

Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary

Jelle W.F. Reumer

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Plio-Pleistocene Soricidae have been studied from Tegelen (The Netherlands) and from seven Hungarian localities: Osztramos 1, 3, 7, 9, 13, Csarnóta 2, and Villány 3.

The subdivision of the subfamily Soricinae into tribes is revised. Of the three tribes recognized by Repenning (1967), two have been retained, viz. the Soricini Fischer von Waldheim, 1817 and the Blarinini Kretzoi, 1965. The third tribe (Neomyini Repenning, 1967) is split into four new (or resurrected) tribes: Soriculini Kretzoi, 1965 (this name having preference over Neomyini Repenning, 1967); Beremendiini new tribe, Amblycoptini Kormos, 1926, and Notiosoricini new tribe. In addition, the Allosoricini Fejfar, 1966 replaces the formerly separate subfamily Allosoricinae, but it includes taxa included earlier in the Neomyini (*Petenyiella gracilis*) and in the Limnoecinae (*Paenelimnoecus*). Two new genera are described: *Mafia* and *Sulimskia*, both belonging to the Blarinini. Five new species are described: *Sorex bor*, *Deinsdorfia janossyi*, *Deinsdorfia kordosi*, *Blarinella europaea*, and *Mafia csarnotensis*.

Some new terms are introduced for the dental morphology. In the P⁴, the connective ridge between the parastyle and the paracone is called the parastylar crest. For the lower incisor, names (adjectives) are introduced to describe the number of cuspules on the dorsal edge: acuspulate (for an I inf. without cuspules), monocuspulate (1), bicuspulate (2), tricuspulate (3), and tetracuspulate (4 cuspules). Furthermore, the degree of posterior emargination in M¹ and M² has been quantified by means of a formula; the result is the PE-index.

Some palaeoecological conclusions are drawn. The observed differentiation of the climate during the Csarnótian and the Villányian is of particular interest. For two genera it has been possible to reconstruct migratory trends. It is noted that in Central Europe *Episoriculus* gradually retreated southwards. This retreat started in the Ruscinian and continued into the Pleistocene; it might have been caused by the gradual deterioration of the climate. *Crocidura* originates from Africa and invaded Europe, starting in Asia Minor in the Ruscinian and ending its invasion in England during the last interglacial. It has since withdrawn from England, but still occurs in Europe below c. 53°N.

Finally, it can be concluded that during the Ruscinian the Soricidae were a very successful group, showing an explosion in species diversity. The Villányian climatic decline caused many extinctions and a considerable impoverishment of the soricid diversity. Of the — at least — eleven genera found in the late Ruscinian, four became extinct at the Ruscinian-Villányian boundary, two during the Villányian and two at the Villányian-Biharian boundary. At present only four genera are found in Europe; only one of these (*Sorex*) was already in Europe during the early Ruscinian, the others immigrated later.

Jelle W.F. Reumer, Instituut voor Aardwetenschappen, Rijksuniversiteit Utrecht, Postbus 80.021, 3508 TA UTRECHT, The Netherlands. Present address: Station de Zoologie Expérimentale, Route de Malagnou 154, CH 1224 Chêne-Bougeries (Genève), Switzerland.

Introductory part	2
Introduction	2
Material and methods	3
Localities	8
Taxonomical part	13
Subfamilies and tribes	13
Descriptions	18
<i>Crocidura</i>	18
<i>Sorex</i>	22
<i>Drepanosorex</i>	38
<i>Deinsdorfia</i>	44
<i>Petenya</i>	55
<i>Blarinella</i>	66
<i>Zelceina</i>	74
Soricini gen. et sp. indet.	77
<i>Mafia</i> gen. nov.	78
<i>Blarinoides</i>	83
<i>Sulimskia</i> gen. nov.	86
<i>Episoriculus</i>	89
Soriculini gen. et sp. indet.	100
<i>Beremendia</i>	101
<i>Amblycoptus</i>	110
<i>Paenelimnoecus</i>	114
Soricinae gen. et sp. indet.	119
The PE-index	120
Taxonomical conclusions	121
Concluding part	123
Palaeoecology	123
Interpretations of our soricid associations	125
Palaeogeography	131
Conclusion	134
Distribution in time	135
References	137
Tables	141

Introductory part

INTRODUCTION

When compared to other groups of small mammals, notably the Rodentia, the Soricidae are a somewhat neglected group in palaeontological studies. Most Neogene and Quaternary mammal localities have yielded remains of the Soricidae, which are usually only tentatively identified at family or subfamily level. As a result, unstudied collections of soricids are abundant.

The reason for this neglect is mainly their comparatively slow rate of evolution and the fact that the Soricidae are supposedly less useful for biostratigraphical purposes.

However, even from the preliminary determinations some interesting phenomena can be noted in the Plio-Pleistocene record of the Soricidae. For instance, Ruscinian shrew associations are rich in species, whereas the Villányian to Recent associations are poor. Furthermore, fossil associations of about the same age may differ strongly in the relative proportions of individual species, suggesting palaeoecological and/or palaeogeographical differentiation.

Study of such phenomena is hampered by our often poor taxonomical knowledge of fossil Soricidae. The last revision of European Soricidae (Friant, 1947) is by now highly outdated. Repenning (1967) gave a revision of the whole family, but he did not pay much attention to the species-level. However, it is still the most successful attempt to subdivide the Soricidae into subfamilies and tribes.

Since then, several investigators have dealt with separate species or genera of the Soricidae; Barbara Rzebik has made the most notable contributions (Rzebik-Kowalska, e.g. 1975, 1976, 1981). Still, it is felt that there is a considerable gap in our knowledge of this family; the present paper is an attempt to fill part of this gap.

Our investigation originally started as a part of the revision of the smaller mammals from Tegelen. It then appeared necessary to investigate material from other localities as well, not only for taxonomical reasons, but also for palaeoecological and palaeogeographical interpretations.

The author had access to rich Hungarian collections (including many type specimens). From these, a number of samples have been chosen, ranging in age from the earliest Ruscinian to the Tiglian/Villányian. These are Osztramos 9, 13, 1, 7, Csarnóta 2, Villány 3, and Osztramos 3. The Soricidae from these localities had been studied in rather a preliminary way, prior to more detailed examination.

In order to gain a better understanding of the taxonomical, palaeoecological and palaeogeographical phenomena, the choice of localities includes faunas from the earliest Ruscinian up to the Villányian and two associations from different geographical and supposedly different palaeoecological settings that are more or less contemporaneous with Tegelen: Villány 3 and Osztramos 3.

MATERIAL AND METHODS

The nomenclature of parts of the upper and lower dentition and of the mandible is given in Figures 1 and 2. The dentition consists of one incisor, three molars and small elements situated between the incisor and the molars: the antemolars (A). In the upper dentition, the P⁴ theoretically is also an antemolar, but it is never designated as such; the number of remaining antemolars may vary between three and five. In the lower dentition there is only one tooth called an antemolar (A₁), the A₂ is generally considered to be the P₄ and hence named as such.

In the literature, the antemolars of the Soricidae are often called 'unicuspids'. This name is considered incorrect, because quite often these teeth possess accessory cusps.

Our nomenclature of the dental pattern is in accordance with the existing literature, but a few new terms are introduced.

Between the parastyle and the paracone in P⁴ there may be a connective ridge. In this paper it is called parastylar crest, as an analogue to the antoconid crest in the lower molars. Furthermore, terms are introduced to describe the lower incisor. On I inf., cuspules may be present on the dorsal/occlusal edge. The number of cuspules (sometimes

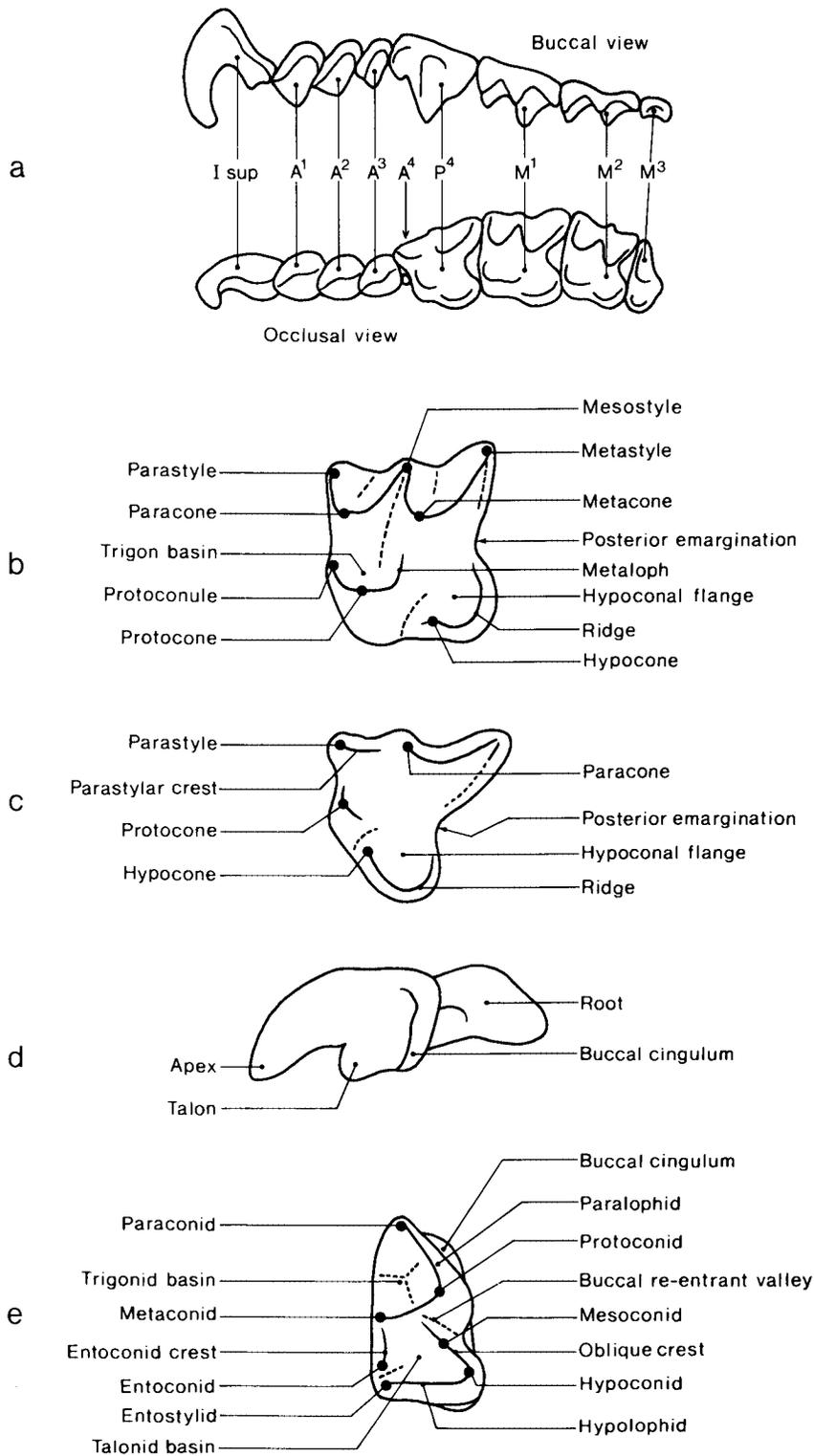


Fig. 1. Nomenclature of parts of the upper dentition and dental elements; a: upper dentition; b: M¹-M²; c: P⁴; d: I sup.; e: M₁-M₃.

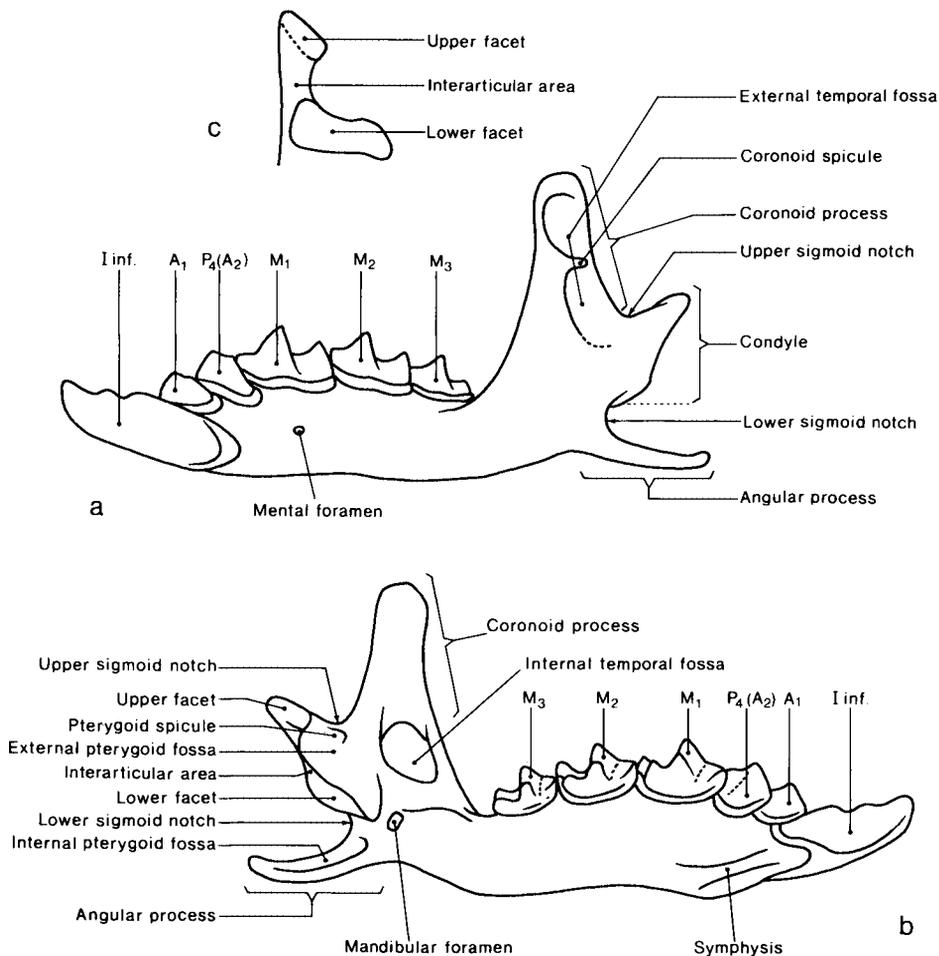


Fig. 2. Nomenclature of parts of the lower dentition and the ramus; a: external/buccal view; b: internal/lingual view; c: condyle.

referred to as serrations, undulations, cuspids or the like) can vary from zero to four. It is here proposed to refer to an incisor without cuspules as 'acuspulate', with one cuspule as 'monocuspulate', with two 'bicuspulate', with three 'tricuspulate', and with four cuspules as 'tetracuspulate'. This is illustrated in Fig. 3.

The following terms for anatomical directions are used:

- anterior — towards the front of the animal;
- posterior — towards the rear of the animal (also: caudal);
- buccal — the side of the dental elements facing the cheek;
- lingual — the side of the dental elements facing the tongue;
- occlusal — the side of dental elements facing the occluding element(s);
- symphyseal — the side of I inf. facing the symphysis of the two mandibular rami;
- dorsal — towards the back of the animal (opposite: ventral);
- medial — towards the midline (or sagittal plane) of the animal.

