

Mészáros: Giant shrews

Hantkeniana 9, 107–116, Budapest, 2014  
András Galács Jubilee volume

## A possible taphonomical evidence for the palaeoecological role of the giant shrews (Mammalia, Soricidae) in the Carpathian Basin

Lukács MÉSZÁROS

Eötvös University, Department of Palaeontology  
H-1117 Budapest, Pázmány Péter sétány 1/C, Hungary  
E-mail: salpin@freemail.hu

(with 11 figures, and 1 table)

The study on some toothmarks on the medial surface of the right ulna of a middle sized carnivore mammal are present in this paper. It is shown here as a possible taphonomical evidence of carrion-eating diet of the Late Miocene *Crusafontina endemica* GIBERT, 1974 shrew (Mammalia, Soricidae) from Sümeg locality (Western Hungary). Also other palaeoecological relations (nutrition and ecotype preference) of the giant shrews (the members of Anourosoricini and Beremendiini tribes of family Soricidae) from the Late Miocene to Middle Pleistocene age of the Carpathian Basin are overviewed in the present article.

### Introduction

Shrews are relatively small animals, but we can find quite large sized fossil species in several groups of them. Some of these taxa have recent representatives as well, like the Asian “mole shrew” (*Anourosorex squamipes*) in tribe Anourosoricini.

We can find “giant shrews” among the fossil Soricidae species of the Carpathian Basin from the Late Miocene to the Middle Pleistocene ages. These “giants” could have been more than duplicated dimensions than the average sized shrews of Hungary in the present (Figures 1-2). These forms belong to two different phylogenetic lines (tribes Anourosoricini and Beremendiini, Figure 3), but they could play similar ecological roles in the different ages of the Carpathian Basin in consequence of their convergent adaptive development.

We can suppose them to have special diets in comparison with the most of the recent shrews on the basis of their extraordinary largeness and increased claim to the nutritive material.

Some tooth-marks on a fragmentary bone of a middle sized mammal from the Late Miocene Sümeg locality could give a new evidence to the carrion-eating diet of the large sized Anourosoricini shrew, *Crusafontina endemica*.

This taphonomical evidence is shown in the present paper and also an overview on the ecological role of the giant shrews (the members of tribe Anourosoricini and Beremendiini) is given here.

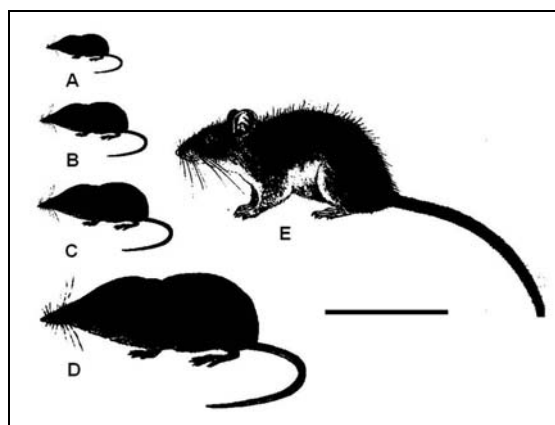


Figure 1. Comparison of the measurements of the giant shrews with that of the most common recent ones in Hungary and a big sized rodent. A = *Sorex minutus* (ca. 5 cm), B = *Sorex araneus* (ca. 7 cm), C = *Neomys fodiens* (ca. 9 cm), D = *Kordosia topali* (ca. 18 cm), E = *Rattus rattus* (Scale bar = 10 cm).

