kamp – circle) and Last Interglacial (Aveluy – black/white rectangle). They point to its migration in the northwestern direction during warmer phases of the Plio-Pleistocene.

MN16 zone in Europe, however, *Crocidura* is also known at Deutsch-Altenburg 9 in Austria (MAIS, RABEDER 1977b) and at Tourkobounia in Greece (REUMER, DOUKAS 1985). ROCA thinks, that two invasions of *Crocidura* into Europe probably occurred, one from the east, and one across Spain.

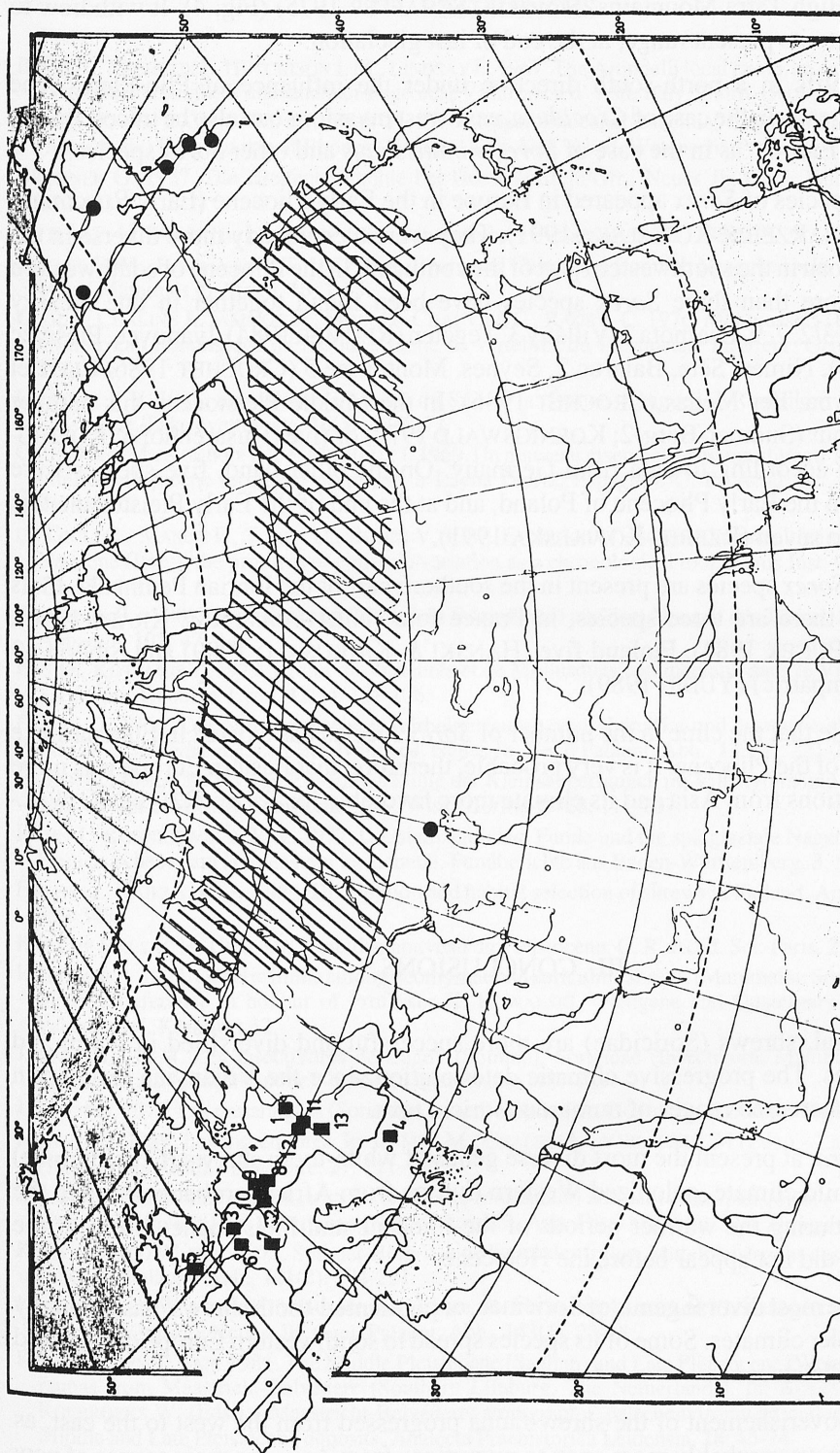
According to present records, *Crocidura*, a good indicator of mild climates, expanded northwards during warmer phases of the Plio-Pleistocene (Fig. 3). In the Villanyan *Crocidura* reached the Carpathian Basin, where it is known as *Crocidura kornfeldi* KORMOS, 1934 from the Hungarian localities Osztramos 3/2 and Villány 3 (MN17) (REUMER 1984) as well as from Včeláre 3 in Slovakia (MN17) (FEJFAR & HORÁČEK 1983). In the Early Pleistocene (Early Biharian) it is still present in Spain, at Orce 3 (ROCA unpublished), as well as at Soave in North Italy (*C. zorzii* PASA, 1947) and at the end of the Early Pleistocene (Late Biharian) at Stránská Skála I in Czech Republic (RZEBIK-KOWALSKA 1972). In the Middle Pleistocene it was found in Breitenberghöhle (near Erlangen) in Germany (BRUNNER 1957) and in Belvédere 4 and Wageningen-Fransche Kamp II in The Netherlands (KOLFSCHOTEN 1985, 1991). During the last interglacial it advanced northwards, reaching the British Isles. I have identified it at Tornewton Cave in Devon (RZEBIK 1968) and STUART (1976) at Avely in Essex.