Measurements were taken with a Leitz Ortholux microscope fitted with a movable stage and measuring clocks. They are presented in the form of tables (1-53) and in diagrams, if relevant.

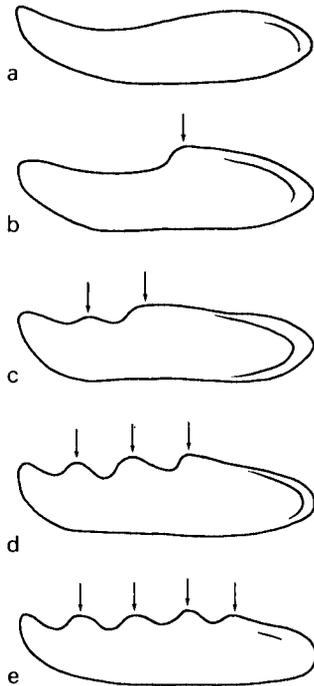


Fig. 3. Terminology of the lower incisor; a: acusulate; b: monocusulate; c: bicusulate; d: tricuspulate; e: tetracusulate.

The following measurements were taken (see Fig. 4):

I sup.: length (L), height (H) and length of the talon (LT). The line of orientation is the dorsal edge of the tooth; the measurements are taken either parallel or perpendicular to this line.

P⁴: length to the posterior emargination (PE), lingual length (LL), buccal length (BL), and width (W). P⁴ is oriented along its buccal edge, parallel to the line parastyle-posterobuccal corner.

M¹ and M²: PE, LL, BL, anterior width (AW), and posterior width (PW). These molars, as well as M³, are oriented along the anterior edge.

M³: length (L) and width (W).

I inf.: greatest length (L).

M₁ and M₂: trigonid width (TRW), talonid width (TAW) and length (L).

M₃: width (W) and length (L). The three lower molars are oriented along their lingual margins; cingula are included in the measurements.

The overall length (L) of M₁-M₃.

The mandibular ramus: the height of the coronoid process (H), measured from the uppermost point P of the arch in front of the angular process to the tip of the coronoid process; the length from P to the posterior rim of the mental foramen (L); the height of the condyle (HC); the lengths of the condylar upper facet (LUF) and of the lower facet (LLF). For measuring HC, the condyle is oriented along its buccal edge in caudal view. In the case of a lingual shift of the lower condyle, the narrow strip of the lower sigmoid notch is not included in LLF, except in the genera *Beremendia* and *Blarinoides*, where the boundary between the sigmoid notch and the lower facet is not clear.

A newly introduced index is the PE-index, which quantifies the degree of emargination of the large upper teeth. It has been calculated for M¹ and M², by means of the formula: $\frac{LL + BL}{2 \cdot PE} - 1$.

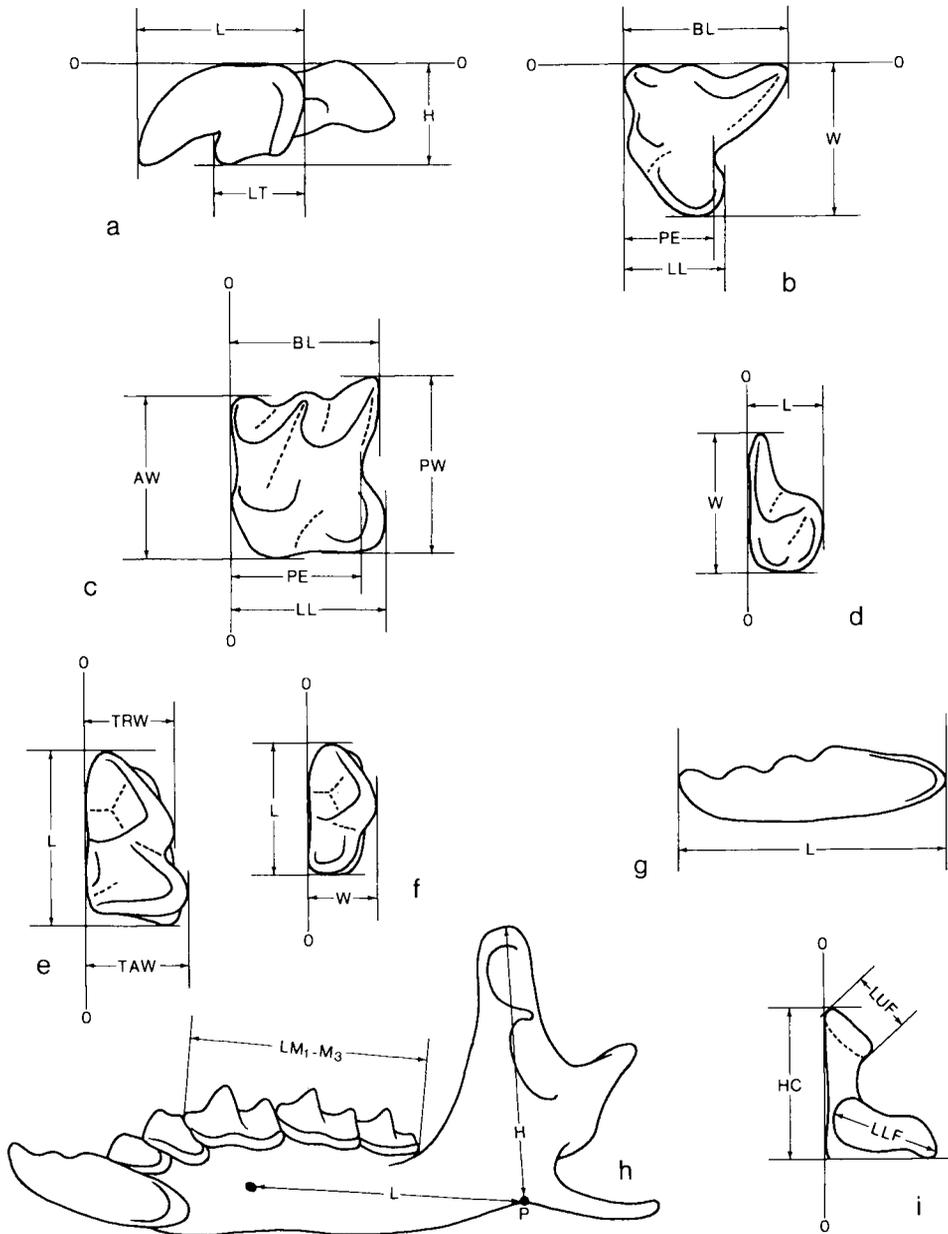


Fig. 4. Measurements taken for: a: I sup.; b: P⁴; c: M¹ and M²; d: M³; e: M₁ and M₂; f: M₃; g: I inf.; h: ramus; i: condyle; for abbreviations see text.

The mean of LL and BL is divided by PE, then 1 is subtracted; the result is a number that could theoretically lie between 0 and about 1. It will be clear that if the index is 0, there is no posterior emargination, i.e. the posterior edge of the tooth is straight. If the index is 1, then the emargination extends halfway along the tooth. The results of the calculations are presented in Table 54 and in Fig. 18.

Material has been studied from Tegelen (The Netherlands) and from the series of Hungarian localities mentioned above (Fig. 5).

None of the samples has been collected by the author; they were already processed and in some cases had been sorted. In order to obtain a good quantitative picture, most of the samples have been picked again by the author. In some cases the material had to be hardened with a plastic solution in acetone (Archaeoderm).

The Tegelen material is stored in the Rijksmuseum van Geologie en Mineralogie (abbreviated RGM) at Leiden, The Netherlands, and was made available by Dr M. Freudenthal.

The material from Csarnóta 2 is stored in the Magyar Állami Földtani Intézet (Hungarian State Geological Survey, abbreviated MÁFI) at Budapest, Hungary. It was made available by Dr László Kordos.

The other Hungarian material (from Villány 3 and the five Osztramos localities) is in the collections of the Természettudományi Múzeum (Natural History Museum, abbreviated TTM), also at Budapest and could be studied thanks to Dr Dénes Jánossy. The type materials from Villány 3 (or Villány Kalkberg) are stored in the MÁFI, not in the TTM.

For comparison, the author studied collections of Deutsch-Altenburg in the Paläontologisches Institut der Universität Wien (Vienna, Austria), curated by Dr Gernot Rabeder and the Hinton type materials (1911) in the British Museum (Natural History), London, England, curated by Dr Jeremy Hooker.

The Tegelen material has been mounted on Lego toy-bricks with Gimborn typewriter cleaner. The Hungarian material was only temporarily mounted on glass slides, also with typewriter cleaner; after being studied it was dismantled again.

LOCALITIES

Tegelen (Te)

The Tegelen Clay is exposed in about half a dozen clay pits, situated between the village of Tegelen and the Dutch-German border. The Dutch palaeontologist Eugène Dubois was the first to excavate and describe vertebrate fossils from these deposits (Dubois, 1904).

Since then, many publications have appeared on various aspects of the flora and fauna; most important of these are papers about the seeds (van der Hammen, 1951), pollen (Zagwijn, 1963), wood (van der Burgh, 1974), fish (Gaudant, 1979), molluscs (Meijer, in Freudenthal et al., 1976), and mammals (Bernsen, 1930, 1930-34; Schreuder, e.g. 1935, 1945; van der Meulen, in Freudenthal et al., 1976). An extensive, but now outdated survey of both flora and fauna was given by van der Vlerk & Florschütz (1950).

The first description of an insectivore was given by Schreuder (1940) for some skeletal fragments of a water-mole. Soricidae were first mentioned by van der Meulen (in Freudenthal et al., 1976).

The sample I studied is from the pit Russel Tiglia Egypte and forms part of the collection discussed in Freudenthal et al., 1976. The geology of the locality was extensively treated by Kortenbout van der Sluijs & Zagwijn (1962); their article contains a map showing the position of the locality. Our material was collected in the early seventies by a team under the leadership of Dr M. Freudenthal of the Rijksmuseum van Geologie en Mineralogie at Leiden, and is stored at the Museum. Freudenthal et al. (1976) described the methods of sampling and processing of the material.

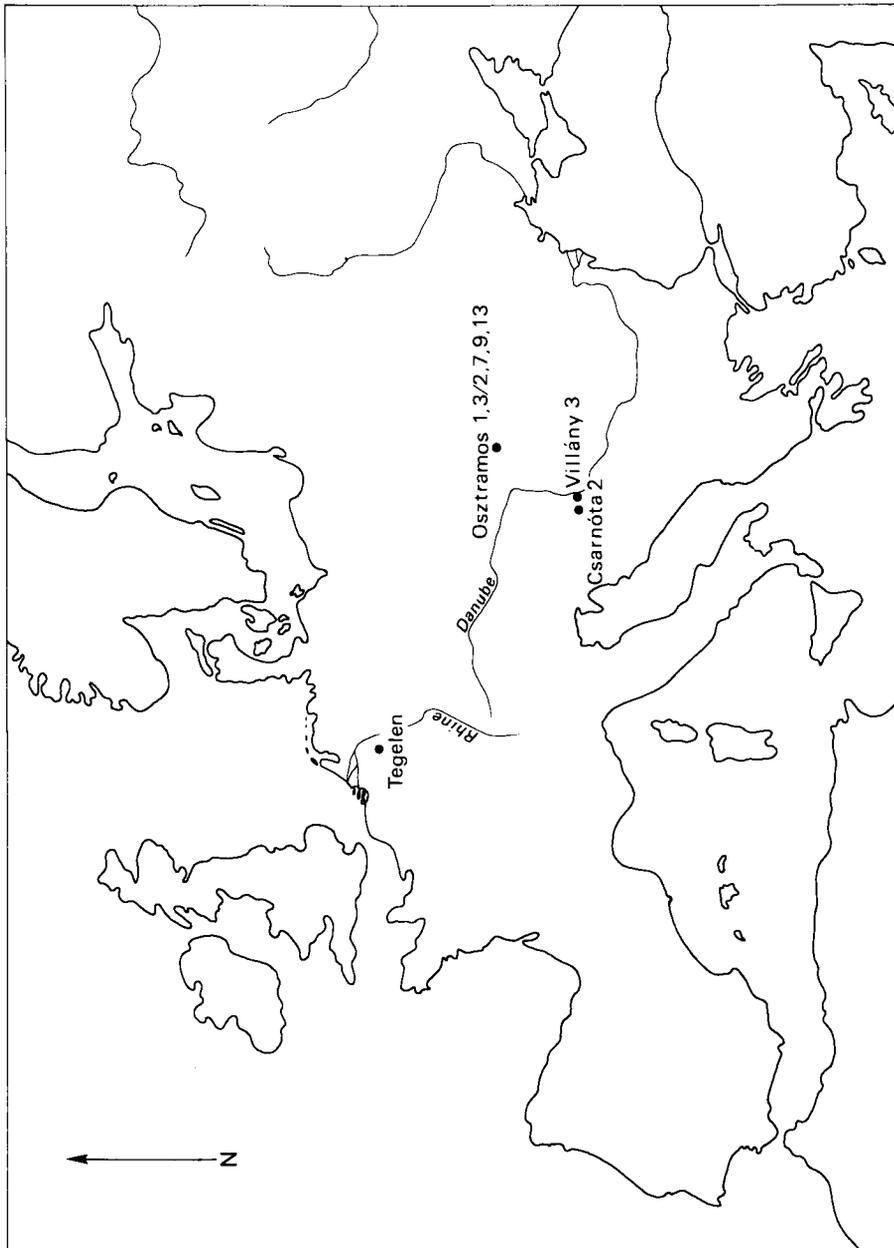


Fig. 5. Map showing the localities studied.

Stratigraphically, the main fauna of Tegelen is placed in pollen zone TC5 of the Tiglian (Zagwijn, 1963) and it is correlated with the late Villányian (van der Meulen, 1974; Freudenthal et al., 1976).

Villány 3 (Vi3)

This and the following locality are situated in the South Hungarian Villány Hills, near the Hungarian-Yugoslavian border. The area consists of limestones of Callovian and Oxfordian (Late Jurassic) age (Kormos, 1937b), which are strongly karstic. It has proved to be one of the richest mammal-yielding areas of Hungary; the various localities of Villány, Csarnóta, Beremend, Nagyharsányhegy, Somssichhegy are all situated in the Villány Hills.

Villány 3 is the same locality as Villány Kalkberg (Nordseite) of Kormos (e.g. 1937b). It is located in a small hill near the Villány railway station, the Templomhegy or Mésköhegy, which is partly quarried away. Maps of the situation are given by Jánossy (1979, figs. 5, 7), photographs of the quarry and its breccias are shown in Jánossy (1979, fig. 8) and Kormos (1937b, figs. 1-4). Lists of the faunal contents of Vi3 were published by Kormos (1937b), Kretzoi (1956) and Jánossy (1979).

The older collections are scattered all over Europe, so nothing could be said about the relative frequency of the various species. The sample we studied was collected in recent times by Dr D. Jánossy; it made it possible for us to perform quantitative studies.

The sample has been taken in three separate parts: Villány 3 alsó (alsó, Hung. = low) from the lower part, Villány 3 felső (felső = high) from the higher part and a sample just called Villány 3. Material from these three samples is lumped in the taxonomical and biometrical studies, but it is treated separately in the palaeoecological part as it shows slight differences in faunal content.