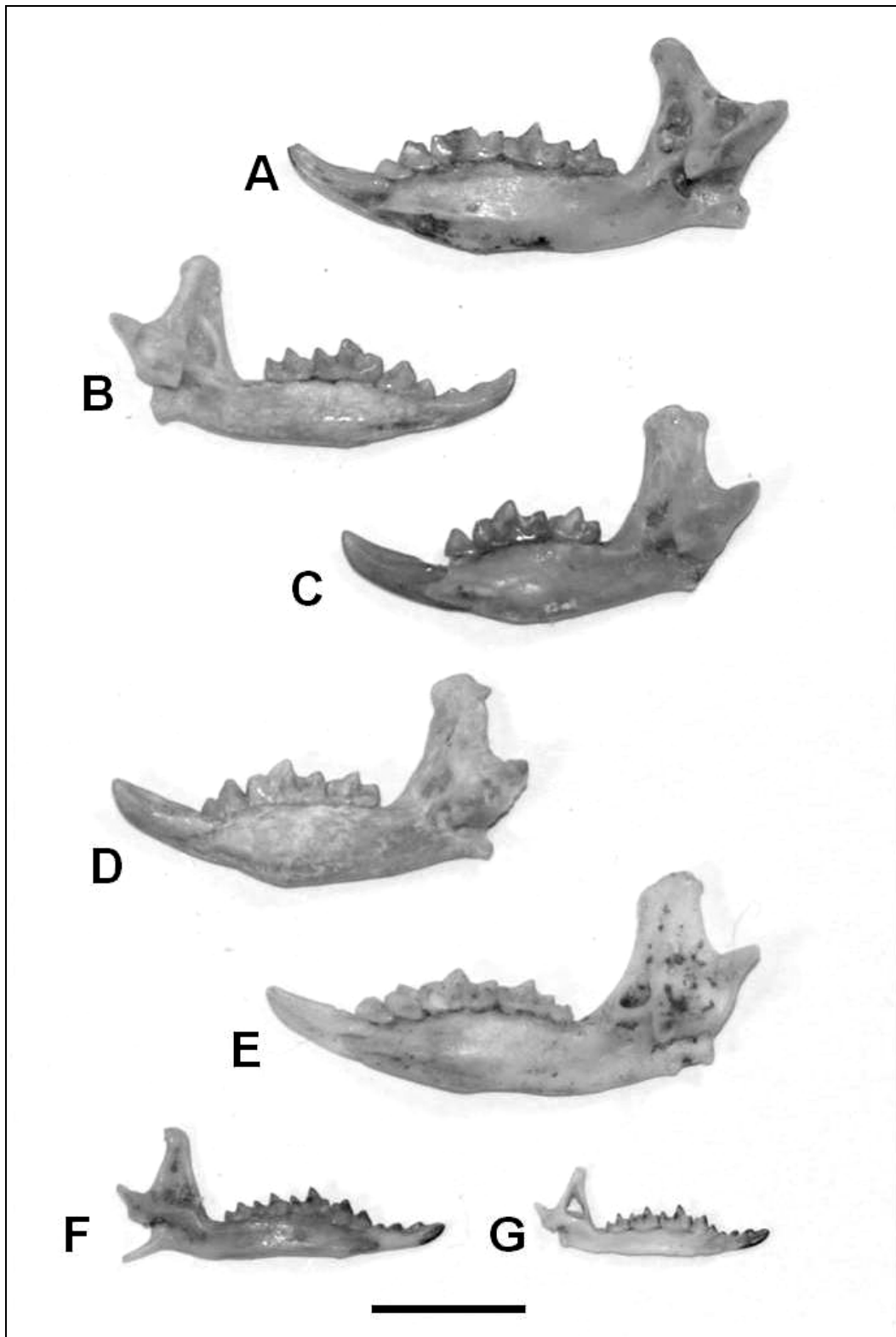


Figure 2. The jaws of the giant shrews of the Carpathian Basin (A-D) and for comparison the recent Anourosoricini form (E), an average and a small sized living *Sorex* species (F-G). All the photos were taken in lingual view and in the same magnitude (scale bar = 5 mm). A: *Beremendia fissidens* (PETÉNYI, 1864), right mandible, Villány 3. B: *Crusafontina kormosi* (BACHMAYER & WILSON, 1970) left mandible, Polgárdi 4. C: *Amblycoptus oligodon* KORMOS, 1926, right mandible, Polgárdi 4. D: *Kordosia topali* (JÁNOSSY, 1972), right mandible, Polgárdi 5. E: *Anourosorex squamipes* MILNE-EDWARDS, 1872, right mandible, Vietnam. F: *Sorex araneus* LINNAEUS 1758, left mandible, Vaskapu 2. G: *Sorex minutus* LINNAEUS 1766, left mandible, Vaskapu 2.

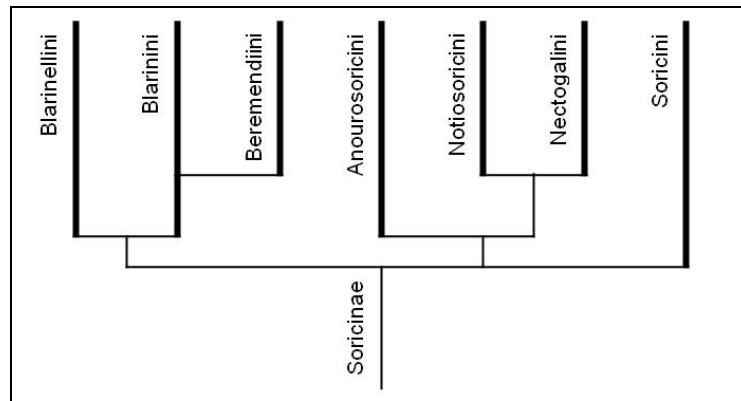


Figure 3. Phylogenetic relations between Anourosoricini and Beremendiini tribes, the two giant shrew groups of the Carpathian Basin (after VAN DAM 2010).

### Localities and stratigraphy

Tribe Anourosoricini is represented in Hungary by three genera: *Crusafontina*, *Amblycoptus* and *Kordosia*. The tribe appears with Genus *Crusafontina* in the Carpathian Basin in the Late Miocene Alsótelekes and Rudabánya localities (MN 9 Zone) (MÉSZÁROS 2000a).

*Crusafontina* occurs with two species in the Carpathian Basin: *C. endemica* is present from MN 9 Zone to the first part of MN 10 Zone, in Alsótelekes (MÉSZÁROS 1999b), and Sümeg (MÉSZÁROS 1996) localities and perhaps in Rudabánya (ZIEGLER & MÉSZÁROS 2004), while *C. kormosi* appears in the end of MN 11 Zone and disappears in the middle of MN 13 Zone. It was found in Kohfidisch (BACHMAYER & WILSON 1970), Tihany (MÉSZÁROS, 2008), Csákvár (MÉSZÁROS 1996), Tardosbánya (MÉSZÁROS 1998a) and Polgárdi 4 (MÉSZÁROS 1999a) sites. The taxonomical status of the Rudabánya form is not clear, it could have been ranged to an other species.

Genus *Amblycoptus* contains only one species: *A. oligodon*. It is reported from MN 12-13 Zones, Tardosbánya (MÉSZÁROS 1998a), Egyházsdengeleg (HÍR & MÉSZÁROS 1995), Széchenyi Hill (MÉSZÁROS 1996), Polgárdi 2 and 4 (MÉSZÁROS 1999a) localities.

Only *Kordosia topali* occurs among the *Kordosia* species in Hungary, in Polgárdi 5 (MÉSZÁROS 1999a) and Osztramos 1 (MÉSZÁROS 1997b) sites. It appears in the middle of MN 13 Zone and disappears in the Lower Pliocene MN 14 Zone.

