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Palaeogeography and environment of the Late Miocene Soricidae (Mammalia) faunae of the Pannonian Basin

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(with 7 figures)

Abstract

The article presents the palaeobiogeographical and palaeoecological results of the examinations of eleven Vallesian and Turolian shrew faunae found in the Pannonian Basin. While in the MN 9-11 Zones of the Late Miocene in the greater part of Europe a subtropical climate was dominant, the Soricidae and other vertebrate fauna elements in the Pannonian Basin's northern and western areas which had become lands reflect much more extreme conditions; forests and grassland plains alternated with each other, and in places desert tracts may have appeared. Probably the wind-sheltering effect of the Alps and Carpathians, which by the MN 9 Zone already had profiles of high mountain ranges, created the drier and, from the point-of-view of temperature, more extreme climate. This is supported by the fact that the migrations and evolutionary connections of the Soricidae faunae show the Pannonian Basin to have been closed to the north and west, and open to the south. In the MN 10-11 Zones the parts of Transdanubia which had become island sometimes became isolated from the eastern mainland of the Pannonian Basin.

Introduction

Shrews, in all probability of Asian origin, appeared in Europe approximately 33 million years ago at the end of the Early Oligocene. From the beginning of the Miocene they became very common, although as an effect of the dry and cold climatic event at the boundary of the Early-Middle Miocene their diversity

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temporarily declined. Compared to the damp subtropical climate of Europe in the Early and Middle Miocene, the Late Miocene brought a significant deterioration in the climate. The Soricinae and Allosoricinae shrews which adapted better to the drier and more extreme climate migrated into the area from Asia, and displaced the hitherto widespread species of the subfamilies Crocidosoricinae and Heterosoricinae (RZEBIK-KOWALSKA, 1995).

At the same time the Late Neogene orogene movements created several smaller basins in Europe. These basins, because of their unusual relief situation and possible isolation, have preserved fossilised faunae from which it can be concluded that the environment differed from the average. The Pannonian Basin was one of these areas in the Late Miocene, the Soricidae faunae of which differed significantly from other European shrew communities.

The author studied eleven shrew fauna of Upper Miocene localities in Hungary between 1994-1998 (Figs 1-2). The taxonomic description of the faunae has since been published (HÍR & MÉSZÁROS, 1995, MÉSZÁROS, 1996, 1997, 1998a, 1998b, 1999a, 1999b, ZIEGLER & MÉSZÁROS, 2000). The changes of shrew faunae and the migratory and autochthonal evolutionary processes which occurred in the Pannonian Basin make it possible to draw numerous palaeobiogeographical and palaeoecological conclusions. These results are presented in the current article.

The biocoenotic preference of the studied genera

Among the shrews which are used to define the environment *Crusafontina*, *Paenelimnoecus* and *Amblycoptus* are the indicators of arboraceous vegetation with a good water supply. Although *Paenelimnoecus*, *Crusafontina* and *Amblycoptus* became extinct, a relative of the latter two, recent *Anourosorex squamipes*, lives in the highland forests of South-East Asia (REPENNING, 1967). *Crusafontina* and *Paenelimnoecus* occur together in Kohfidisch (BACHMAYER & WILSON, 1970) and Dorn-Dürkheim (STORCH, 1978), although the former mainly represents large, extensive grassland plains, with small patches of forest grouped around open water surfaces, and the latter was an area of arboraceous vegetation in the Late Miocene.

According to REUMER (1984) *Episoriculus* (*Asoriculus*) indicates the proximity of an open water surface which is bordered by dense plant cover. The Osztramos and Csarnóta finds (JÁNOSSY & KORDOS, 1977, KRETZOI, 1962) support this supposition.