Villány 3 is placed in the lower part of the late Villányian (MN 17); it is the type locality of the so-called *Mimomys-Lagurodon* Zone (Kretzoi, 1956; van der Meulen, 1973, 1974; Jánossy, 1979). It is of the same age as the Tegelen deposits (van der Meulen, 1974; Freudenthal et al., 1976).

Csarnóta 2 (Cs2)

Csarnóta 2 is situated some 18 km west of Villány, in a hill called Cserhegy (see photographs in Kormos, 1937b and the map in Jánossy, 1979). Faunal lists were published by Kormos (1937b), Kretzoi (1956, 1962, annotated) and Jánossy (1979).

The locality has been excavated in layers of 25-30 cm thickness (Kretzoi, 1962); the whole section is several metres high (Kordos, pers. comm.). Individual layers are numbered in the present paper, from 0 through 25 and designated Cs2/0, Cs2/1, etc., Cs2/0 being the highest. In the taxonomic descriptions the locality is treated as a whole.

Kretzoi (1962) already had 21 layers at his disposal and gave a rodent-spectrum for these (op. cit., p. 320). To this, a shrew-spectrum is added here (Figs. 19, 20).

Csarnóta 2 is the type-locality of the Csarnótian of Kretzoi (1959a), a stage originally meant to be situated above the Astian and below the Villányian/Villafranchian and corresponding to the uppermost Pliocene (Kretzoi, 1959a). In 1962, Kretzoi gave a more detailed diagnosis of the Csarnótian; it was correlated with part of the Astian and put above the Ruscinian, which he introduced in the same paper.

Van de Weerd et al., 1982, consider the Csarnótian (erroneously spelled Csarnotian) to be the upper half of the Ruscinian, corresponding to MN zones 15b and 16a. However, they place the type-locality, Csarnóta 2, in the upper half of their Csarnótian (MN 16a). In our paper, the Csarnótian is considered to be the uppermost part of the Ruscinian (MN 16a). Its upper boundary is placed at the onset of the Villányian (Beremend phase) with its cooler faunas. Its lower boundary is not defined (see Fig. 23).

Osztramos

The mammal-bearing localities of Osztramos are found in a large quarry on the hill Osztramos (or Esztramos), where limestones of Ladinian (Middle Triassic) age are exploited. The hill is part of the Rudabánya Mountains, close to the Hungarian-Czechoslovakian border, north of the town of Miskolc. Numerous karst fissures and caves in the rock have been exposed by the quarrying activities; they contain sediments and faunas ranging in age from the early Ruscinian to the Biharian.

The first collection of fossil mammals from Osztramos was made by Kretzoi c.s. in 1955 and published the year after (Kretzoi, 1956). A survey of the localities (by then 20) was given by Jánossy & Kordos, 1977. In that paper, and in Jánossy (1979) there are maps of the Osztramos quarry. Due to continued quarrying, the situation has changed since. The following localities are studied here (in numerical order):

Osztramos 1 (Osz1)

In fact, Osztramos 1 is an accumulation of several fossiliferous deposits in a very long but narrow karstic fissure; its length is about 400 m, with a width of 3-4 m (Jánossy, 1972). The various fossiliferous pockets in this fissure were designated 1A through 1F. Here, they are treated as belonging to one locality, Osz1.

A map showing the position of Osz1 and its subdivisions was given by Jánossy & Kordos (1977) and Jánossy (1979); in the former publication two photographs (figs. 6, 7) were given showing the locality. The small mammals from Osz1 were described in a separate paper (Jánossy, 1972).

Osztramos 1 is the type locality of the Estramontian Stage of Jánossy, 1972. The Estramontian is here considered to be the lowermost part of the Ruscinian (\pm MN 14). Its lower boundary is the Turolian-Ruscinian boundary. Jánossy (1972) stressed the difference between Osztramos 1 and the late Turolian Polgárdi fauna. The upper boundary of the Estramontian is not defined. It is not possible to use the (not fixed) beginning of the Csarnótian as the upper boundary of the Estramontian. There is a large gap between the Estramontian and the Csarnótian, roughly corresponding to MN 15. So far, no Hungarian mammal-bearing locality is known from this zone, so there is still a gap in the local biostratigraphy. Jánossy (1973a) calls this gap Ruscinian, but this is not followed here.

Osztramos 3 (Osz3/2)

Osztramos 3 is a cave containing deposits 10 m high and 5-6 m wide (Jánossy & Kordos, 1977). Photographs of the locality appeared in Jánossy & Kordos (1977, fig. 10) and Jánossy (1979, photo 7). The former paper (op. cit., fig. 20) contains a drawing showing the section and the individually sampled levels. For the present study only material from level 2 has been used; this level is designated Osz3/2.

Osztramos 3 represents the uppermost part of the Kisláng phase, when a cooling trend corresponding to the Eburonian glaciation became apparent (Jánossy & van der Meulen, 1975; Jánossy & Kordos, 1977). Osztramos 3 is somewhat younger than Tegelen and Villány 3 (Freudenthal et al., 1976).

Osztramos 7 (Osz7)

Osztramos 7 is a fissure filling some 30 m high and 1-2 m wide (Jánossy & Kordos, 1977). 'The upper part of the sediment was more dark red, the lower one more yellowish, both intercalated by calcite beds' (op. cit.). This difference in facies and the presence of calcite floors suggest that the sedimentation of Osz7 took place over a long period of time, and

was perhaps even discontinuous Jánossy (1973a) stated that about twenty metres of the section had been explored, and furthermore that 'any mix up is wholly excluded'. This does not apply to the collected samples. Personal observations by the author revealed that the fissure is exposed from the side, i.e. a rather large surface is available for collecting. Since bits and pieces of the section have fallen down and are being collected, it is quite likely that fossils have been displaced and have become mixed up in the collections.

Jánossy (1973a) and Jánossy & Kordos (1977) consider Osztramos 7 to yield a marker fauna for the Pliocene-Pleistocene boundary. This is based on the presence of *Lemmus* teeth in the fauna, indicating the onset of a cooler climate.

In our paper, several presumedly Estramontian fauna elements are described from Osztramos 7 (*Sorex bor*, *Amblycoptus* sp.). This fact together with the supposedly long sedimentary history lead us to the conclusion that Osztramos 7 spans a rather long period of time, coinciding mainly with the Csarnótian. Its lower part could reach down into the Estramontian; its upper part may reach the Villányian. In Fig. 23, Osztramos 7 is indicated by a bar in order to stress this supposition. The Ruscinian-Villányian boundary should be present somewhere in the section.

A faunal list was published by Jánossy (1979); the book also includes a photograph of the locality (photo 5). Jánossy & Kordos (1977) give two photographs (figs. 15, 16) and a general map showing the position of the locality in the quarry (fig. 19).

Osztramos 9 (Osz9)

This is the oldest locality studied. Its sediments have been penetrated by the fissure of Osztramos 1, suggesting that Osz9 is older (Jánossy & Kordos, 1977). The fauna confirms this assumption.

Osztramos 9 is here considered to belong to the lowermost Estramontian. A list of the fauna was published by Jánossy (1974); to this list Topál (1975) added a bat. A photograph of Osz9 is included in Jánossy & Kordos (1977, fig. 12)

Osztramos 13 (Osz13)

The locality of Osztramos 13 has yielded a very peculiar faunule, consisting only of bats and one specimen of *Episoriculus gibberodon* (originally described as *E. tornensis* by Jánossy, 1973b).

The position of the deposit in the quarry is indicated on the map in Jánossy & Kordos (1977) and Jánossy (1979). Jánossy (1974) considered Osz13 to be of the same age as Osz9. There is no way to confirm or deny this assumption.

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Taxonomical part

SUBFAMILIES AND TRIBES

The most recent comprehensive revision of the taxonomy of the Soricidae was made by Repenning (1967). He acknowledged the presence of five subfamilies: the Heterosoricinae, Limnoecinae, Allosoricinae, Crocidurinae, and Soricinae. The first three subfamilies are extinct, the latter two are still extant.

Repenning divided the Soricinae into three tribes: the Soricini, Blarinini and Neomyini. Essentially, these three tribes are based on differences in two morphological characters: the presence or absence of an entoconid crest in M_1 and M_2 and the shape of the interarticular area of the condyle. If the entoconid crest is absent and the interarticular area is broad, then a soricine shrew belongs to the tribe Blarinini. In the other two tribes the entoconid crest is present. If the interarticular area is rather broad we are dealing with a member of the Soricini; if this area is narrow, we have a representative of the Neomyini.

In our present revision, these characters are used too, but we also consider a combination of several other characters, such as the absence or presence of pigmentation, the reduction or absence of the entoconid, the fissidenty of the upper incisor, and the morphology of the condylar process.

The present study follows Repenning's classification, except in the case of the Allosoricinae and the Neomyini.

The group of genera comprised in the tribe Neomyini of Repenning, 1967 shows a wider variation than any of the non-soricine subfamilies. The difference between several genera of the Neomyini appears to be of a similar magnitude as that between the other two tribes in the Soricinae. Therefore, the tribe Neomyini is here replaced by four tribes: the Soriculini, Beremendiini, Amblycoptini, and Notiosocini. In addition, the subfamily Allosoricinae Fejfar, 1966 is here considered to be a soricine tribe. This conclusion is supported by the morphology of the P_4 , which has a postero-lingual basin characteristic for the Soricinae.

Together with the Soricini and the Blarinini, this makes a total of seven tribes within the subfamily Soricinae.

Part of the newly defined tribe Allosoricini was included in Repenning's Neomyini, viz. in the genus *Petenyiella* (this material is here assigned to *Paenelimnoecus*).

The relation between the old classification of the Soricinae and the one proposed here is shown in Fig. 6. Our determination key to the Soricidae is as follows.

- | | |
|--|----------------------------|
| 1a. Internal temporal fossa of the mandible not pocketed | Subfamily Heterosoricinae. |
| 1b. Internal temporal fossa of the mandible pocketed | 2. |
| 2a. Interarticular area of the condyle not emarginated lingually | 3. |
| 2b. Interarticular area of the condyle emarginated lingually | Subfamily Soricinae 4. |
| 3a. Teeth not pigmented, P_4 tetrahedral; restricted to the Old World (Africa and Eurasia) | Subfamily Crocidurinae. |
| 3b. Teeth pigmented, P_4 with a central blade, restricted to North America | Subfamily Limnoecinae. |
| 4a. Entoconid crests absent | 5. |
| 4b. Entoconid crests present | 7. |

- 5a. Condyle with broad interarticular area, entoconids present, teeth pigmented, I sup. not fissident
Tribe Blarinini.
- 5b. Condyle with narrow interarticular area and triangular upper facet 6.
- 6a. Interarticular area of condyle very narrow, teeth unpigmented, M3 reduced or missing, M¹ with parastyle, teeth rather stout and bulbous
Tribe Amblycoptini.
- 6b. Interarticular area not very narrow, teeth may be pigmented, entoconids either extremely reduced or absent, metaconids close to protoconids, parolophid forming a carnassial blade
Tribe Allosoricini.
- 7a. Interarticular area very broad, lower facet strongly shifted anteriorly, I sup. strongly fissident, teeth pigmented
Tribe Beremendiini.
- 7b. Interarticular area less broad, lower facet at least partly visible from the side 8.
- 8a. Lower condylar facet reaching the lower sigmoid notch, interarticular area not very narrow, teeth pigmented
Tribe Soricini.
- 8b. Lower condylar facet separated from the lower sigmoid notch by a groove 9.
- 9a. Upper condylar facet large, triangular or ovoid, interarticular area short, I sup. not fissident, teeth pigmented; restricted to North America
Tribe Notiosoricini.
- 9b. Upper facet cylindrical, interarticular area high and narrow, I sup. fissident, teeth pigmented; restricted to Eurasia
Tribe Soriculini.

Selected genera	Tribes (this paper)	Tribes (according to Repenning, 1967)	Subfamilies (according to Repenning, 1967 and Baudelot, 1972)	Subfamily (this paper)
<i>Sorex</i> <i>Drepanosorex</i> <i>Deinsdorfia</i> <i>Petenya</i> <i>Blarinella</i> <i>Dimylosorex</i> <i>Zelceina</i> <i>Crocidosorex</i> <i>Oligosorex</i>	SORICINI Fischer von Waldheim, 1817	SORICINI Fischer von Waldheim, 1817	SORICINAE	SORICINAE
<i>Blarina</i> <i>Blarinoides</i> <i>Shikamainosorex</i> <i>Cryptotis</i> <i>Sulimskia</i> gen.nov. <i>Mafia</i> gen.nov.	BLARININI Kretzoi, 1965	BLARININI (Stirton, 1930)		
<i>Notiosorex</i> <i>Hesperosorex</i> <i>Megasorex</i> <i>Bechiasorex</i>	NOTIOSORICINI new tribe	NEOMYINI Repenning, 1967		
<i>Neomys</i> <i>Macroneomys</i> <i>Soriculus</i> <i>Episoriculus</i> <i>Nesiottilis</i> <i>Chimarrogale</i> <i>Chodsigoa</i> <i>Nectogale</i>	SORICULINI Kretzoi, 1965			
<i>Beremendia</i>	BEREMENDIINI Gureev, 1971			
<i>Amblycoptus</i> <i>Anourosorex</i> <i>Anourosoricodon</i> <i>Paranourosorex</i> <i>Crusafontina</i>	AMBYCOPTINI Kormos, 1926			
<i>Paenelimoecus</i> (ex- <i>Petenyiella</i>)	ALLOSORICINI Fejfar, 1966	X		
<i>Paenelimoecus</i>			ALLOSORICINAE	
" <i>Sorex</i> " <i>gracilidens</i> <i>Allosorex</i>				

Fig. 6. Diagram showing the relations between the tribal and subfamilial taxonomy of Repenning (1967) and Baudelot (1972) and the classification proposed here.

SORICIDAE Gray, 1821

Subfamily Heterosoricinae Viret & Zapfe, 1951

For an extensive revision of this extinct subfamily the reader is referred to Repenning (1967) for New World genera and to Engesser (1975) for Old World genera. This subfamily is not dealt with in this paper.

Subfamily Limnoecinae Repenning, 1967

This extinct subfamily is restricted to the New World and appears to be the American analogue for the Old World Crocidurinae in several respects, notably in the structure of the condyle and the reduced talonid in M_3 . It should be noted here that assignments of European soricids to this subfamily (e.g. Baudelot, 1972) are highly questionable (see Engesser, 1979). This subfamily is not dealt with in this paper.

Subfamily Crocidurinae Milne-Edwards, 1874.

The Crocidurinae are restricted to the Old World and nowadays have their main distribution in Africa, where it is the only soricid subfamily present. The subfamily is characterized by: P_4 of tetrahedric shape; no pigmentation of the dental elements; facets of the mandibular condyle more or less united along the lingual side of the condyle, which therefore shows a buccal emargination. In Europe, representatives of the Crocidurinae are known from the early Miocene onwards up to the present; in the time span covered by the present study (earliest Pliocene-early Pleistocene) the only genus found in Europe is *Crocidura* (late Ruscinian-Recent).