Tribe Beremendiini is a monogeneric group which contains only genus *Beremendia*. Two forms, *B. fissidens* and *B. minor* were found in Hungary from its four species. Both of them appear here in the Lower Pliocene Osztramos 1 locality (MN 14 Zone, REUMER 1984, JÁNOSSY 1986). *Beremendia fissidens* disappears in the

middle Pleistocene. It is reported also from Csarnóta (REUMER 1984), Beremend (JÁNOSSY 1986), Villány (REUMER 1984), Dunaalmás (JÁNOSSY 1986), Nagyharsányhegy (JÁNOSSY 1986), Újlak Hill (JÁNOSSY 1986), Süttő 19 (PAZONYI et al. 2014), Somssich Hill 2 (BOTKA & MÉSZÁROS 2014 a, b) and Tarkó (JÁNOSSY 1986). *Beremendia minor* is known to the late Early Pleistocene (Somssich Hill 2, BOTKA & MÉSZÁROS 2014b). For the stratigraphical ranges see Figure 4.

The ages, and the Anourosoricini or Beremendiini occurrences with the reporting references are summarized in Table 1. The ages of the Late Miocene localities were pointed out in MÉSZÁROS 2000a. The stratigraphical position of the Pliocene and the Pleistocene sites are used here as it was stated in BOTKA & MÉSZÁROS (2014b).

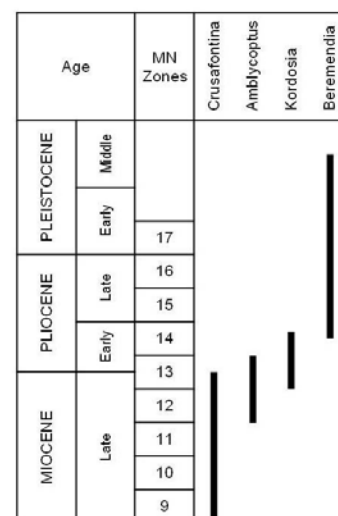


Figure 4. Stratigraphical occurrence of the studied genera in the Carpathian Basin.

Table 1. The age of the studied localities with the Anourosoricini or Beremendiini occurrences and the reporting references.

Locality	Age	Species	Reference
Alsótelekes	MN 9	<i>Crusafontina endemica</i>	MÉSZÁROS 1999b
Rudabánya	MN 9	<i>Crusafontina endemica</i>	ZIEGLER & MÉSZÁROS 2004
Sümeg	MN 10	<i>Crusafontina endemica</i>	MÉSZÁROS 1996
Kohfidisch	MN 10	<i>Crusafontina kormosi</i>	BACHMAYER & WILSON 1970
Tihany	MN 11	<i>Crusafontina kormosi</i>	MÉSZÁROS 2008
Csákvár	MN 11	<i>Crusafontina kormosi</i>	MÉSZÁROS 1996
Tardosbánya	MN 12	<i>Crusafontina kormosi</i> <i>Amblycoptus oligodon</i>	MÉSZÁROS 1998a
Egyházasdengeleg	MN 12	<i>Amblycoptus oligodon</i>	HIR & MÉSZÁROS 1995
Széchenyi Hill	MN 12	<i>Amblycoptus oligodon</i>	MÉSZÁROS 1996
Polgárdi 2,4,5	MN 13	<i>Crusafontina kormosi</i> <i>Amblycoptus oligodon</i> <i>Kordosia topali</i>	MÉSZÁROS 1999a
Osztramos 1,2,3,4,7,8,14	MN 14, MN 16 – Middle Pleistocene	<i>Kordosia topali</i> <i>Beremendia fissidens</i> <i>Beremendia minor</i>	REUMER 1984, JÁNOSSY 1986, MÉSZÁROS 1997b
Csarnóta 1,2,4	MN 15, MN 17	<i>Beremendia fissidens</i>	REUMER 1984
Beremend 1,2,3,4,5,8,9,11,15	MN 16 – Early Pleistocene	<i>Beremendia fissidens</i>	JÁNOSSY 1986
Villány 1,2,3,5,6,7,8,11	MN 17 – Middle Pleistocene	<i>Beremendia fissidens</i>	REUMER 1984, JÁNOSSY 1986
Dunaalmás 4	MN 17 – Early Pleistocene	<i>Beremendia fissidens</i>	JÁNOSSY 1986
Nagyharsányhegy 2,3,4,5	MN 17 – Early Pleistocene	<i>Beremendia fissidens</i>	JÁNOSSY 1986
Újak Hill	Early Pleistocene	<i>Beremendia fissidens</i>	JÁNOSSY 1986
Süttő 19	Early Pleistocene	<i>Beremendia fissidens</i>	PAZONYI et al. 2014
Somssich Hill 2	Early Pleistocene	<i>Beremendia fissidens</i> <i>Beremendia minor</i>	BOTKA & MÉSZÁROS 2014a, b
Tarkó	Middle Pleistocene	<i>Beremendia fissidens</i>	JÁNOSSY 1986

## Taxonomy

Nomenclature for the morphological descriptions are used after REUMER (1984) and MÉSZÁROS (1997) in the taxonomical part.

Phylum Vertebrata LINNAEUS, 1758  
 Classis Mammalia LINNAEUS, 1758  
 Order Eulipotyphla WADDELL et al., 1999  
 Family Soricidae FISCHER VON WALDHEIM, 1817  
 Subfamily Soricinae FISCHER VON WALDHEIM,  
 1817

### Tribe Anourosoricini ANDERSON, 1879

The common characters of Anourosoricini species are as follows: Large dimensions, upwardly widening coronoid process, tight internal temporal fossa, trigonal upper condyloid facet, oblong-shaped lower one, very narrow interarticular area. They have two or three upper antemolars, their lower incisor is acusulate or bicusulate. Dental formula may be 142/123, 133/123, 142/122 and 132/122 (MÉSZÁROS 1997b).

By this time six valid genera is ranged in the tribe Anourosoricini (VAN DAM 2010), but three of

them (*Darocasorex*, *Paranourosorex*, and the only recent *Anourosorex*) were not reported from the Carpathian Basin (Figure 5).