This colonization of Western Europe in the Pliocene and Pleistocene proceeded along a route south of the Carpathians, because in Poland where two species of *Crocidura* are currently living, their remains are unknown before the Holocene (RZEBIK-KOWALSKA 1994).

The glaciations probably caused the retreat of *Crocidura* southwards. It is, however, well documented only during the last one. Relict populations probably survived during that period only in Southern Europe. It repopulated middle European latitudes during the Holocene. At present it does not live at above ca. 53 latitude, apparently avoiding low temperatures. It is absent from the British Isles, even though these in their southern part have regained a mild climate. The English Channel probably blocked its reinvasion (REUMER 1984).

During the cold episodes of the Pleistocene the shrew fauna of Europe was dominated by the genus *Sorex*, which is today the most diverse genus in the Holarctic. A particularly good indicator of boreal conditions is *Sorex minutissimus*. This, the smallest of all *Sorex* species (the juveniles of which weigh less than 2 g, being comparable in size to the smallest living mammal *Suncus etruscus* SAVI, 1822) is associated with the taiga zone. It lives from Finland to eastern Siberia, Kamchatka and Sakhalin Island (Fig. 4), in very cold regions, where the average January temperature is not above -10°C (MEZHHERIN 1965).

At the end of the Early Pleistocene, this species inhabited Poland (Kozi Grzbiet; RZEBIK-KOWALSKA 1991) and Germany (Husarenhof 4; KOENIGSWALD 1973). In the cold periods of the Middle Pleistocene it reached as far south as northern France (Cagny; JAMMOT 1974) and Bulgaria (Moravitsa Cave; POPOV 1989). During the Late Pleistocene it was still present in England (Tornewton Cave; RZEBIK 1968), France (Bavay; HEIM DE BALSAC 1940, La Baume de Gigny; JAMMOT 1989), Germany (Breitenberghöhle, Gönnerdorf, Kleine Scheuer; BRUNNER 1957, MALEC 1978, HAHN et al., 1977) as well as Poland (Mamutowa and Nietoperzowa Caves; RZEBIK-KOWALSKA 1991) and in the



Sorex minutissimus

Fig. 4. Map showing the recent (hatched and circles) and Pleistocene – Holocene (rectangles) distribution of *Sorex minutissimus*. 1 – Kozi Grzbiet, 2 – Husarenhof 4 (End of Early Pleistocene), 3 – Cagny, 4 – Moravitsa (Middle Pleistocene), 5 – Tormewton Cave, 6 – Bovay, 7 – La Baume de Gigny, 8 – Breitenberghöhle, 9 – Grönerdorf, 10 – Kleine Scheuer, 11 – Nietopierzowa Cave, 12 – Mamutowa Cave (Late Pleistocene), 13 – High Tatra (Holocene).

Holocene in High Tatra Mountains, Slovakia (SCHAEFER 1975) (Fig. 4). It withdrew to the northeast, to its present range, at the end of last glaciation.

Besides shifts in a north-south direction under the influence of Plio-Pleistocene climatic changes as in the case of *Crocidura*, east-west invasions can also be traced among the shrews of Europe, as in the case of *Sorex minutissimus* and other *Sorex* species.

The first species of *Sorex* appeared in Europe in the Early Pliocene (Early Ruscinian) (REUMER 1984, RZEBIK-KOWALSKA 1991). They were then already more diverse in the northeastern than in the southwestern part of the continent. In the Pliocene of southwestern Europe no more than three *Sorex* species have been found together in one locality (Osztramos 1, 3/2, 7, 9, Csarnóta 2, Villány 3, Tegelen (REUMER 1984), Ivanovce, Plešivec (FEJFAR 1966), Nîmes, Sète, Balaruc 2, Seynes, Montoussé 5 (CROCHET 1986, CLOT et al. 1976), Layna, Iles Medas (CROCHET 1986). In the Middle Pleistocene this number increased to four (Sudmer-Berg-2; KOENIGSWALD 1972) or five (Husarenhof 4; KOENIGSWALD 1973) according to data from Germany. On the other hand, five species were described from the Early Pliocene of Poland, and at the end of the Early Pleistocene this number rose to seven (RZEBIK-KOWALSKA 1991).

Today no *Sorex* species are present in the southern part of the Iberian Peninsula. In its northern part there are three species, in France four (NIETHAMMER & KRAPP 1990), Poland four (PUCEK 1984), Finland five (HANSKI & KAIKUSALO 1989) and Siberia 13 (6-8 being sympatric) (YUDIN 1989).

It is possible that the cline in the number of *Sorex* species has existed in Eurasia since the beginning of the Pliocene. It is very probable, therefore, that Eastern Europe was more open to migrations from Asia and its climate more favorable for *Sorex* (RZEBIK-KOWALSKA 1994).

III. CONCLUSIONS

1. In general, shrews (Soricidae) are more successful and diversified in warm and humid climates. The progressive climatic deterioration since the Villanyian resulted in extinction or decreased ranges of numerous soricid taxa.

2. *Crocidura*, at present the most diverse genus of white-tooth shrews (Crocidurinae) adapted to a mild climate, colonized Western Europe from Africa, probably through the Middle East, during the warmer periods of the Pliocene and Pleistocene. North of the Carpathians it did not appear before the Holocene.

3. *Sorex*, the most diverse genus of Soricinae, or pigmented-tooth shrews, has gradually adapted to cooler climates. Some of its species spread to southwestern Europe during cold phases of the Pleistocene.

4. The impoverishment of the shrew fauna progressed from the west to the east, as Eastern Europe was probably more open to migrations from Asia, the main source of new taxa for European continent.

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