Subfamily Soricinae Fischer von Waldheim, 1817

This is by far the most diverse soricid subfamily. It is characterized by a P^4 , which has a postero-lingual basin and a buccal overhang of the crown over the root; condyle with two, usually separated, articular facets; the connective part (the interarticular area) has a lingual emargination. This subfamily is divided into the following seven tribes.

Tribe Soricini Fischer von Waldheim, 1817

Type genus — The type genus is *Sorex* L., 1758.

Diagnosis — Teeth pigmented (except in *Crocidosorex*); articular separation small to moderate with a relatively broad interarticular area; internal temporal fossa large and triangular; lower first and second molars with an entoconid crest; the upper incisor may be fissident.

Distribution — The tribe has an Holarctic distribution. The following European genera are here attributed to this tribe: *Crocidosorex* Lavocat, 1951 (late Oligocene - early Miocene, Europe); *Oligosorex* Kretzoi, 1959 (late Oligocene - early Miocene, Europe);

Sorex L., 1758 (early Ruscinian - Recent, Europe; early Blancan - Recent, North America); *Drepanosorex* Kretzoi, 1941 (Villányian - Biharian, Europe); *Dimylosorex* Rabeder, 1972 (Biharian, Europe); *Petenya* Kormos, 1934 (early Ruscinian - early Pleistocene, Europe); *Blarinella* Thomas, 1911 (early Turolian - late Ruscinian, Europe; Recent, Asia); *Zelceina* Sulimski, 1962 (late Ruscinian, Europe); *Deinsdorfia* Heller, 1963 (early Ruscinian - early Pleistocene, Europe).

Tribe Blarinini Kretzoi, 1965

Type genus — *Blarina* Gray, 1838.

Synonym — Blarinini Repenning, 1967; not *Blarina* group Stirton, 1930.

Diagnosis — Teeth pigmented; articular separation pronounced with a broad interarticular area; lower facet placed towards the anterior and the lingual when compared to the Soricini; internal temporal fossa of moderate size; entoconid crest lacking in the lower molars; upper incisor not fissident.

Distribution — Representatives are known from Eurasia and America; the following European genera are attributed to this tribe: *Blarinoides* Sulimski, 1959 (Ruscinian); *Sulimskia* gen. nov. (late Ruscinian); *Mafia* gen. nov. (Ruscinian).

Remark — Repenning (1967) mentions Stirton (1930) as the original author of the tribe Blarinini. However, Stirton did not formally establish tribes but merely distinguished 'generic groups'. One of these, the *Blarina* group, contained the genera *Neomys*, *Chimarroale*, *Soriculus*, *Cryptotis*, *Blarina*, and *Notiosorex*; these genera are now included in either the Soriculini, Blarinini, or Notiosoricini. The tribe Blarinini sensu Repenning and the *Blarina* group of Stirton are therefore entirely different. The name Blarinini was formally introduced by Kretzoi (1965) with a brief description and was considered to contain the genera *Blarina*, *Blarinella*, *Beremendia*, *Paracryptotis*, *Cryptotis*, *Shikamainosorex*, *Petenya*, and (probably) *Peisorex*. This group of genera is to a large degree the same as the one included in the Blarinini sensu Repenning. Therefore, Kretzoi, 1965, is here considered to be the author of this tribe.

Tribe Soriculini Kretzoi, 1965

Type genus — *Soriculus* Blyth, 1854.

Synonym — Neomyini Repenning, 1967 (partim).

Diagnosis — Upper incisor fissident; teeth lightly pigmented; strong articular separation emphasized by a narrow interarticular area which is present only at the buccal side of the condyle; lower facet elongated lingually and offset from the lower sigmoid notch at its buccal side; entoconid crests in M_1 - M_2 present but sometimes low; lower incisor never tricuspluate.

Distribution — The tribe is known from Eurasia only; included are: *Neomys* Kaup, 1829 (early Pleistocene - Recent, Europe; Recent, Asia); *Episoriculus* Ellerman & Morrison-

Scott, 1951 (late Turolian - early Pleistocene, Europe; Recent, Asia); *Chodsigoa* Kastschenko, 1907 (Pleistocene - Recent, Asia); *Nesiotites* Bate, 1944 (late Pliocene - Holocene, Europe); *Nectogale* Milne-Edwards, 1870 (Recent, Asia); *Soriculus* Blyth, 1854 (Recent, Asia); *Macroneomys* Fejfar, 1966 (Ruscinian, Europe); *Neomysorex* Rzebik, 1981 (early Ruscinian, Europe).

Remark — It will be clear that the name *Soriculini* Kretzoi, 1965 (which tribe includes *Neomys*) has priority over *Neomyini* Repenning, 1967.

Tribe Beremendiini new tribe

Type genus — *Beremendia* Kormos, 1934.

Synonyms — Subtribe *Beremendina* Gureev, 1971; *Neomyini* Repenning, 1967 (partim).

Diagnosis — Upper incisor strongly fissident; teeth heavily pigmented; Blarinini-like condyle with broad interarticular area and anteriorly placed lower facet; lower incisor acusulate; entoconid crests present.

Remark — This is the only monogeneric tribe amongst 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 the *Soriculini* (fissident I sup., entoconid crests) and the *Blarinini* (structure of the condyle, intense pigmentation).

Tribe Amblycoptini Kormos, 1926

Type genus — *Amblycoptus* Kormos, 1926.

Synonyms — *Amblycoptinae* Kormos, 1926; *Anourosoricini* Stirton, 1930, in: Sulimski et al., 1979; *Neomyini* Repenning, 1967 (partim).

Diagnosis — Upper incisor not fissident; lower incisor acusulate; teeth not pigmented and more or less bulbous; M¹ with a well-developed parastyle; M₃ reduced or absent; internal temporal fossa a narrow and small foramen only; interarticular area of condyle reduced to a narrow ridge.

Distribution — This tribe appears to be the most specialized supra-generic group within the Soricidae. To this tribe are attributed: *Anourosorex* Milne-Edwards, 1870 (early Turolian, Europe; middle Pliocene - Recent, Asia); *Amblycoptus* Kormos, 1926 (late Turolian - early Ruscinian, Europe); *Crusafontina* Gibert, 1974 (Vallesian, Europe); *Anourosoricodon* Topachevsky, 1966 (Pliocene, Europe); *Paranourosorex* Rzebik-Kowalska, 1975 (early Ruscinian, Europe).

Tribe Allosoricini Fejfar, 1966

Type genus — *Allosorex* Fejfar, 1966.

Synonyms — Allosoricinae Fejfar, 1966; Neomyini Repenning, 1967 (partim).

Diagnosis — Upper incisor may be fissident; entoconid and entoconid crest virtually or completely absent; hence hypolophid ends in the entostylid, which parallels the entoconid of other Insectivora in function and in position; metaconid low and close to the protoconid; paralophid long and nearly parallel to the longitudinal axis of the jaw, resembling a carnassial blade, particularly in M_1 . Condyle with short interarticular area and triangular upper facet.

Distribution — This tribe is known from Europe only and is now extinct. Attributed taxa are: *Allosorex* Fejfar, 1966 (Ruscinian); '*Sorex*' *gracilidens* Viret & Zapfe, 1951 (Miocene); *Paenelimnoecus* Baudelot, 1972 (= *Petenyiella* sensu Kretzoi, 1959a, non Kretzoi, 1956) (Miocene - late Ruscinian).

Remark — The proposed inclusion of *Petenyiella* sensu Kretzoi, 1959a in *Paenelimnoecus* will be dealt with in the description of the genus.

Tribe Notiosoricini new tribe

Type genus — *Notiosorex* Baird, 1877.

Synonym — Neomyini Repenning, 1967 (partim).

Diagnosis — Upper incisor not fissident; teeth pigmented; entoconid crests in M_1 - M_2 present but low; condyle with oval or triangular upper facet and broad oval lower facet; interarticular area broad and short; lower facet clearly separated from the lower sigmoid notch by a groove due to lingual displacement; internal temporal fossa narrow.

Distribution — Its distribution is restricted to North America; to this tribe are attributed: *Hesperosorex* Hibbard, 1957 (Hemphillian); *Beckiasorex* Dalquest, 1972 (late Pliocene); *Notiosorex* Baird, 1877 (early Blancan - Recent); *Megasorex* Hibbard, 1950 (Recent).

DESCRIPTIONS

Subfamily Crocidurinae Milne-Edwards, 1874.

Genus *Crocidura* Wagler, 1832

Type species — *C. leucodon* (Hermann, 1780).

Crocidura kornfeldi Kormos, 1934
Pls 1, 2.

Holotype — A skull with partial dentition (of which the left A^4 got lost after 1934), coll. MÁFI no. Ob. 3686 (Pl. 1, fig. 1).

Type locality — Villány Kalkberg (= Vi3), Hungary.

Studied localities — Villány 3, Osztramos 3/2.

Selected other localities — Villány 5, Somssichhegy 1, Osztramos 2, 8 and 14, Nagyharsányhegy 2 (all Hungary, compare Jánossy, 1979).

Stratigraphic range — Late Villányian - early Biharian (Kisláng and Betfia phases).

Synonymy (only concerning the studied localities)

Crocidura Kornfeldi, in: Kormos, 1934 p. 304 (Vi3), fig. 37.

Crocidura Kornfeldi Korm., in: Kormos, 1937b, p. 1090 (Vi3).

Crocidura kornfeldi Kormos, in: Kretzoi, 1956, pp. 61 and 184 (Vi3).

Crocidura cf. kornfeldi Kormos, in: Jánossy & Kordos, 1977, p. 44 (Osz3).

Crocidura kornfeldi Kormos, in: Jánossy, 1979, p. 34 (Vi3).

Crocidura cf. kornfeldi Kormos, in: Jánossy, 1979, p. 36 (Osz3).

Original description — Kormos (1934) did not give a formal diagnosis, but only a description, from which the following items may be used as diagnostic features: P⁴, M¹ and M² relatively short and broad, molars with a short emargination; I inf. acuspulate; A₁ and A₂ broad; there is a thick bar between the anterior base of the coronoid process and the condyle, underneath the internal temporal fossa; a deep groove is present below this bar.

Emended diagnosis — Relatively small *Crocidura* species; P⁴ and molars relatively short and broad; of the upper antemolars, A¹ is much larger than A² and A³, and A² is slightly smaller than A³. A³ is nearly as high as the parastyle of P⁴ in buccal view. P⁴ has a protocone which is situated buccally, away from the antero-lingual corner. Lower molars with a narrow, undulating cingulum. Ascending ramus stout, internal temporal fossa bordered ventrally by a thick bar. Condyle relatively large.

Studied material

Villány 3: 7 I sup., 8 AA sup., 4 P⁴, 3 M¹, 2 M², 2 M³, 17 I inf., 13 A₁, 18 P₄, 33 M₁, 33 M₂, 27 M₃, 21 condyles.

Villány 3 alsó: 10 I sup., 2 AA sup., 8 P⁴, 7 M¹, 6 M², 7 I inf., 4 A₁, 9 P₄, 30 M₁, 27 M₂, 14 M₃, 21 condyles.

Villány 3 felső: 4 I sup., 8 AA sup., 10 P⁴, 10 M¹, 5 M², 13 I inf., 8 A₁, 12 P₄, 31 M₁, 33 M₂, 26 M₃, 19 condyles

In addition, the holotype has been studied (see above).

Osztramos 3/2: 3 fragmentary mandibles, each with M₁-M₃, one with the ascending ramus; one maxilla with I sup.-M¹.

Measurements — See Tables 1-2; the measurements for Villány 3 include all material from this locality.

Description

I sup. — The cingulum along the posterior buccal margin is narrow but well pronounced; usually it is undulate.

AA sup. — Of the three upper antemolars, the first one is by far the largest, the two posterior ones are considerably smaller; A² is slightly smaller than A³. The elements overlap only to a small degree. Between A³ and P⁴ a short diastema is sometimes present. The upper antemolars are provided with cingula on both sides. When seen from the buccal side, the A³ and the parastyle of the P⁴ are of about equal height (see Pl. 1, figs. 4b, 6b).

P⁴ — The parastyle of P⁴ is protruding and separated from the paracone by a deep valley; a parastylar crest is not present. The protocone is small and situated buccally of the antero-lingual corner (which is therefore rounded). The hypocone is not visible as a distinct cusp. Instead, a cingulum-like ridge runs along the lingual margin of the tooth. This hypoconal ridge is separated from the protocone by a valley. The posterior emargination is strong.

M^1 and M^2 — The two larger upper molars are relatively broad and short and of slender appearance. The protocone is connected to the paracone, but between the protocone and the metacone there is a wide and deep valley. The hypocone is situated postero-lingually of the protocone. It is poorly individualized and separated from the protocone by a valley. In M^1 the postero-buccal corner protrudes strongly, while in the antero-buccal corner a little parastyle is sometimes present. The shape of M^2 is trapezoidal. In a few M^1 a small cusplule is found in the valley between mesostyle and metastyle (see Pl. 1, fig. 3). A similar cusplet may be found in several Recent African species of the genus *Crocidura* (see for example Hutterer & Jenkins, 1980).

M^3 — Protocone and hypocone are united into a ridge surrounding the lingual basin of the tooth; the paracone is the best developed cusp.

I inf. — The apex is upturned; the upper (dorsal) margin is sometimes slightly monocuspulate or bicuspulate (the illustrated specimen, Pl. 2, fig. 4, is an extreme). The buccal cingulum is narrow but pronounced. I inf. reaches back to the posterior end of A_1 , underneath P_4 (Pl. 2, fig. 3).

A_1 — This element is quite elongate antero-posteriorly; only a small part of it is hidden underneath P_4 . The cingulum is weak buccally, but well developed at the lingual side.

P_4 — P_4 is typical for *Crocidura*: a high, pointed, tetrahedron-shaped tooth. The cingulum is equally strong on both sides.

M_1 and M_2 — The lower molars are also typical for *Crocidura*; the buccal re-entrant valley opens high above the cingulum; the entoconid crest is low to nearly absent. The buccal cingulum is narrow but well pronounced; it is undulate in practically all specimens, particularly in M_1 . Lingual cingulum weak.

M_3 — The talonid in M_3 is reduced to a single cuspid, the hypoconid. The development of the cingula is as in M_1 and M_2 .

Mandible — The coronoid process is blunt and low, the coronoid spicule is either absent or small, hardly developed and situated high. The anterior part of the coronoid process leans slightly backward, and sometimes has a somewhat rough spot in the middle. The external pterygoid fossa is strongly excavated. The pterygoid boss is well developed. The whole condyle reaches far backward and is comparatively large. The internal temporal fossa is large and open, reaching to halfway up the coronoid process. The region underneath the internal temporal fossa is excavated, separated from the fossa by a protruding ridge. The mandibular foramen is small; the mental foramen is situated underneath the P_4/M_1 transition.

Plate 1

Crocidura kornfeldi Kormos, 1934.