#### Genus *Crusafontina* GIBERT, 1974

This genus has the most complete dentition in the tribe Anourosoricini. Dental formula is 143/123.  $M^3$ , and  $M_3$  are reduced, but always are present. Upper condylar facet is triangular or oval, lower one is oblong, interarticular area is very narrow. Internal temporal fossa is subtriangular to round or oval.  $I^1$  is with buccal cingulum.  $A^1$  is without parastyle.  $P^4$  is pentagonal because of the projecting parastyle.  $P^4$  and  $M^1$  are with distinct posterior emargination.  $M^1$  parastyle is projecting less or equally far buccally compared to metastyle.  $M^2$  with complete talon.  $I_1$  is mono-, bi-, or tricuspidate.  $P_4$  is with posterolingual depression.  $M_1$  and  $M_2$  are with entocristid.

Two of the *Crusafontina* species are definitely reported from the Carpathian Basin (VAN DAM 2004).

#### *Crusafontina endemica* GIBERT, 1974.

The  $I^1$  apex is long, with L/H not smaller than about 1.40. Metastyle of  $M^1$  is extending more buccally than parastyle, and hypoconal flange is not protruding lingually. The  $I_1$  is bi- to tricuspidate. The  $M_3$  talonid contains a small basin.  $M_3$ – $M_1$  length ratio is not smaller than about 0.40 (VAN DAM 2004).

#### *Crusafontina kormosi* (BACHMAYER & WILSON, 1970)

Medium-sized *Crusafontina* species. The  $I^1$  apex is long, with L/H ratio smaller than about 1.40.  $M^1$  metastyle and parastyle is extending buccally about equally far and hypoconal flange not protruding lingually.  $I_1$  is bicuspidate.  $M_3$  talonid is either with closed basin, with terminal heel or missing.  $M_3$ – $M_1$  length ratio is smaller than about 0.40 (VAN DAM 2004).

#### Genus *Amblycoptus* KORMOS, 1926

Large sized Anourosoricini, but somewhat smaller than *Kordosia*. The third lower and upper antemolars are missing, but  $A^3$  is present.  $I_1$  is acuspulate, the parastyle of  $A^1$  is missing.  $P^4$  is pentagonal in occlusal view. Dental formula is 142/122 (MÉSZÁROS 1997b).

#### *Amblycoptus oligodon* KORMOS, 1926

For *A. oligodon* is the only known species of the genus, the morphological characters are the same as there.

#### Genus *Kordosia* MÉSZÁROS 1997

*Kordosia* has the most reduced dental formula in the tribe Anourosoricini: 132/122.  $A^3$ ,  $M^3$  and  $M_3$  is always missing, ventral profile of  $P^4$  is much like an oblong. PW of  $M^1$  is far less than AW,  $I_1$  is acuspulate. On the mandible the internal temporal fossa is extremely tight. Dental formula is 132/122. (MÉSZÁROS 1997b)

Two species, *Kordosia jessiae* (DOUKAS 1995) and *Kordosia topali* is ranged here. By this time only *K. topali* is found in the Carpatian Basin.

#### *Kordosia topali* (JÁNOSSY, 1972)

Larger sized *Kordosia* species, than *K. jessiae*.  $I^1$  may be without cingulum and with convex margin (MÉSZÁROS 1997b).

#### Tribe Beremendiini REUMER, 1984

This is the only monogeneric tribe among the Soricinae, comprising only the extinct genus *Beremendia*. Separation of this tribe from the other tribes is based on the intermediate position of its morphology between Soriculini (bifid  $I^1$  and presence of entoconid crests) and Blarinini (structure of the condyle and intense dark red pigmentation) (REUMER 1984).

#### Genus *Beremendia* KORMOS, 1934

Upper incisor is strongly fissident, teeth are heavily pigmented, it has Blarinini-like condyle with broad interarticular area and anteriorly placed lower facet, the lower incisor is acuspulate, the entoconid crests are present (REUMER 1984).

The genus contains four valid species (*B. fissidens*, *B. minor*, *B. pohaiensis* and *B. jiangnanensis*) but the two latter do not occur in Europe.

#### *Beremendia fissidens* (PETÉNYI, 1864)

Teeth are intensively stained a dark red. The  $I^1$  is strongly fissident with a bifid apex. Four upper antemolars are present.  $A^1$  and  $A^2$  are of about equal size,  $A^3$  is smaller and  $A^4$  is smaller again. The  $A^4$  is reduced, hidden and not visible in buccal view or is lacking. The posterior emargination is moderate on the  $P^4$ ,  $M^1$  and  $M^2$ . The parastyle of the  $M^1$  is moderately developed. The  $M^3$  is relatively small. The  $I_1$  is grooved, acuspulate, the apex curves upwards. The  $A_2$  is bicuspid and has a posterolingual basin. The  $M_3$  is reduced. The ramus is strong and robust. The coronoid process is stout, anterolaterally curved, the angle of the curve may vary. The angular process is short and flat. The external pterygoid fossa is definitely or

less deeply pocketed. The upper facet is narrow, its shape may vary from elliptic to oval. The interarticular area is broad with a lingual margin. The lower facet leans strongly anteriorly and it is not visible in buccal view. The internal temporal fossa is small, deep and pocketed (REUMER 1984).

*Beremendia minor* RZEBIK-KOWALSKA, 1976

The dimensions of the species are significantly smaller than that of *B. fissidens* (not only the dental elements but also the size of the mental foramen, its anterior basin and the parameters of the symphysis fossa). The angle of the  $I^1$  is smaller between the ventral part of the apex and the anterior margin of the talon. The  $I_1$  has a more pointed apex and a more curved lower incisor. The  $M_3$  has a high entoconid, a rounded hypolophid and its posterior margin of the talonid is round (BOTKA & MÉSZÁROS 2014b).