Kordosia likes open grassland associations. Although REUMER (1984) believes that the genus could have lived in a forest environment, the author does not accept this. Its occurrence at Osztramos does not prove anything in itself, as

according to JÁNOSSY (1972) locality 1 has a "mixed ecology" containing both steppe and forest elements. The Mediterranean occurrence (DOUKAS et al., 1995) and presence of *Kordosia* in the Polgárdi 5 fauna of unusual components (see below) can only be explained by the fact that it lived in a climate warmer than the average of the area (e.g. on the exposed southern karstic mountainsides) and was able to tolerate the drier conditions.

Blarinella, although today forced back to the mountain forests of Asia (Repenning, 1967), was a typical "opportunist" genus in the Late Neogene (MÉSZÁROS, 1999a); it occurred both in drier, open grassland and wetter, forest associations.

The biocoenotic relations of the studied faunae

Soricidae communities, considering other fauna elements, usually indicate a local forested ecotope with a good water supply connected with an open mass of water, or a highland environment in a drier climate.

Alsótelekes: Among modern Soricinae only *Crusafontina* is present which makes arboraceous vegetation probable. The more ancient members of the biocoenosis (*Florinia, Miosorex*) suggest that the environment could not have been dry.

Rudabánya: The presence of *Dinosorex* and *Crusafontina*, as at Alsótelekes, suggests wet conditions with lush vegetation. The appearance of *Paenelimnoecus* and perhaps *Blarinella* (KRETZOI et al., 1976) further strengthens this view. The supposition of a wet environment is supported by other insectivores also found in the fauna (ZIEGLER & MÉSZÁROS, 2000). This all agrees with the statement of KRETZOI et al. (1976) according to which remains were collected in marshland in the environment of which there were also grassland plains and patches of forest.

Sümeg: *Dinosorex*, *Crusafontina* and *Paenelimnoecus* suggest a similar environment to the previous locality. Here, however, the presence of an open water surface cannot be proved unambiguously, as although Anura can be found in the fauna, the proportion of amphibians is very low and fish do not occur at all (KRETZOI, 1984).

Tihany: Only three *Crusafontina* were found at the locality, which suggests arboraceous vegetation, but the few remains are not enough to clear exactly the palaeoecological statement.

Csákvár: *Crusafontina* and *Paenelimnoecus* indicate dense, lush vegetation. In the area of the locality there must have been a water environment association. Fish, turtles, beavers, otters and water birds all occur at the locality. Ungulates (types of deer, pygmy antelopes) were also rather forest-dwellers than steppe-dwellers (KRETZOI, 1954).

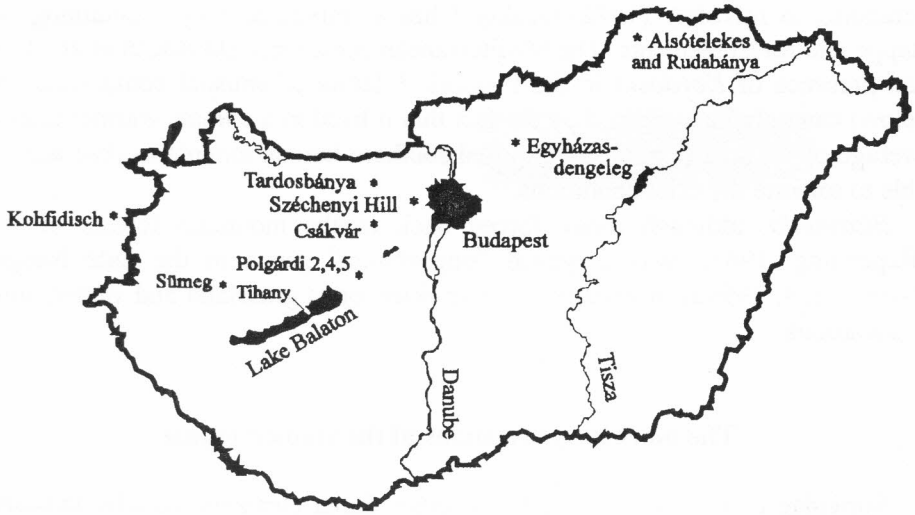

Fig. 1. Upper Miocene Soricidae localities studied in the Pannonian Basin.