1. Holotype, Vi3 (Villány Kalkberg), coll. MÁFI no. Ob.3686.

2. Left. I sup., Vi3 alsó.

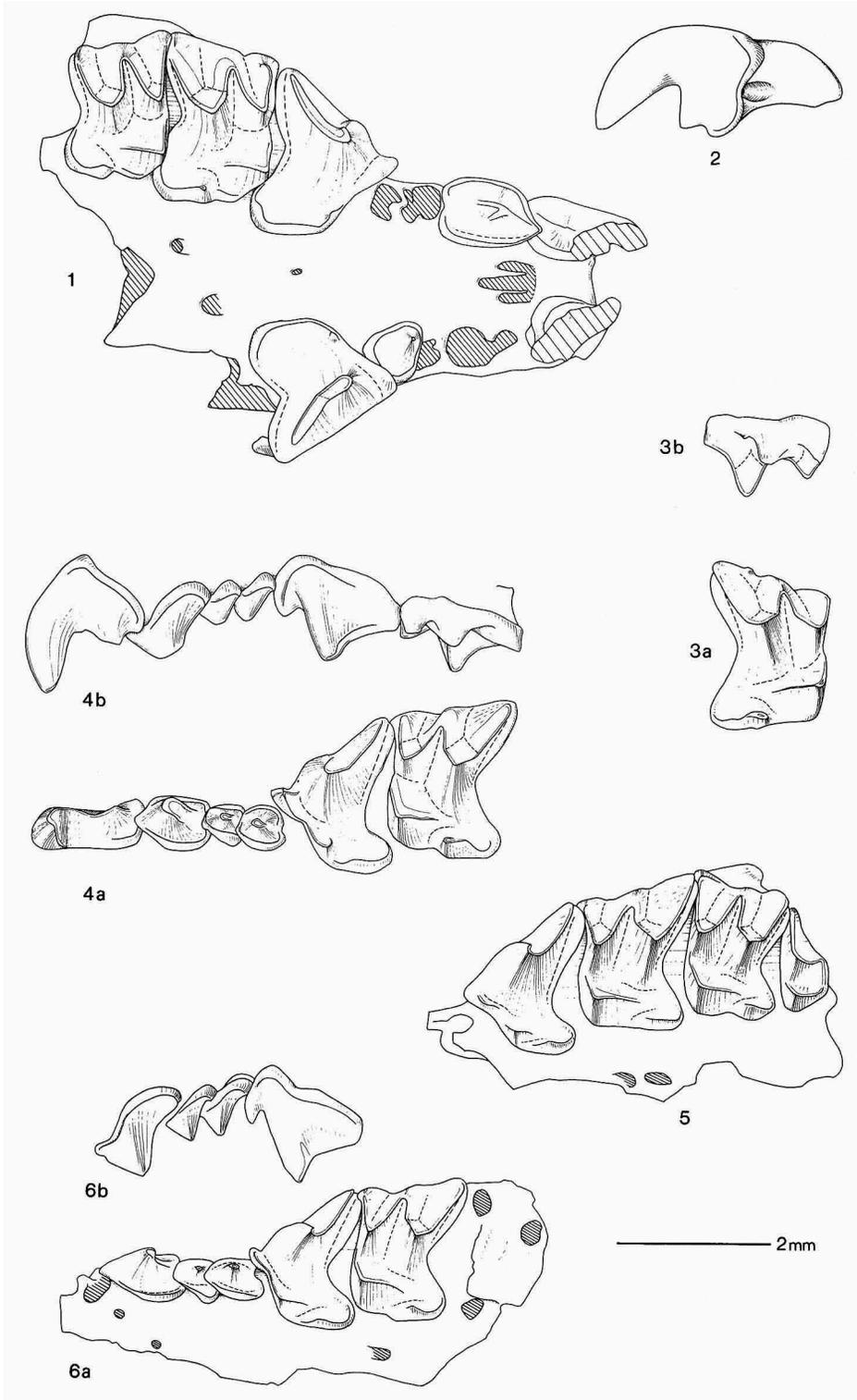
3. Right M^1 with small extra cusplule between mesostyle and metastyle, Vi3 alsó; a: occlusal view; b: buccal view.

4. Left I sup.- M^1 , Osz3/2; a: occlusal view; b: buccal view.

5. Left P^4 - M^3 , Vi3.

6. Left A^1 - M^1 , Vi3 felső; a: occlusal view; b: buccal view.

Plate 1



Remarks — *Crocidura kornfeldi* Kormos, 1934 is the oldest *Crocidura* species recorded from the European mainland. At present, the genus is represented in Europe by a number of (more or less closely related) species, such as *C. russula*, *C. leucodon* and *C. suaveolens*. For a few biogeographical remarks, the reader is referred to the final chapter of this paper.

Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Soricini Fischer von Waldheim, 1817

Genus *Sorex* L., 1758

Type species — *S. araneus* L., 1758.

Remarks — The genus *Sorex* L., 1758 has long been the waste-basket for soricid remains. Large numbers of 'Sorex' species have been described, many of which belong to other genera, tribes or even to other subfamilies. For instance, *Sorex tasnadii* Kretzoi, 1941, *Sorex pachyodon* Pasa, 1948 and *Sorex savini* Hinton, 1911 have been assigned to *Drepanosorex*; *Sorex dehneli* Kowalski, 1956 belongs to the tribe Blarinini; *Sorex pusilliformis* Doben-Florin, 1964 and *Sorex dehmi* Viret & Zapfe, 1951 are referred to the subfamily Crocidurinae.

Sorex is now well defined thanks to Repenning (1967), who set morphological limits that are comparable with those for other genera in the Soricidae. Nevertheless, *Sorex* is still a very large genus, with many species and a wide distribution both in space and time.

A thorough revision of the genus is definitely needed, as is a revision of related groups. This, however, would be beyond the scope of this paper. A problem arises for instance, concerning the generic status of *Drepanosorex*. Rabeder (1972a) concludes that *Drepanosorex* is a distinct genus 'without doubt', although resembling *Sorex* in essential characters. Rabeder's conclusion is accepted here, but the following considerations are worth noting.

Drepanosorex is based mainly on the combination of a fissident upper incisor and exoedaenodont ('bulbous') antemolars. However, some Eurasian representatives of the genus *Sorex* (sensu stricto) also have fissident upper incisors, e.g. *S. minutus* L., 1766 (see below) and *S. mirabilis* Ognev, 1937 from Siberia (Hoffmann, 1971).

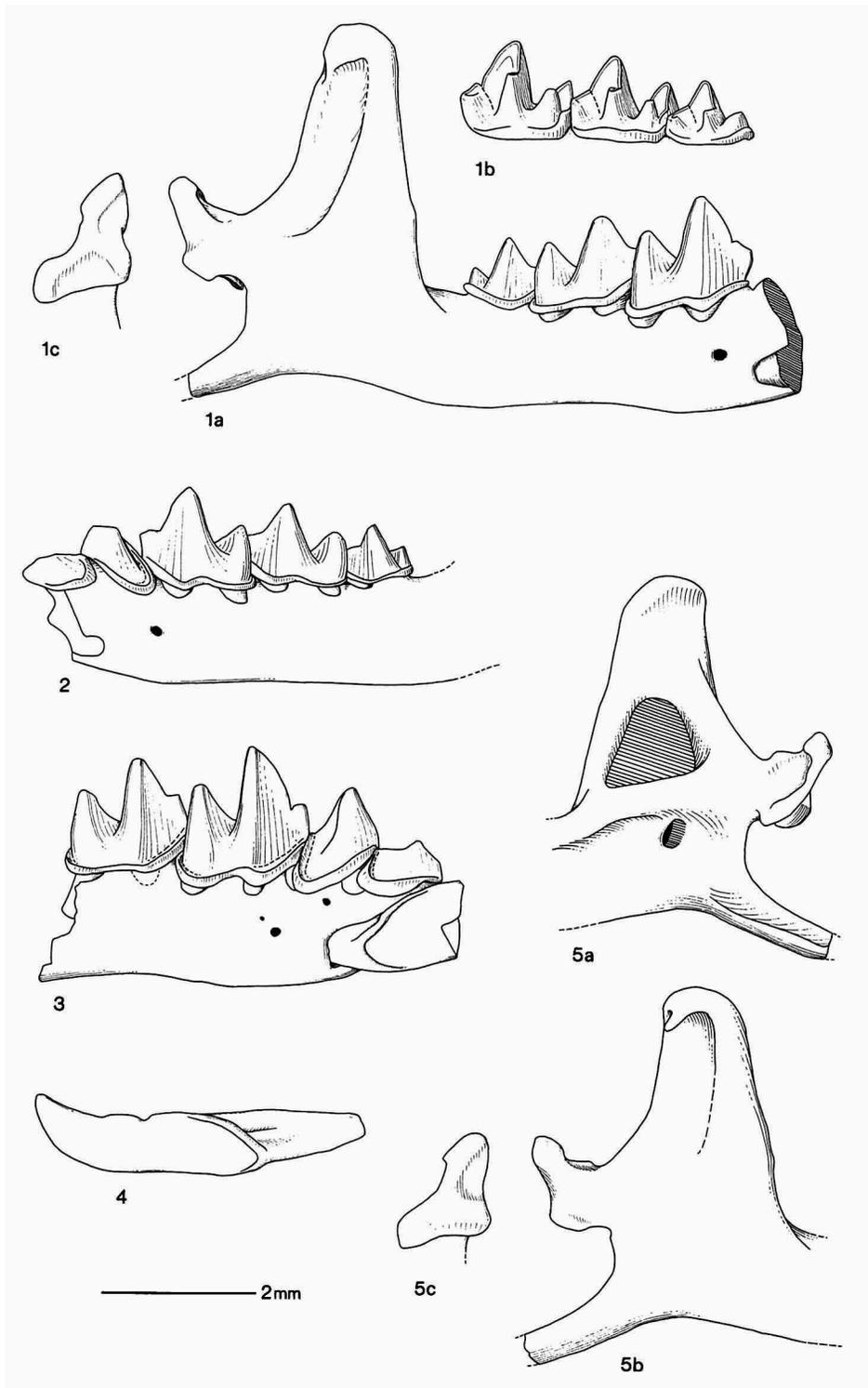
Similarly, many American species of *Sorex* have fissident upper incisors (e.g. the *vagrans-obscurus* group, Hoffmann, 1971; see also Merriam, 1895); Rabeder (1972b) also discussed the fissident incisor. Other North American *Sorex* species may show a slight degree of exoedaenodontology in the upper antemolars (e.g. *S. pacificus* Coues, 1877, see Merriam, 1895).

Plate 2

Crocidura kornfeldi Kormos, 1934.

1. Right ramus with M₁-M₃, Osz3/2; a: buccal view; b: lingual view of dentition; c: caudal view of condyle.
2. Left A₁-M₃, Vi3, smallest specimen.
3. Right I inf. - M₂, Vi3 also, largest specimen.
4. Left I inf., Vi3 felső.
5. Right ascending ramus, Vi3 felső; a: lingual view; b: buccal view; c: caudal view of condyle.

Plate 2



As a consequence of our conservative treatment, *S. praeareneus* is transferred to *Drepanosorex*. Other 'Sorex' species that are here referred to other genera are: *S. kretzoi* Sulimski, 1962 to *Sulimskia* gen. nov., *S. hibbardi* Sulimski, 1962 to *Deinsdorfia* Heller, 1963 and *S. dehneli* Kowalski, 1956 to *Mafia* gen. nov.

The diagnosis given by Repenning, 1967 for *Sorex* is followed here, with two additions: 1) the angular process is long and slender, 2) the ventral margin of the elongate mandible is slightly curved upwards (concave).

Sorex minutus L., 1766

Pls 3-6

Studied localities — Osztramos 7, Csarnóta 2, Villány 3, Tegelen, and Osztramos 3/2.

Stratigraphic range — Late Ruscinian (MN 15) - Recent.

Synonymy (only concerning the studied localities)

Sorex minutus L., in: Kormos, 1937c (Vi3).

Sorex cf. *minutus* L., in: Kretzoi, 1956, pp. 47 and 170 (Cs2).

Sorex minutus L., in: Kretzoi, 1956, pp. 61 and 184 (Vi3).

Sorex (s.l.) sp. indet., in: Kretzoi, 1962, pp. 306 and 353 (Cs2).

Sorex sp., in: Freudenthal et al., 1976, p. 14 (Te).

Sorex cf. *praeminutus* Sulimski ¹⁾, in: Jánossy & Kordos, 1977, p. 44 (Osz3).

Sorex cf. *subminutus* Sulimski, in: Jánossy, 1978, p (Osz7).

Sorex s.l. sp. (partly?), in: Jánossy, 1979, p. 23 (Cs2).

Sorex minutus L., in: Jánossy, 1979, p. 34 (Vi3).

Sorex cf. *praeminutus* Sulimski ¹⁾, in: Jánossy, 1979, p. 36 (Osz3).

Available material

Osztramos 7: 5 AA sup., 7 P⁴, 9 M¹, 6 M², 2 M³, 5 I inf., 4 A₁, 6 P₄, 18 M₁, 17 M₂, 12 M₃, 3 condyles.

Csarnóta 2: 2 I sup., 2 P⁴, 1 P₄, 16 M₁, 15 M₂, 7 M₃, 12 condyles.

Villány 3: 1 P⁴, 1 I inf., 1 A₁, 1 P₄, 1 M₁, 2 M₂, 2 M₃, 1 condyle.

Villány 3 felső: 1 P⁴, 1 M₁, 2 M₂, 2 M₃.

Tegelen: 3 I sup.: RGM 257 201, 313, 369.

10 P⁴: RGM 257 034, 039, 050, 168, 183, 212, 242, 243, 382, 387.

15 M¹: RGM 257 034, 035, 036, 038, 077, 122, 135, 137, 183, 231, 232, 280, 283, 383, 400.

9 M²: RGM 257 034, 035, 037, 179, 211, 235, 284, 380, 414.

5 I inf.: RGM 257 043, 170, 260, 317, 318.

2 P₄: RGM 257 190, 191.

13 M₁: RGM 179 050, 257 033, 057, 129, 151, 164, 190, 191, 197, 274, 275, 291, 292.

14 M₂: RGM 179 050, 257 032, 033, 042, 057, 151, 190, 248, 274, 275, 293, 303, 347, 395.

8 M₃: RGM 257 032, 033, 057, 274, 275, 287, 289, 395.

5 condyles: RGM 179 050, 257 151, 190, 274, 275.

Osztramos 3/2: 1 P⁴, 3 M¹, 1 M², 4 I inf., 6 A₁, 13 P₄, 28 M₁, 35 M₂, 24 M₃, 27 condyles, and a nearly complete skull with mandibles and all four molar sets, not detached.