*Remarks*

We know further large sized shrews (for example *Dinosorex*) from the Miocene of the Carpathian Basin (MÉSZÁROS 2000a). As these

species today is not ranged in family Soricidae, and their ecological role in this area is less clear, they are not discussed here.

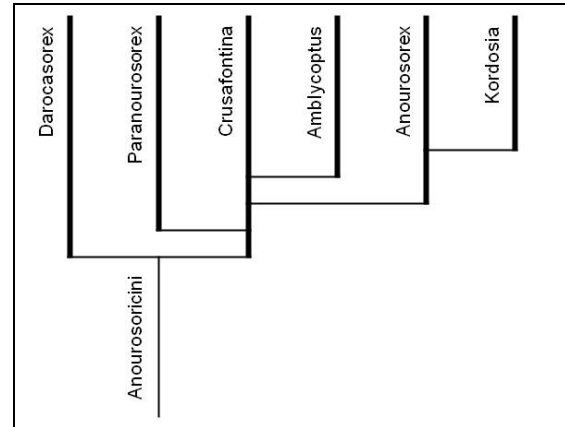


Figure 5. Phylogenetic relations between the genera of the Anourosoricini tribe. This sketch was made after the data of VAN DAM (2010, fig. 3), but in the case of *Amblycoptus* and *Kordosia* it was modified on the basis of the phylogenetic analysis of MÉSZÁROS (1997a, fig. 12-13) and the occurrences of the Anourosoricini species in the Carpathian Basin (MÉSZÁROS 1997b and 1998b).

### Taphonomical results

László Kordos and Ray Bernor lead an excavation in the Late Miocene Sümeg palaeontological locality in the summer of the 2001st year. Miranda Armour-Chelu and the present author were the members of the researcher team. She discovered some tooth-marks on a fragmentary bone and called the author's attention to this taphonomical remain. She raised, that these bites could have been caused by a large sized soricid.

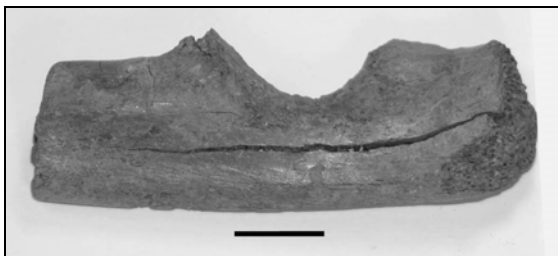


Figure 6. Proximal fragment of the right ulna of a middle sized carnivore mammal, from medial view, Sümeg, working number in the excavation: R2, 1974/131, C.482. (Scale bar = 10 mm).

The bites were seen from medial view on a proximal fragment of the right ulna of a middle sized carnivore mammal (Figure 6), of which

working number in the Sümeg excavation was R2, 1974/131, C.482. There are some thin tooth-marks and many extensive, shallow nibble-marks on this surface. Moreover, we can see two deep, parallel grooves, which are the only well-identifiable tooth-marks on it (Figure 7).

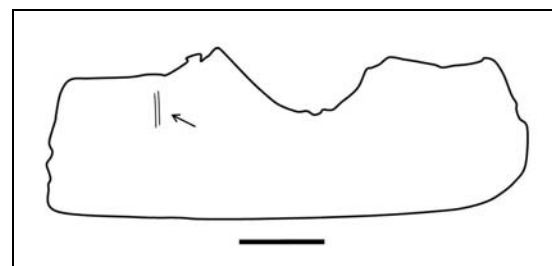


Figure 7. The position of the parallel tooth-marks on the medial surface of the ulna fragment from Sümeg locality. The distance between them is 0.3 mm, which is corresponding to the gap between the upper incisors' apices of *Crusafontina*. (Scale bar = 10 mm).

Merely the insectivorous mammals are so little sized as they were able to make the studied marks. Otherwise, the smaller shrew species of the Sümeg fossil assemblage were evidently too small to bite those (MÉSZÁROS 1996).

However the upper incisor's apexes of giant shrews, represented in the age of the Sümeg site by *Crusafontina*, perfectly fit into the grooves. The distance between the tooth-marks is 0.3 mm, which is corresponding to the gap between the in-situ upper incisors' apexes in the complete *Crusafontina* maxillae (Figure 8).

In spite of the fact that shrews can kill little vertebrates (HABERL 2002), the middle sized

mammal species, whose bone fragment is studied here, was surely too big as to be a prey of *Crusafontina*. The big shrew probably fed on its carcass, eating the soft tissues and scratching the surface of the bone under it. Therefore we can take into consideration this taphonomical finding as an evidence to the carrion-eating diet of the giant shrews of the Carpathian Basin.