Tardosbánya: Apart from *Crusafontina*, *Paenelimnoecus* and *Amblycoptus* which suggest a forest environment, *Asoriculus* is present, the first Late Miocene Soricinae in the Pannonian Basin which definitely lived near open water. The fish, frogs and desmans in JÁNOSSY's manuscript faunal list, made in 1981, suggest the proximity of a larger stretch of water.

Egyházasdengeleg: The obvious dominance of *Amblycoptus* indicates a forest biocoenosis developed in a dry broader surrounding as the result of a local effect. The same can be said of the Gastropods of the locality as well (KROLOPP E., pers. comm.). However, the development of local areas of desert or semi-desert can be deduced from certain rodent finds (HÍR & MÉSZÁROS, 1995). Taking into consideration the full group of remains and the taphonomic characteristics, the Soricidae fauna of the cross-stratified sand at Egyházasdengeleg lived in a gallery forest on the margins of a river situated in a very dry broader area.

Széchenyi-hegy: Only *Amblycoptus* represents the shrews in the examined material. KRETZOI (1980), not taking the Soricidae into account, believes that, with the exception of one tapir tooth, there was nothing to suggest a waterside, forested environment. However, taking into consideration the ecological requirements of *Amblycoptus*, greater significance must be attributed to the tapir find. To this the "Trimylinae ind." remains mentioned by Kretzoi must be added, which on the basis of the description is probably *Paenelimnoecus*, which, like *Amblycoptus*, adapted to a forest environment.

Polgárdi 2, 4, 5: KORDOS (1991) on the basis of the Cricetidae fauna placed all three localities in the MN 13 Zone so that localities 4 and 5 were of about the

same age, while locality 2 was somewhat younger than them. In spite of this the shrew community of localities 4 and 2 are largely similar to each other (the presence of *Crusafontina*, *Paenelimnoecus*, *Amblycoptus* and *Asoriculus* indicates arboraceous vegetation); locality 5, however, differs fundamentally from them. 7 species of shrew occur at locality 4; at locality 5 the diversity is drastically reduced. Among the former only *Blarinella dubia* remains, and together with the here first occurring *Kordosia topali* the total number of species is two.

Myr	Age	Central Paratethys Stage	Mammal faunal unit	MN	Soricidae localities in the Pannonian Basin	Selected other Soricidae Localities
6 _	L					Maramena
	a	Pontian		13	Polgárdi 2	
					Polgárdi 5	
7 _	t				Polgárdi 4	
	e		Turolian	12	Széchenyi Hill Tardosbánya	
					Egyházas-dengeleg	
8 _	M				Csákvár	
	i			11	Tihany	
						Dorn-Dürkheim
9 _	o	Pannonian				
	c			10	Kohfidisch Sümeg	
10 _	e		Vallesian			
					Rudabánya	
	n			9	Alsótelekes	
						Belchatów A
11 _	e					Can Llobateres

Fig. 2. The stratigraphical position of the studied Upper Miocene Soricidae localities.

The divergence of the Polgárdi 5 fauna from that of 4 is probably not caused by macroclimatic changes but microclimatic ones. This could have been, for example, the development of the vegetation of a forested karst area into an open biocoenosis which was accompanied by the large-scale decline in the diversity of the shrew community. In the fauna of Polgárdi 5 the opportunist *Blarinella*

remained, but the forest genera disappeared and *Kordosia*, which likes warmer conditions characteristic of the Mediterranean, appeared. In parallel with the forestation that followed lusher vegetation again developed on this mountainside in which the forest genera (*Paenelimnoecus* and *Amblycoptus*) reappeared, but perhaps not with its original diversity. Locality 2 represents this period.