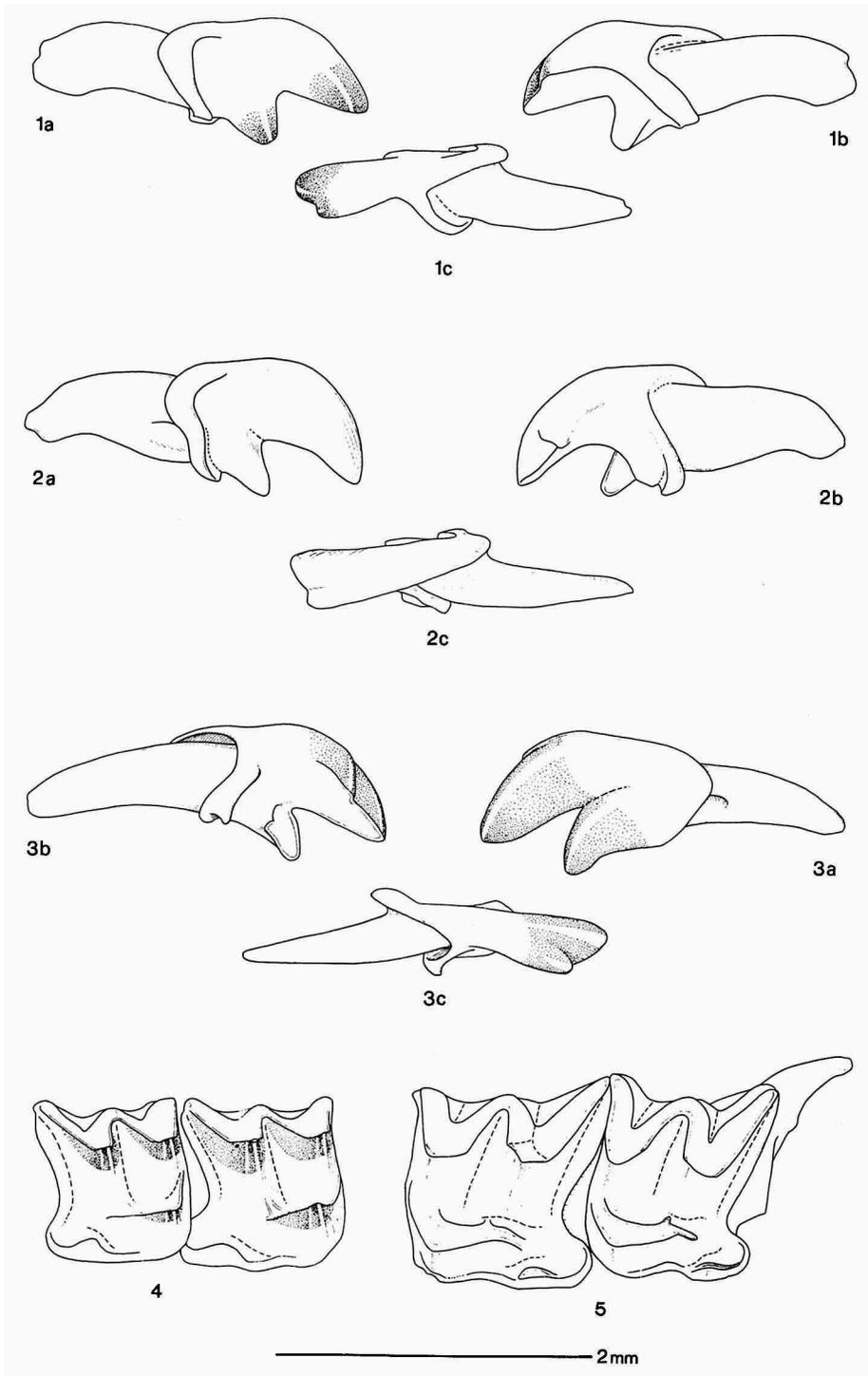
¹⁾An obvious mistake: it should either be *subminutus* Sulimski, 1962 or *praeminutus* Heller, 1963.

Plate 3

Sorex minutus L., 1766

1. Right I sup., Recent, Netherlands, author's coll. no. 8201; a: buccal view; b: medial view; c: dorsal view.
2. Right I sup., Cs2/20, same views as fig. 1.
3. Left I sup., Te, coll. RGM 257 313, same views as fig. 1.
4. Right M¹-M², Osz3/2.
5. Left M¹-M², Te, coll. RGM 257 035.

Plate 3



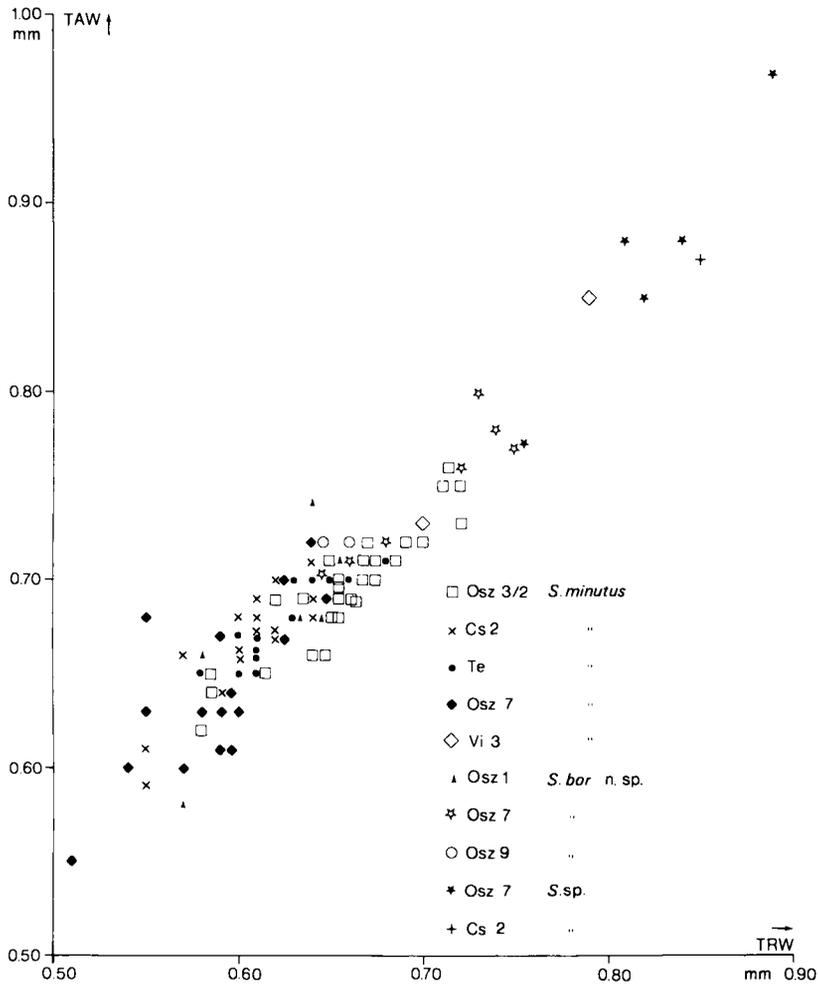


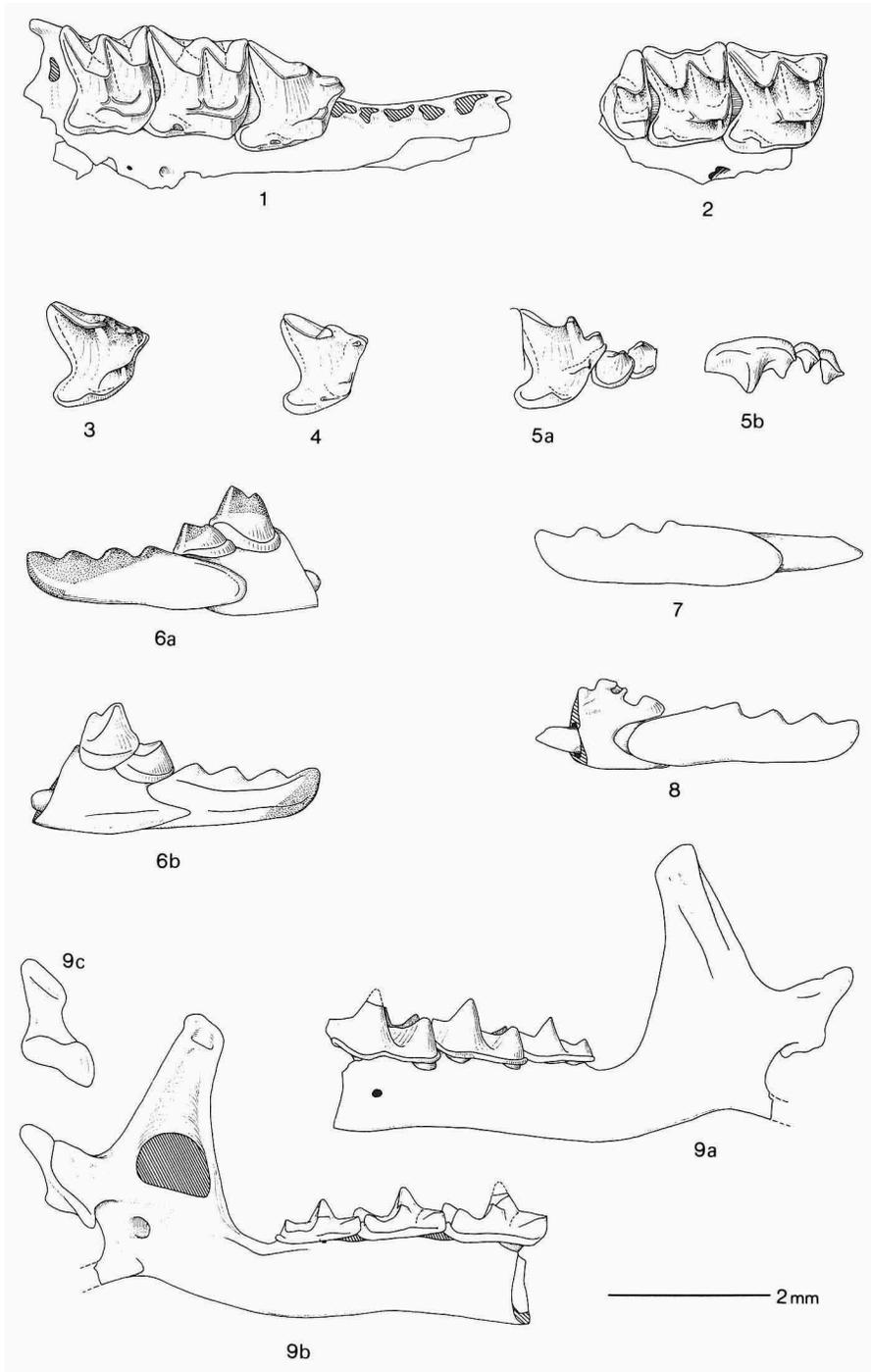
Fig. 7. Scatter diagram of the relation between talonid width (TAW) and trigonid width (TRW) in M_1 of the studied *Sorex* samples.

Plate 4

Sorex minutus L., 1766

1. Right P^4-M^2 , Te, coll. RGM 257 034.
2. Right M^1-M^3 , Osz7.
3. Right P^4 , Vi3 felső.
4. Right P^4 , Cs2/20.
5. Right A^4-P^4 , Osz7; a: occlusal view; b: buccal view.
6. Left I inf.- P^4 , Osz3/2; a: buccal view; b: lingual view.
7. Left I inf., Te, RGM 257 318, tricuspluate.
8. Right I inf., Te, RGM 257 043, tetracuspluate.
9. Left ramus with M_1-M_3 , Te, RGM 257 274; a: buccal view; b: lingual view; c: caudal view of condyle.

Plate 4



Measurements — See Tables 3-7 and Figs. 7-8.

Description — The dental elements are stained.

I sup. — All available upper incisors (from Csarnóta 2 and Tegelen) have a small but distinct medial cuspule, i.e. they are fissident (see Pl. 3, figs. 2, 3). The talon is well-developed, pointed and reaches farther downwards than does the apex. The buccal posterior edge is placed at a sharp angle to the dorsal margin. A cingulum runs right along the buccal posterior edge, but sometimes (Tegelen) it is hardly detectable. The cingulum is well-developed at the medial side.

AA sup. — Five upper antemolars are present, as can be concluded from the number of alveoles (Pl. 4, fig. 1). Only A⁴ and A⁵ are preserved, however (in Osz7, Pl. 4, fig. 5). They are of about equal size, with well-developed cingula all around.

P⁴ — The hypocone is hardly individualized and only detectable as a 'rise' on the lingual cingulum. It is separated from the protocone by a wide valley. The parastyle is surrounded by a cingulum; as a rule the parastyle is connected to the paracone by a parastylar crest (not in Cs2). The protocone is L-shaped, with a short crest running in the posterior direction.

M¹ and M² — As in P⁴, the hypocone in M¹ and M² is only weakly developed as a cuspule on the cingulum which surrounds the hypoconal flange. Hypocone and protocone are separated by a wide valley which is bordered lingually by a small but distinct cingulum running from the hypocone to underneath the protocone. The ridge running from the protocone towards the posterior bifurcates into a Y-shape and thus closes off the trigon valley at its posterior side (metaloph).

M³ — The last upper molar is only preserved in Osztramos 7 (Pl. 4, fig. 2); it is rather long and stout. A hypocone is not present but the protocone is well developed.

I inf. — Tricuspluate, with a tendency to be tetracuspluate in some specimens (Pl. 4, fig. 8) due to a small protrusion on the dorsal edge behind the posterior-most cuspule. A weak cingulum may be present along the buccal posterior margin. The lower incisor extends backwards at the buccal side of the mandible to half-way along P₄, before of just underneath the paraconid of M₁.

A₁ — The A₁ is rather long at the buccal side, and essentially single-cusped. It is hidden underneath P₄ for less than half its length.

P₄ — The P₄ is slender and high in unworn specimens; its postero-lingual basin is well developed but the edges of the basin are usually faint. The element is two-cusped, with the anterior cusp always considerably higher than the posterior cusp.