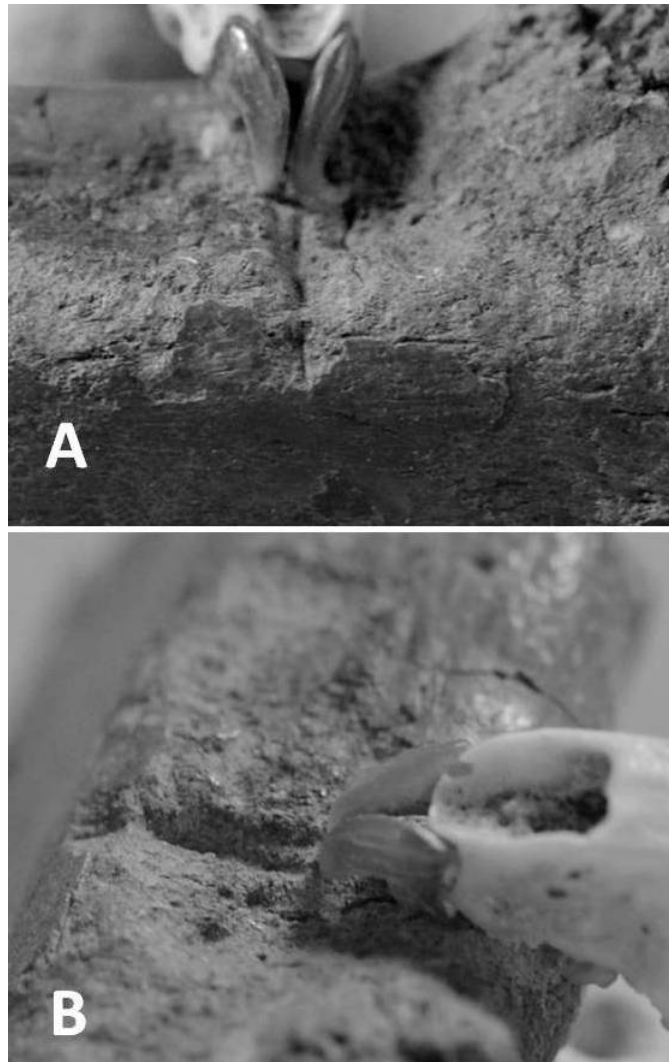


Figure 8. Parallel tooth-marks on the medial surface of the ulna fragment, with the upper incisors of a *Crusafontina* skull remain.

## Palaeoecological overview

### *Nutrition*

In its dental formula and structure *Crusafontina* is the less specialized species of tribe Anourosoricini in the Hungarian fossil record. In spite of this, its P<sup>4</sup> shows the signs of characteristic adaptation. There is a strong edge on its buccal

margin, formed by the paracone and its posterior prolongation. (Figure 9). This structure is very similar to the cutting edge of the carnivore molars. We suppose, that *Crusafontina* adapted to diversified diet, eating not only insects, worms and snails, but often vertebrate carcasses. Among the recent shrews we can also find examples for such nourishment (*Neomys*, in HABERL 2002).

However, on the basis of its dental structure we suppose *Crusafontina* to be more adapted to carrion eating than *Neomys*. This hypothesis is supported by the taphonomical finding shown in the present article.

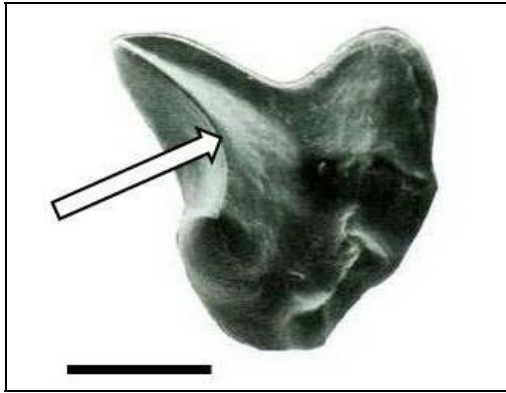


Figure 9. *Crusafontina kormosi* (BACHMAYER & WILSON, 1970), left P<sup>4</sup> in occlusal view from Tardosbánya (after MÉSZÁROS 1998b). The cutting edge is marked by the white arrow. Scale bar = 1 mm.

The climate of the Carpathian Basin turned drier and more extreme after MN 13 Zone (MÉSZÁROS 2000b). The climatic changes yielded decreasing in the insect fauna in some of the ecotypes of the area. This ecological crisis caused significant evolutionary changes in tribe Anourosoricini (MÉSZÁROS 2014).

In the line of *Amblyoptus*, the missing insects were supplied with the vertebrate carcasses, while *Kordosia* adapted to snail-eating. The evolution of the latter genus could have been in progress outside of the Carpathian Basin, in the phylogenetic line of the ancient *Anourosorex* forms (Figure 5), if so they immigrated here later.

The nutrition changes yielded transformations in the dental morphology. The cutting edge became stronger on the pentagonal *Amblyoptus* P<sup>4</sup> but disappeared on the oblong and plate *Kordosia* one (Figure 10).

From the MN 14 Zone the Anourosoricini genera disappeared from the Carpathian Basin, but the empty ecological niche (the role of the giant shrew with diversified nourishment) was filled by the new raising *Beremendiini* (JÁNOSSY & KORDOS 1997).

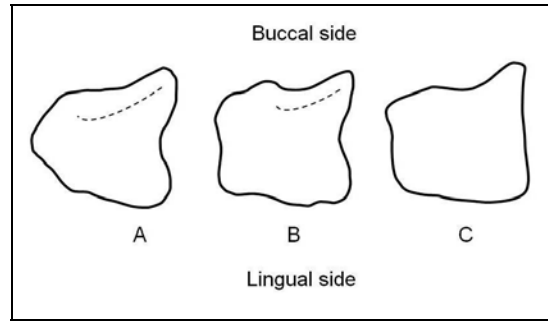


Figure 10. The outline of the occlusal surface of P<sup>4</sup>. A – The “pentagonal” form of *Crusafontina* and *Amblyoptus* with strong cutting edge marked by the dotted line (this edge becomes more stronger at *Amblyoptus*). B – The “square” outline of recent genus *Anourosorex* with shorter edge which is ranged to the ectoloph of M<sup>1</sup>. C – The “square” form becomes “oblong” but without distinct cutting surface at *Kordosia*. (After MÉSZÁROS 1994, figs 7, 10, 16 and 19.)

Today *B. fissidens* is said to be venomous. This hypothesis is induced by its specially adapted lower incisor on which there is a well-marked “venom groove” running along the medial side of its crown (Figure 11).



Figure 11. *Beremendia fissidens* (PETÉNYI, 1864), left I<sub>1</sub> in lingual view from Somssich Hill 2 (after BOTKA & MÉSZÁROS 2014a). The venom groove is marked by the white arrow. Scale bar = 1 mm.

FURIÓ et al. (2010) analyzed the anatomical characters of *Beremendia*. According to them the diet of this form was highly specialized in coleopterans and gastropods.