The Carpathian-Alpine biogeographical barrier

On the basis of the change of shrew faunae MÉSZÁROS (2000b) defined four Late Miocene 'Soricidae fauna intervals' in the Pannonian Basin. The boundary between the first two (Alsótelekes and Kohfidisch intervals) lies within the MN 9 Zone. On this boundary three genera disappear, and two new ones appear; the number of surviving genera is three. On the lower boundary of the third and fourth intervals (Tardosbánya, MN 12, Polgárdi, MN 13) two new genera appear in each. In the Soricidae fauna of the Pannonian Basin the change which indicates the drying of the climate and the rise in the mean annual temperature fluctuation had already happened in the MN 9 Zone. The minute Crocidosoricinae shrews which adapted to the subtropical climate became extinct, and their place was taken by Soricinae migrating in from Asia which also tolerated continental conditions well. Somewhat later the Heterosoricinae also disappeared. On the lower boundary of the MN 12 and MN 13 Zones new species of Soricinae migrated into the region which likewise suggests changes in the climate (Figs 3-4).

In spite of this it cannot be stated that the climate of the Pannonian Basin in the MN 9-11 Zones would have been extremely dry. Taking into account that the temperature could have been somewhat warmer than today's (*Sorex* or other shrews which definitely tolerate cold are missing), the quantity of precipitation probably more or less corresponded to current values. Generally, conditions reminiscent of present day savannahs could have been dominant, where gallery forests grew along larger water-courses and on the coasts of the Pannonian Lake (KRETZOI, 1954, 1984, KRETZOI et al., 1976, KÁZMÉR, 1990). Besides the provision of the necessary wetness, the Lake also could have moderated the annual fluctuation of temperature to a slight degree. Although on the basis of the Soricinae dominance a more extreme climate can be clearly shown, the occurrences of shrews are most often connected with the gallery forests already mentioned.

Age	Late Miocene					Soricidae subfamilies
Unit	Vallesian		Turolian			
MN	9	10	11	12	13	
SFI	I.	II.		III	IV	
gen. nr.	2	0	0	0	0	Crocidosoricinae
	1	1	0	0	0	Heterosoricinae
	4	3	3	6	7	Soricinae
	2 FAD, 3 LAD		2 FAD	2 FAD		Simultaneous events in the Soricidae fauna

Fig. 3. The change in the Soricidae faunae of the Pannonian Basin in the Late Miocene. Abbreviations: SFI = Soricidae Fauna Intervals according to Mészáros (in press); I = Alsótelekes SFI; II = Kohfidisch SFI; III = Tardosbánya SFI; IV = Polgárdi SFI; gen. nr. = number of genera; FAD = First Appearance Date; LAD = Last Appearance Date.

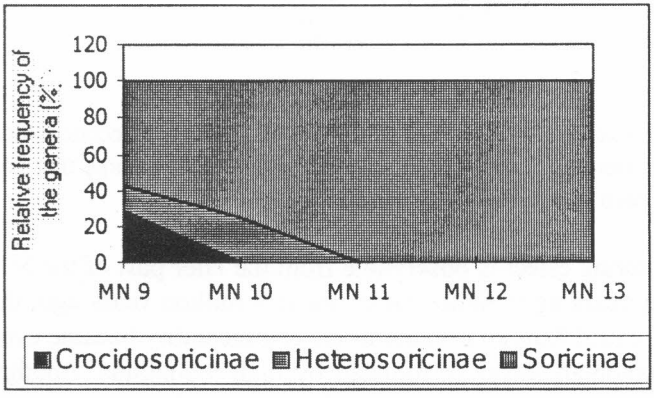

Fig. 4. The change in the relative frequency of the Soricidae subfamilies in the Late Miocene MN 9-13 Zones.

While the climate of the Pannonian Basin became more continental, in other parts of Central Europe in the Vallesian and at the start of the Turolian subtropical forests and faunae still occurred (FORTELIUS et al., 1996, BERNOR et al., 1997) such as those of the Pannonian Basin in the Middle Miocene (MÉSZÁROS, 2000a). The drier climate which developed in the Pannonian Basin can only be explained if we assume that as a consequence of the Late Neogene

orogene movements the Alps and the Carpathians had already risen so much by the Early Vallesian MN 9 Zone as to obstruct the passage of the moist air masses arriving from the Atlantic Ocean to the region (Fig. 5).