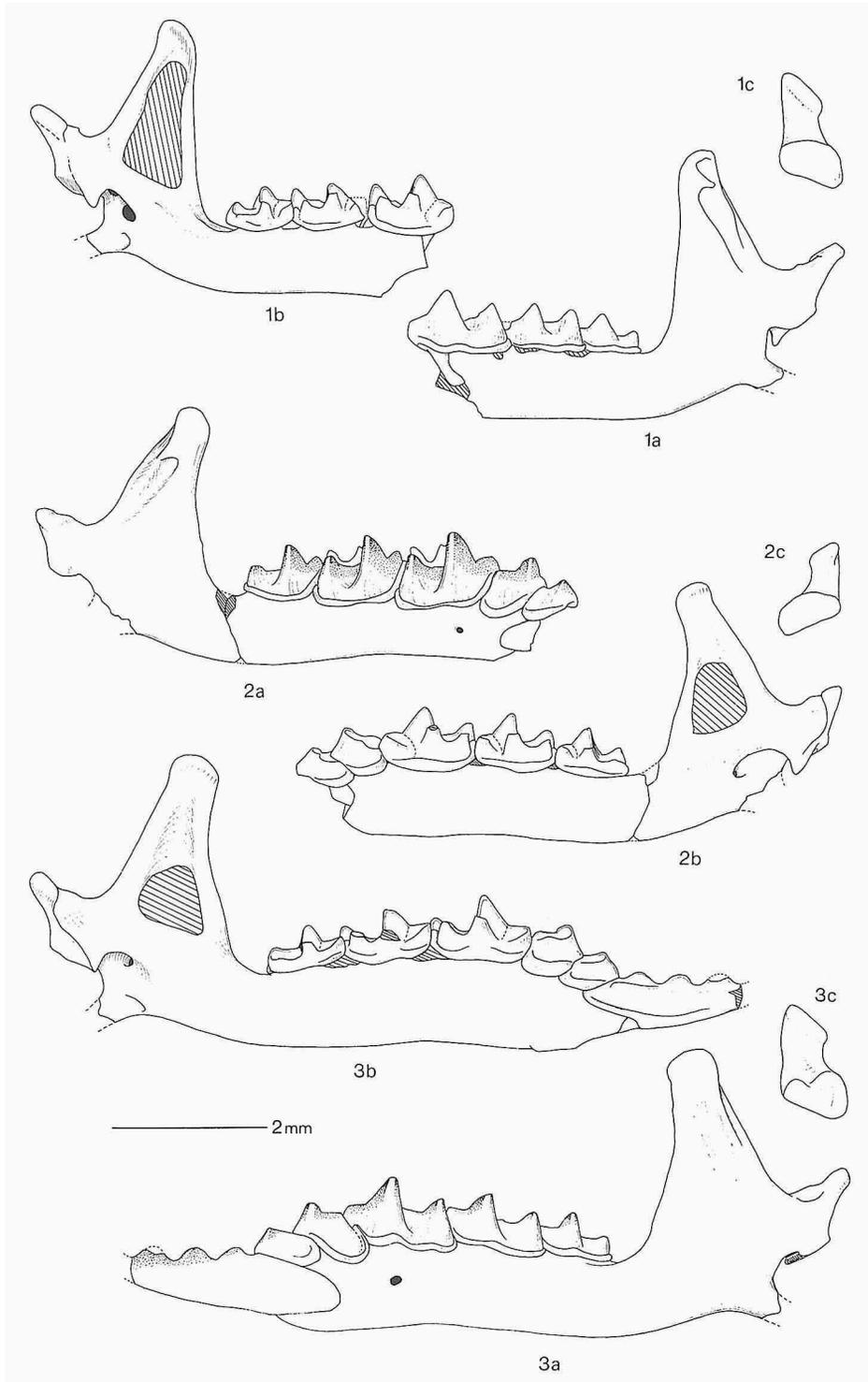
M₁ and M₂ — The sharply-cusped elements resemble each other to a large degree; the oblique crest bears a mesoconid in unworn specimens. The entoconid crest is usually rather high and slightly comma-shaped in occlusal view. The buccal re-entrant valley opens at some distance above the buccal cingulum; this buccal cingulum is well-developed but narrow and usually undulate. The lingual cingulum is broader but hardly pronounced from the side of the teeth.

Plate 5

Sorex minutus L., 1766

1. Left ramus with M₁-M₃, Cs2/23; a: buccal view; b: lingual view; c: caudal view of condyle.
2. Right ramus with A₁-M₃, Osz7, same views as fig. 1.
3. Left ramus with I-M₃, Vi3, same views as fig. 1.

Plate 5



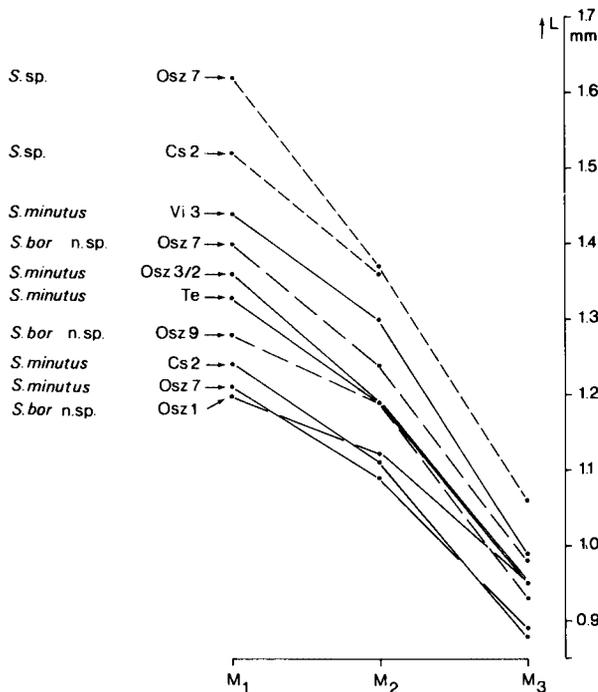


Fig. 8. Diagram showing the mean lengths of M_1 , M_2 , M_3 of the studied *Sorex* samples.

M_3 — The talonid is well-developed, basined and provided with both hypoconid and entoconid. The buccal cingulum is well individualized, but the lingual one hardly so, or it is even absent.

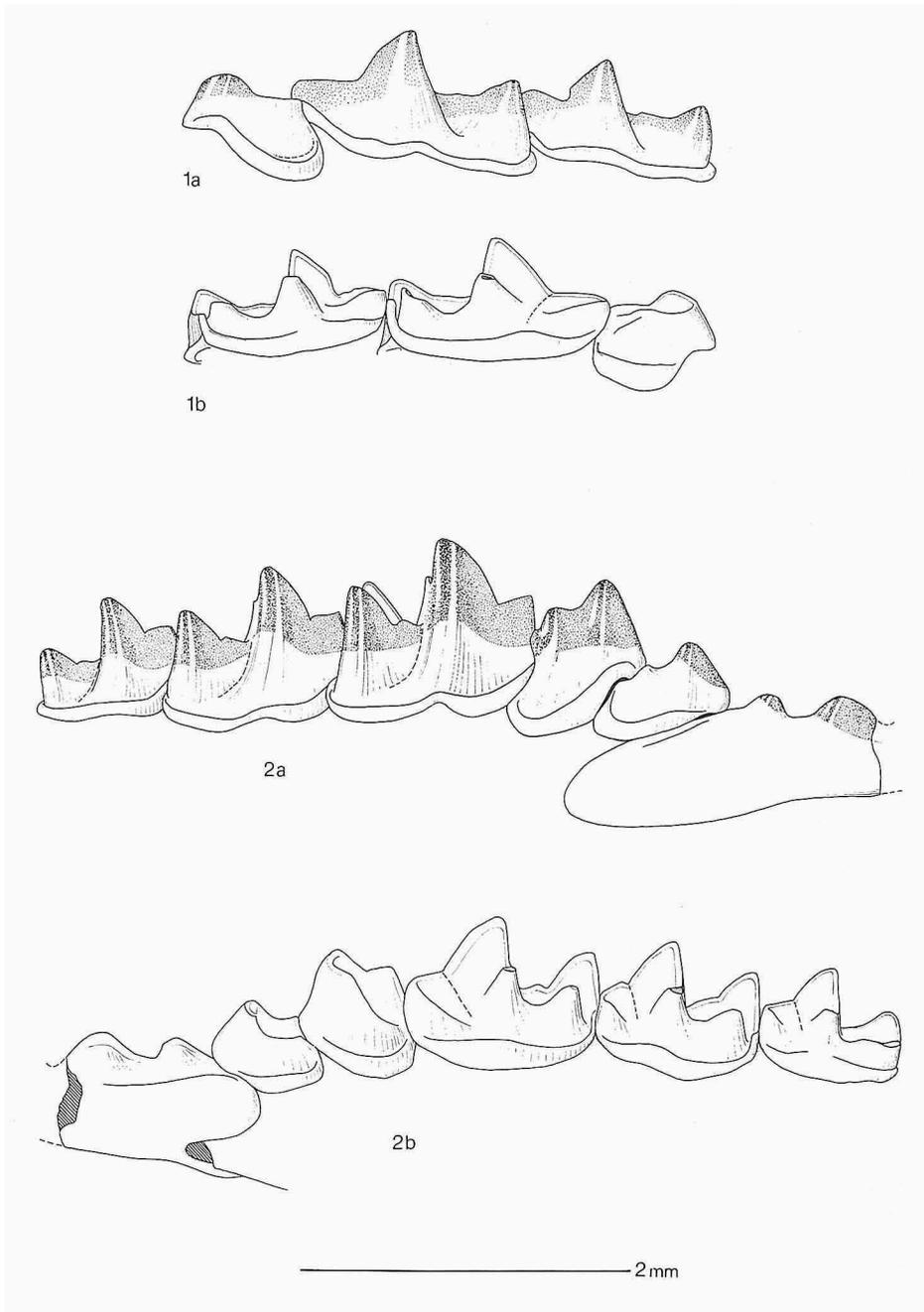
Mandible — The anterior edge of the coronoid process is concave, the apex bends slightly towards the anterior. The apex is narrow and pointed. As a rule, a coronoid spicule is absent (only faintly present in Cs2). The external temporal fossa is developed as a longitudinal groove, running parallel to the posterior edge of the coronoid process; it is provided with a central ridge in its upper half (see Pl. 4, fig. 9a, Pl. 5, figs. 1a, 2a, 3a). The fossa reaches to below the upper sigmoid notch. The internal temporal fossa is high and triangular, continuing to the tip of the coronoid; its lower margin points to the upper facet of the condyle. The condyle is placed far backwards; the upper facet is cylindrical; the lower facet widens towards the median. The interarticular area is broad to moderately narrow. The mandibular foramen is large and situated below the posterior corner of the internal temporal fossa. The mental foramen is placed below the trigonid of M_1 .

Plate 6

Sorex minutus L., 1766

1. Left P_4 - M_2 , Te, RGM 257 190; a: buccal view; b: lingual view.
2. Right I inf.- M_3 , Osz3/2, same views.

Plate 6



Remarks — This is the first time it is mentioned that *S. minutus* possesses a fissident upper incisor. This feature is also present in Recent material: Pl. 3, fig. 1 depicts a specimen from the island of Terschelling, the Netherlands. See also the discussion on the genus (above).

The sizes of the individual elements from the five localities studied do not show much variation (see Figs. 7, 8). One specimen from Villány 3 is quite large but it is tentatively included for its morphological resemblances. It is worth noting that the Ruscinian material is slightly smaller than that from the Villányian localities (see Fig. 8).

The material has been attributed to the Recent *S. minutus* mainly because of the presence of a fissident upper incisor and also on the basis of the resemblances in size and morphology.

The upper incisor of *S. subminutus* Sulimski, 1962 is not fissident and its P⁴ has a well-developed hypocone (more molarized according to Sulimski, 1962). *S. praeminutus* Heller, 1963 from Deinsdorf is probably a synonym of *S. minutus*, since the only difference mentioned by Heller (1963) is in the shape of the internal temporal fossa (his 'fossa pterygoidea'), which is not very diagnostic and does not seem to differ from our *minutus* material.

Since *S. minutus* occurs in the Ruscinian it is the first of the extant shrews to appear in Europe.

Sorex bor sp. nov.

Pl. 7.

Holotype — A right mandible with complete lower dentition, coll. TTM no. V.83.12 (Pl. 7, fig. 4).

Etymology — Bor, Hungarian for wine, which the author enjoyed much during his visits to Hungary.

Type locality — Osztramos 9.

Studied localities — Osztramos 1, 7 and 9.

Stratigraphic range — Ruscinian.

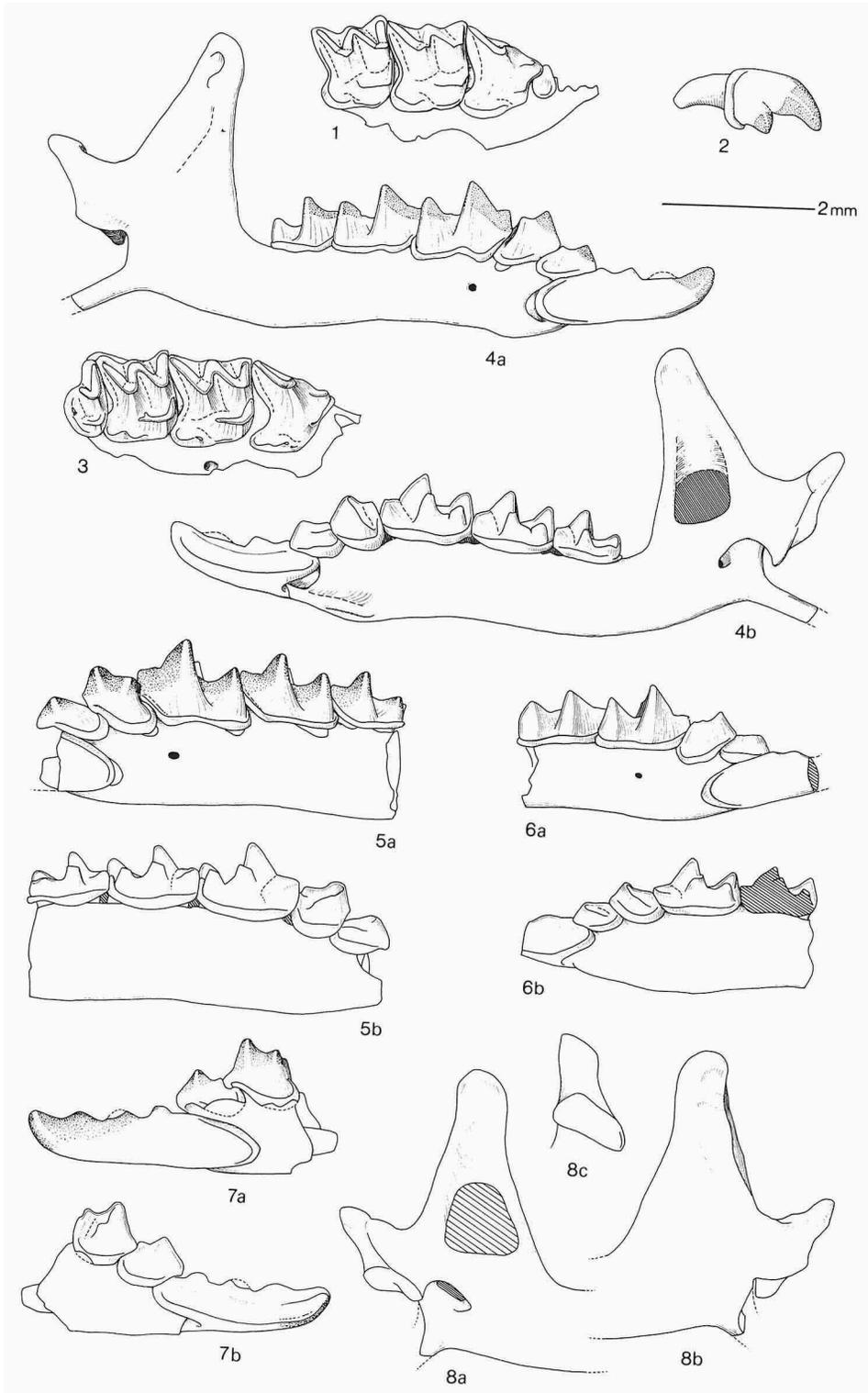
Diagnosis — A small *Sorex* species; upper incisor not fissident; lower incisor with upturned apex, tricuspluate and provided with a narrow cingulum. A₁ long and flat, P₄ deeply basined; lower molars typically *Sorex*-like, with large talonids. Coronoid spicule small and close to the tip of the coronoid process. Mandibular foramen large; mental foramen under the trigonid of M₁. Condylar facets parallel or nearly so.

Plate 7

Sorex bor sp. nov.

1. Right A⁵-M², Osz9.
2. Right I sup., Osz9.
3. Right P⁴-M³, Osz1E.
4. Right mandible with complete dentition, Osz9, holotype, coll. TTM no. V.83.12; a: buccal view; b: lingual view.
5. Left A₁-M₃, Osz7, same views as fig. 4.
6. Right I inf.-M₂, Osz1C, coll. TTM no. V.73.19, same views as fig. 4.
7. Left I inf.-P₄, Osz7, same views as fig. 4.
8. Left ascending ramus, Osz7; a: internal view; b: external view; c: caudal view of condyle.