However its nutrition could have been more complete, because BENNÁSAR *et al.* (2014) have found taphonomical evidences of that *B. fissidens* may have had the capacity to bite prey larger than itself (small mammals e.g. moles). The addition of small vertebrates to complement a diet based on insects and snails could have been a way of responding to the needs of the high metabolic rate characteristic of the giant shrews.

#### *Ecotype preference*

After the climatic changes in the Carpathian Basin, beside the large grasslands, there were gallery forests and bushy areas along the larger



water-courses and on the coasts of the Pannonian Lake (KÁZMÉR, 1990 MÉSZÁROS 2000b). On the basis of their very close relation to the extant *Anourosorex squamipes*, living in the mountain forests of SE Asia, the Anourosoricini genera may be indicate these well-watered, forested environments.

They are described from wooded or at least partly wooded areas. (MÉSZÁROS 1998c). Further, the morphometrical analyses, made by KERNER (2003) on the limb-bones of *Crusafontina*,

*Amblycoptus* and *Kordosia*, showed that these animals can move equally well in the water and on the land.

*B. fissidens* is reported as well from ecotypes nearby open water bodies (lakes or rivers) by several authors (for example AGUSTÍ et al. 2011, CUENCA-BESCÓS et al. 2005, FURIÓ et al. 2010, GARCIA et al. 2014, PAZONYI et al. 2013, SZENTESI 2014). That is why we suppose, that it lived in similar ecotypes in the Carpathian Basin as the earlier Anourosoricini shrews.

## Acknowledgements

The authors is indebted to László Kordos, the former director of the Hungarian Geological Institute and Miranda Armour-Chelu for the chance to make a study on the here described material from Sümeg locality and their valuable

suggestions. Special thanks go to Máté Polgári for his kind help in making the photos. The work was supported by Hungarian Research Found (OTKA K104506 project).

## References

- AGUSTÍ J., SANTOS-CUBEDO A., FURIÓ M., DE MARFÁ R., BLAIN H.-A., OMS O. & SEVILLA P. (2011): The late Neogene-early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Castellón, Eastern Spain): Chronologic and paleoclimatic context. *Quaternary International*, 243: 183-191.
- BACHMAYER F. & WILSON R. W. (1970): Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch fissures of Burgenland, Austria. *Annalen des Naturhistorischen Museums in Wien*, 74: 533-587.
- BENNÁSAR M., CÁCERES I., CUENCA-BESCÓS G., HUGUET R., BLAIN H.-A. & ROFES J. (2014): Exceptional biting capacities of the Early Pleistocene fossil shrew *Beremendia fissidens* (Soricidae, Eulipotyphla, Mammalia): new taphonomic evidence. *Historical Biology* (ahead-of-print): 1-9.
- BOTKA D. & MÉSZÁROS L. (2014a): A Somssich-hegy 2-es lelőhely (Villányi-hegység) alsó-pleisztocén *Beremendia fissidens* (Mammalia, Soricidae) maradványainak taxonómiai és paleoökológiai vizsgálata. Taxonomical and palaeoecological studies on the Lower Pleistocene *Beremendia fissidens* (Mammalia, Soricidae) remains of the Somssich Hill 2 locality (Villány Mountains). *Földtani Közlöny – Bulletin of the Hungarian Geological Society*, 144 (4), in press.
- BOTKA D., MÉSZÁROS L. (2014b): *Beremendia* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (South Hungary) and their taxonomical, biostratigraphical, palaeoecological and palaeobiogeographical relations. *Fragmenta Palaeontologica Hungarica*, 32, in press.
- CUENCA-BESCÓS G., ROFES J. & GARCIA-PIMIENIA J. (2005): Environmental change across the Early-Middle Pleistocene transition: small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain. *Geological Society, London, Special Publications*, 247(1): 277-286.
- DOUKAS C. S. (1995): *Amblycoptus jessiae* n. sp. - In: Doukas C. S.; Van Den Hoek-Oostende L. W.; Theocharopoulos D. & REUMER J. W. F.: The Vertebrate Locality Maramena (Greece) at the Turolian-Ruscinian boundary (Neogene) 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia). – *Münchner Geowissenschaftlichen Abhandlungen*, 28: 43-64.
- FURIÓ M., AGUSTÍ J., MOUSKHELISHVILI A., SANISIDRO O. & SANTOS-CUBEDO A. (2010): The Paleobiology of the Extinct Venomous Shrew *Beremendia* (Soricidae, Insectivora, Mammalia) in Relation to the Geology and Paleoenvironment of Dmanisi (Early Pleistocene, Georgia). *Journal of Vertebrate Paleontology*, 30(3): 928-942.
- GARCIA J., MARTÍNEZ K., CUENCA-BESCÓS G. & CARBONELL E. (2014): Human occupation of Iberia prior to the Jaramillo magnetochron (>1.07 Myr). *Quaternary Science Reviews*, 98: 84-99.
- HABERL W. (2002): Food storage, prey remains and notes on occasional vertebrates in the diet of the Eurasian water shrew, *Neomys fodiens*. *Folia Zoologica*, 51 (2): 93-102.
- HÍR J. & MÉSZÁROS L. (1995): Late Miocene Microvertebrata from Egyházásdengeleg. *Nógrád Megyei Múzeumok Évkönyve*, 20: 167-200.
- JÁNOSSY D. (1986): Pleistocene Vertebrate Faunas of Hungary. *Akadémiai Kiadó, Budapest*, 208 pp.
- JÁNOSSY D. & KORDOS L. (1977): Az Osztramos gerinces lelőhelyeinek faunisztikai és karsztmorfológiai áttekintése (1975-ig). Faunistical and karstmorphological review of palaeontological localities for vertebrates at Osztramos (Northern Hungary). *Fragmenta Mineralogica et Palaeontologica*, 8: 39-72.
- KÁZMÉR, M. (1990): Birth, life and death of the Pannonian Lake. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 79: 171-188.