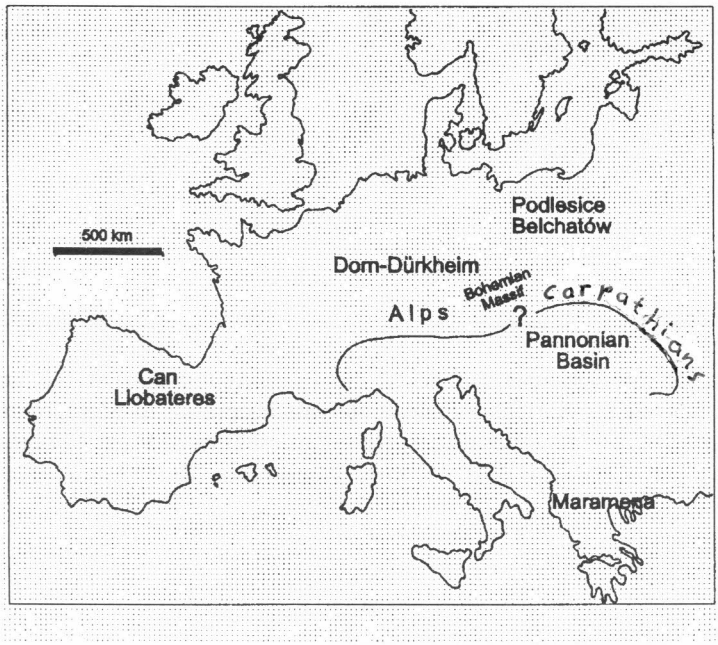

Fig. 5. The biogeographical barrier formed at the beginning of the Late Miocene which obstructed the further migration to the west and north of the Soricidae groups that had arrived in the Pannonian Basin. See text for explanation.

The precipitation-sheltering effect is observable from the later part of the MN 9 Zone (about 11 million years ago). When later, about 8 million years ago, the whole of the climate of Central Europe became drier, continentality became even more apparent in the Pannonian Basin surrounded by high mountains. Another Soricinae migration started into the region and in places small deserts appeared. At this time too gallery forests ran along the margins of the larger rivers from the Carpathians towards the Pannonian Lake (HÍR & MÉSZÁROS, 1995).

The development of the high mountain profile at the same time represented the appearance of a biogeographical barrier, which on the one hand isolated the populations of species already present from those found to the north and west, and on the other hand hindered those coming from Asia in migrating further.

There is a significant difference in the comparison of the sizes of the *Crusafontina* finds from the Pannonian Basin and the Spanish and Polish forms. A monotonous trend in the growth of size is typical of the populations of the

Pannonian Basin into which individuals of more western populations cannot be accommodated (Fig. 6). On the basis of the differing evolution it can be assumed that the stocks living in the Pannonian Basin were isolated from the aspect of morphological evolution from the communities of other areas, thus a biogeographical barrier separated the two areas.

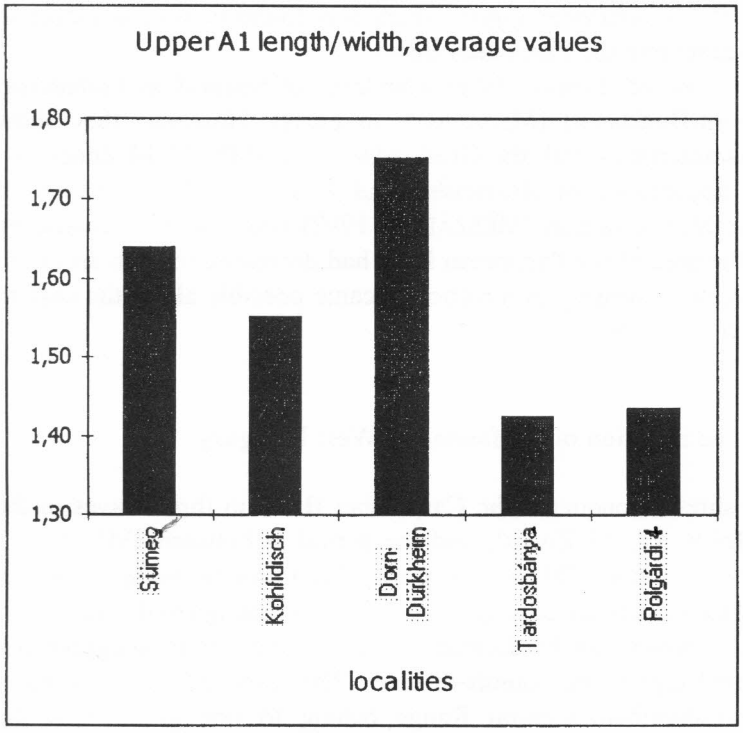

Fig. 6. The divergence in the trend of the growth in size of the *Crusafontina* populations in the Pannonian Basin from the trends of other European regions.

According to MÉSZÁROS (2000b) the shrews of the Pannonian Basin in the Alsótelekes fauna interval show a relationship with the Polish ones, while in the remaining part of the Upper Miocene a great degree of provinciality developed. Unfortunately, there is no known locality for Polish Soricidae in the greater part of the Upper Miocene, thus the exact period of the isolation cannot be established. *Zelceina soriculoides* and *Kordosia topali* appear significantly later in Poland (only after Podlesice, RZEBIK-KOWALSKA, 1994). It is probable that just like today the Eurasian grassland plains due to the effect of the basin stretched the furthest west in the area of Hungary in the Vallesian and Turolian ages; they only appeared in Poland later. Thus the Soricinae shrews which

adapted to a more continental climate only reached Polish territory much later and possibly by a different route.

Provinciality could not have been caused by climatic differences only as it continued in the Pliocene as well when, due to the general climatic change, the differences between the climate of Hungary and other Central European areas may have been smaller. *Amblycoptus oligodon* never occurred outside Hungary, while its relation, *Paranourosorex gigas*, which was found in several places in Poland, did not migrate into the Pannonian Basin.

The Soricidae faunae of Hungary differ from those of Spain (Can Llobateres) and Germany (Dorn-Dürkheim) (MÉSZÁROS, in press). However, they show several similar characteristics with the Greek Maramena (MN 13/14 Zones) as, for instance, the appearance of *Asoriculus* and *Petenyia*. The migration of *Kordosia* from the Mediterranean (MÉSZÁROS, 1997) was possible because by the MN 13 Zone the area of the Pannonian Lake had decreased to such an extent that the fauna flux in a north/south direction became possible along the eastern shores (MAGYAR et al., 1999).

The isolation of the faunae of West Hungary

The Soricinae shrews conquered the Carpathian Basin in three waves in the Late Miocene (MN 9, 12, 13 Zones), and the period in between (MN 10, 11 Zones) was free of migration. This was probably due to the unchanged climate, but neither should the possibility of geographical isolation be ignored (Fig. 7).

The examined localities can be divided into two groups from geographical, sedimentological and taphonomic points-of-view. The fossil infills of the karst recess in the Transdanubian Central Range belong to one group, and the sediments containing fossils accumulated under fluvial, lacustrine or marshy conditions of North Hungary to the other. The shrew remains found in the lacustrine sediment at Tihany constitute an exception. The finds of the migration-free period were found without exception in the Transdanubian Central Range.