- KERNER J. (2003): Új módszer a szárazföldi paleo-ökoszisztémák vizsgálatára: fosszilis cickányok (Mammalia, Soricidae) mozgás-szervrendszerének morfológiai analízise. A new method in the study of the terrestrial paleoecosystems: the morphometrical analysis of the locomotion system of fossil shrews (Mammalia, Soricidae). *Földtani Közlemény – Bulletin of the Hungarian Geological Society*, 133(2): 211-218.
- MÉSZÁROS L. GY. (1994): A magyarországi neogén Amblycoptini (Mammalia, Insectivora) maradványok taxonómiai és filogenetikai vizsgálata. Taxonomy and evolution of the Neogene Amblycoptini shrews (Mammalia, Insectivora) from Hungary. M.Sc. Thesis. Eötvös Loránd University, Budapest, 103 pp.
- MÉSZÁROS L. GY. (1996): Soricidae (Mammalia, Insectivora) remains from three Late Miocene localities in western Hungary. *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae - Sectio Geologica*, 31: 5-25.
- MÉSZÁROS L. (1997a): A magyarországi felső miocén cickány (Soricidae Mammalia) maradványok. The Late Miocene shrew (Soricidae, Mammalia) remains from Hungary. Ph.D. Thesis. Eötvös Loránd University, Budapest, 84 pp.
- MÉSZÁROS L. GY. (1997b): *Kordosia*, a new genus for some Late Miocene Amblycoptini shrews (Mammalia, Insectivora). *Neues Jahrbuch für Geologie und Paläontologie - Monatshefte*, 1997(2): 65-78.
- MÉSZÁROS L. GY. (1998a): Late Miocene Soricidae (Mammalia) fauna from Tardosbánya (Western Hungary). *Hantkeniana*, 2: 103-125.
- MÉSZÁROS L. GY. (1998b): *Crusafontina* (Mammalia, Soricidae) remains from Late Miocene localities in Hungary. *Senckenbergiana Lethaea*, 77(1-2): 145-159.
- MÉSZÁROS L. (1998c): A magyarországi késő miocén cickányok (Soricidae) paleoökológiai jelentősége. Paleocological importance of the Late Miocene shrews (Soricidae) from Hungary. *Állattani Közlemények*, 83(1): 41-52.
- MÉSZÁROS L. GY. (1999a): An exceptionally rich Soricidae (Mammalia) fauna from the Late Miocene localities of Polgárdi (Hungary). *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae - Sectio Geologica*, 32: 5-32.
- MÉSZÁROS L. GY. (1999b): Some insectivore (Mammalia) remains from the Late Miocene locality of Alsótelekes (Hungary). *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae - Sectio Geologica*, 32: 33-42.
- MÉSZÁROS L. GY. (2000a): New results for the Late Miocene Soricidae stratigraphy of the Pannonian Basin. *Newsletters on Stratigraphy*, 38(1): 1-11.
- MÉSZÁROS L. GY. (2000b): Paleogeography and environment of the Late Miocene Soricidae (Mammalia) faunas of the Pannonian Basin. *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae, Sectio Geologica*, 33: 107-120.
- MÉSZÁROS L. GY. (2008): Two *Crusafontina* (Mammalia, Insectivora) fossils from the Miocene of the Transdanubian Central Range (Hungary). *Geologica Pannonica: An International Journal of Earth Sciences*, 36: 227-233.
- MÉSZÁROS L. (2014): Giant Dwarfs, The Evolutionary Center of Extinct Monster-Shrews in the Carpathian Basin. In: BALLA BALOGH A., CSÁKÁNY A., FARKAS J., KALMÁR V. & BALÁZS I. (Eds): OTKA Annual Report 2013. OTKA, Budapest, pp. 69-70.
- PAZONYI P., MÉSZÁROS L., SZENTESI Z., GASPARIK M., VIRÁG A. (2013): Preliminary Results of the Palaeontological Investigations of the Late Early Pleistocene Somssich Hill 2 Locality (South Hungary). In: CAGATAY N., ZABCI C. (Eds): 14th Congress of Regional Committee on Mediterranean Neogene Stratigraphy. Istanbul Technical University, Istanbul, p. 270.
- PAZONYI P., KORDOS L., MAGYARI E., MARINOVA E., FÜKÖH L. & VENCZEL M. (2014): Pleistocene vertebrate faunas of the Süttő Travertine Complex (Hungary). *Quaternary International*, 319: 50-63.
- REUMER J. W. F. (1984): Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. *Scripta Geologica*, 3: 1-173.
- SZENTESI Z. (2014): Előzetes eredmények a késői koraleisztocén Somssich-hegy 2 (Villányi-hegység) ősgérces-lelőhely kétélűtűinek vizsgálatában. Preliminary results in the study of the amphibians from the late Early Pleistocene Somssich Hill 2 palaeovertebrate locality. *Földtani Közlemény, Bulletin of the Hungarian Geological Society*, 144(2): 165-174.
- VAN DAM J. A. (2004): Anourosoricini (Mammalia: Soricidae) from the Mediterranean Region: A Pre-Quaternary example of recurrent climate-controlled North-South range shifting. *Journal of Paleontology* 78(4): 741-764.
- VAN DAM J. A. (2010): The Systematic Position of Anourosoricini (Soricidae, Mammalia): Paleontological and Molecular Evidence. *Journal of Vertebrate Paleontology*, 30/4: 1221-1228.
- ZIEGLER R. & MÉSZÁROS L. (2004): Insectivora. p. 11. In: BERNOR R. L., KORDOS L. & ROOK L. (Eds): Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN 9), Hungary: a compendium. *Palaeontographia Italica*, 89: 3-36.