It can be assumed that the localities of North Hungary were in areas filled up by the deltas of rivers flowing into the Pannonian Lake, while some parts of the Central Range rose above the remaining large water surface as islands or peninsulas. This possible isolation must have already disappeared by the MN 12 Zone as in Tardosbánya and Polgárdi new migrant species had appeared. The island or peninsula theory is supported by the fact that in both Sümeg and Csákvár animals associated with a watery environment can be found. The isolation, however, could not have been continuous towards the west as the faunae of West Hungary and the animal community of Kochfidisch in Burgenland demonstrate a close relationship. The isolation of the two areas

created the possibility for the *Crusafontina-Amblycoptus* evolutionary transition (MÉSZÁROS, 1997). The Carpathian/Alpine biogeographical barrier isolated the *Crusafontina* populations of the Pannonian Basin from other European areas, providing the possibility for the separated morphological evolution and the evolution of endemic *Amblycoptus*. It does not explain, however, how *Amblycoptus* could have evolved in a way that *Crusafontina* could still be found in the Pannonian Basin. This fact is only credible if in the MN 10-11 Zones the populations were also isolated from each other within the Pannonian Basin. *Crusafontina* continued to survive in the western area (Sümeg, Csákvár, Tihany). In the east, perhaps due to the competition provoked by the arrival of further species from Asia (e.g. *Petenyia*, Egyházasdengeleg), the *Amblycoptus* evolved. The isolation disappeared in the MN 12 Zone, the *Amblycoptus* migrated into the Transdanubian region and in Tardosbánya they are found together with *Crusafontina*.

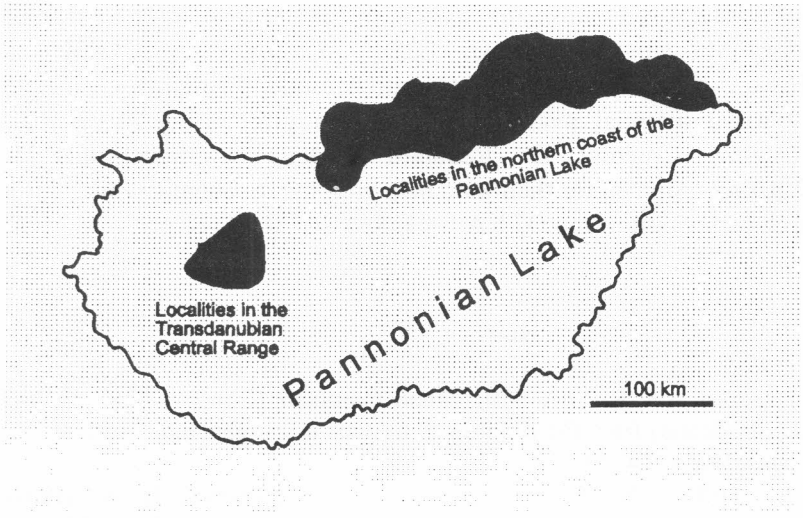

Fig. 7. Isolated Soricidae areas in the MN 10-11 Zones of the Pannonian Basin. See text for explanation.

On the basis of this hypothesis it is possible that MÉSZÁROS's (1998a) stratigraphical statement, according to which the relatively low frequency of the occurrence of *Amblycoptus* at Tardosbánya suggests an older period than Egyházasdengeleg, needs to be revised. The lack of *Crusafontina* at Egyházasdengeleg and the wealth of *Amblycoptus* at the locality may also be the consequence of isolation.

The palaeogeographical picture outlined here agrees with the series of maps prepared on the basis of the palaeontological and geophysical data of MAGYAR et al. (1999) which shows the palaeogeographical evolution of the Pannonian Lake. According to this, 10.8 million years ago (about the start of the MN 9 Zone) the Transdanubian Central Range and north-eastern Hungary were mainland and the two areas were connected. 9.5 million years ago (about the start of the MN 10 Zone) mainland emerged in north-eastern Hungary, but in Transdanubia only a few islands emerged from the Pannonian Lake. 9 million years ago the northern part of Transdanubia and north-eastern Hungary became connected mainland, and the Pannonian Lake receding to the south-east no longer separated the two areas.

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