Plate 7



Differential diagnosis — *S. bor* differs from *S. minutus* by the non-fissident upper incisor, by having a coronoid spicule, by not having a longitudinal bar in the external temporal fossa and by being somewhat larger when found together with *S. minutus* in the same sample. It differs from *S. subminutus* by being considerably larger. *S. bor* differs from other Ruscinian *Sorex* taxa (such as *S. cf. praealpinus* and *S. runtonensis* from Węże) mainly by being distinctly smaller.

Available material

Osztramos 9: 1 I sup., 1 A sup., 3 P⁴, 3 M¹, 2 M², 1 mandible with complete dentition, 1 edentulous mandible, 1 I inf., 1 P₄, 1 M₁, 1 M₂, 1 M₃.

Osztramos 1: 1 A₁, 1 P₄, 1 M₁.

Osztramos 1 B: 1 M¹, 1 M², 1 M³, 1 P₄, 2 M₁, 2 M₂, 1 M₃.

Osztramos 1 C: 1 M¹, 1 M², 1 I inf., 1 A₁, 1 P₄, 2 M₁, 2 M₂, 1 M₃, 1 condyle.

Osztramos 1 E: 1 P⁴, 2 M¹, 1 M², 1 M³, 1 I inf., 1 M₁, 1 M₂, 1 M₃.

Osztramos 7: 1 P⁴, 5 I inf., 2 A₁, 4 P₄, 8 M₁, 7 M₂, 3 M₃, 4 condyles.

Measurements — See Tables 8-10 and Figs. 7-8.

Description — The dental elements are stained a dark orange.

I sup. — Not fissident, the apex and the short talon are placed at right angles. A posterior buccal cingulum is present along the entire margin, but it is narrow and not well pronounced.

AA sup. — Only one A sup. is preserved, an A⁵ from Osz9 (Pl. 7, fig. 1). It appears to be relatively smaller than comparable elements in *S. minutus* (see Pl. 4, fig. 5). The element is unicuspid.

P⁴ — There is a wide and open valley between protocone and hypocone; a cingulum runs from the protocone and surrounds the parastyle. A low parastylar crest is present.

M¹ and M² — The hypocone is either faintly developed or absent. Metalophs are hardly developed and often they are lacking. The upper M¹ and M² closely resemble those of *S. minutus* in morphology.

M³ — Unlike in *S. minutus*, a hypocone is present and distinct (see Pl. 7, fig. 3). It is not directly connected to the protocone.

I inf. — Tricuspluate, the apex is upturned; a narrow cingulum is present along the buccal posterior border. The symphyseal cingulum is wide and smooth. The incisor is short; it ends buccally underneath the anterior half of P₄, and it does not reach M₁.

A₁ — Relatively long and flat, only for a small part hidden below P₄; A₁ is more or less two-cusped. A postero-lingual basin is clearly present, although shallow and faintly bordered. Clear cingula are present on both sides.

P₄ — The postero-lingual basin is deep and bordered by sharp crests that sometimes bear small cusps. P₄ is two-cusped, the anterior cusp is always considerably higher than the posterior one. Clear cingula occur on both sides.

M₁ and M₂ — The lower molars are of a typical *Sorex* shape. A small mesoconid is present on the oblique crest in unworn specimens; the entoconid crest is rather high. In M₁ the metaconid and the protoconid are close together, causing the trigonid to be narrow; in both M₁ and M₂ the talonid is wider than the trigonid. Cingula are well developed on both sides, the buccal cingulum is slightly undulate, particularly in M₁.

M₃ — The talonid in M₃ is well developed, basined and provided with clearly distinguishable hypoconids and entoconids. Cingula are present on both sides, but lingually not as strong as buccally.

Mandible — The anterior edge of the coronoid process is slightly concave to almost straight, the posterior edge is straight. The coronoid spicule is small and very close to the apex. The external temporal fossa is shallow and narrow, reaching the level of the upper

sigmoid notch. The internal temporal fossa is high and triangular. The condyle is placed far backwards, it is entirely visible from the side. The upper facet is cylindrical, the lower facet is provided with a slightly concave upper margin and is nearly parallel to the upper facet. The interarticular area is broad and flat. The angular process is long and dorso-ventrally compressed. A large and open mandibular foramen is placed below the posterior corner of the internal temporal fossa. The mental foramen is situated below the trigonid of M_1 .

Remarks — While studying the Osztramos 7 material, it soon became apparent that a *Sorex* species was present, intermediate in size between *S. minutus* and *S. sp.*, to be described hereafter. This species also differed from *S. minutus* by having a coronoid spicule and by lacking the longitudinal ridge in the external temporal fossa.

When the Osz7 material was compared with material from other localities (Osz1 and Osz9) other differences between *S. minutus* and *S. bor* sp. nov. emerged, such as the non-fissident I sup.

The size data however, show a considerable overlap (see Fig. 7); the size difference originally observed in Osz7 cannot be applied as a good diagnostic difference between the two species, except in the case where *minutus* and *bor* occur together in the same sample.

Sorex bor sp. nov. is different from all other known Ruscinian *Sorex* (s.s.) species in morphology and/or size. Morphologically it seems to be closest to *S. subminutus* Sulimski, 1962.

The only other material that perhaps belongs to *Sorex bor* is that of *Sorex* sp. from Mała Cave in Poland. According to the description (Sulimski et al., 1979) there are minor differences, for instance in the position of the mental foramen, but the sizes appear to be nearly the same.

Sorex sp.

Pl. 8, figs. 1-7.

Attributed material

Osztramos 7: 2 P^4 , 1 M^1 , 1 M^2 , 1 M^3 , 3 I inf., 2 A_1 , 4 P_4 , 5 M_1 , 6 M_2 , 3 M_3 , 1 condyle.

Csarnóta 2: 2 I inf., 1 P_4 , 1 M_1 , 1 M_2 , 1 condyle.

Measurements — See Tables 11, 12 and Figs. 7, 8.

Description — The dental elements are stained.

P^4 — The hypoconal flange is small and flat, bordered by a low cingulum; the hypocone is hardly developed as a distinct cusp. The protocone is well-developed, but lower than the parastyle. There is a wide trench between hypocone and protocone. The parastyle is not surrounded by a cingulum; the parastylar crest is high.

M^1 and M^2 — The hypocone is hardly individualized in the upper molars. The well-developed protocone is connected to the paracone; there is no metaloph.

M^3 — The protocone forms a U-shaped crest surrounding the lingual part of the tooth; a hypocone is not present.

I inf. — Of the lower incisor, only the posterior parts have been found, so the number of cusps cannot be reconstructed. A buccal cingulum is either faintly present or absent. The lower incisor continues on the buccal side of the mandible to half-way along P_4 , and does not reach M_1 .

A_1 — The rather long A_1 is essentially two-cusped and hidden below P_4 for a small part only. A shallow postero-lingual basin is present. The cingulum is broad on both sides, as it is in P_4 .

P_4 — The postero-lingual basin is shallow and bordered only by a faint ridge. The buccal overhang of the root by the crown is only slight.

M_1 and M_2 — The lingual cingulum on the lower molars hardly protrudes; buccally it is better developed. The entoconid crest is quite high. The trigonid valley opens at the level of the lingual cingulum, but the buccal re-entrant valley opens high above the buccal cingulum.

M_3 — In M_3 the talonid is basined and both hypoconid and entoconid are present.

Mandible — The internal temporal fossa is narrow and high; the condyle is large and placed far backwards. The upper condylar facet is narrow and cylindrical; the lower facet is slightly elongated lingually. The interarticular area is broad. The mandibular foramen is small and situated below the middle of the internal temporal fossa; the mental foramen is situated underneath the protoconid of M_1 .

Remarks — The unnamed species described above is smaller than *S. araneus* L., 1758, *S. kennardi* Hinton, 1911, *S. subaraneus* Heller, 1959, and *S. sp.* from Węże (Sulimski, 1959). It is larger than *S. alpinoides* Kowalski, 1956 (referred to *Neomysorex* by Rzebik-Kowalska, 1981), *S. fallax* Heller, 1936 and *S. bor* sp. nov.

Its size agrees well with the sizes of *S. runtonensis* Hinton, 1911, *S. helleri* Kretzoi, 1959 (= *S. araneoides* Heller, 1930) and *S. praealpinus* Heller, 1930.

The present material differs from the type material of *S. runtonensis* in the British Museum (Natural History) having an almost completely free A_1 and high buccal re-entrant valleys in the lower molars; so attribution to that taxon is impossible. The British type material is much younger than our material; it is from the Upper Freshwater Bed (lower Biharian) of West Runton.

Great differences between the present material and the *S. runtonensis* from Węże cannot be distilled from Sulimski's description (Sulimski, 1959, 1962), but his figures (1959, pl. IV, figs. 5a-c) show the same differences as Hinton's type material and also a conspicuous cingulum on the lower incisor, which is not found in our material. The *S. runtonensis* that has been described from Rębielice Królewskie (Kowalski, 1960) is much smaller than our species.

The type of *S. helleri* from Sackdilling is also much younger than our material. It is of the same size, as stated. Heller (1930) gives neither a diagnosis nor a description of this species (which he described as *S. araneoides*). The illustration in Heller (1930) is very small and no maxillary material was available. It is therefore impossible to evaluate the status of *S. helleri* and its possible relation to our Ruscinian material.

Plate 8

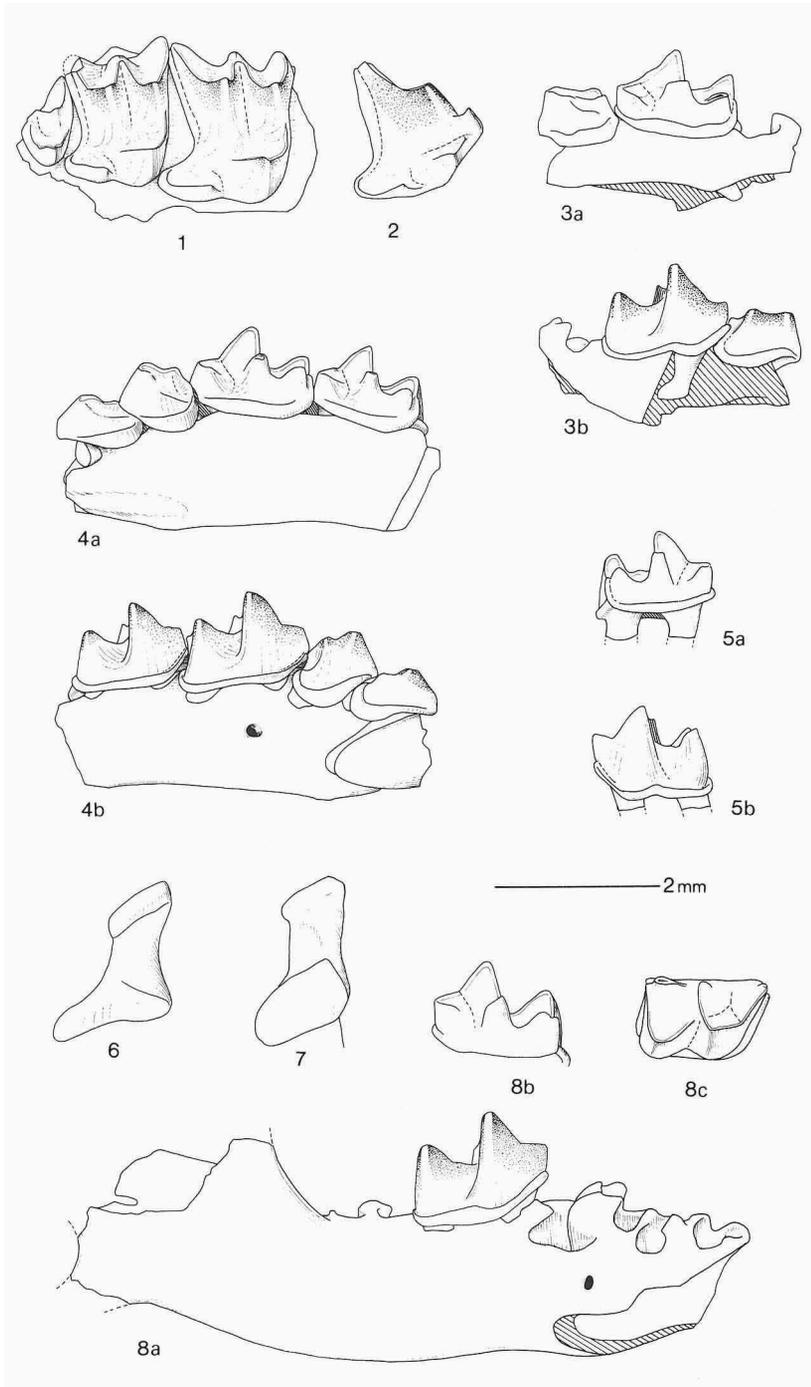
Sorex sp.

1. Right M^1 - M^3 , Os7.
2. Right P^4 , Os7.
3. Right P_4 - M_1 , Cs2/20; a: lingual view; b: buccal view.
4. Right A_1 - M_2 , Os7, same views as fig. 3.
5. Left M_2 , Cs2/22, same views as fig. 3.
6. Right condyle, Os7.
7. Right condyle, Cs2/18.

Soricinae gen. et sp. indet. 1

8. Right horizontal ramus with M_2 , Os7; a: buccal view; b: lingual view; c: occlusal view.

Plate 8



Our *Sorex* sp. is most probably identical to the material from Węże described by Sulimski (1962) as *S. cf. praealpinus*. The attribution of our *Sorex* sp. and of the Węże material to the species *praealpinus* Heller, 1930 is however prohibited by large morphological differences in, for instance, the structure of the condyle and the position of the mental foramen.

Our material cannot be attributed to any of the known species. As the material is rather scanty (e.g. complete mandibles are lacking) we refrain from erecting a new species. If a new species is created in the future, this might best be done on the basis of the material from Węże (*S. cf. praealpinus*, Sulimski, 1962) and not on the basis of the material described here.

Genus *Drepanosorex* Kretzoi, 1941

Type species — *D. tasnadii* Kretzoi, 1941 (= *D. savini* (Hinton, 1911)).

Remarks — A discussion of the generic status of *Drepanosorex* can be found above, under *Sorex*. Kretzoi (1941), Repenning (1967) and Rabeder (1972b) have discussed the genus *Drepanosorex*. The major difference between *Drepanosorex* and *Sorex* is in the development of exoedaenodont dental elements, notably the antemolars.

The genus was based on *D. tasnadii* Kretzoi, 1941 from Gombaszög (now in Czechoslovakia) as the type species. Jánossy (1979) demonstrated that *D. tasnadii* is a synonym of *D. savini* (Hinton, 1911) from West Runton, England.

Drepanosorex praeareneus (Kormos, 1934)

Pls 9-11.

Holotype — A skull with partial dentition, coll. MÁFI no. Ob.3681 (Pl. 9, fig. 1).

Original reference — Kormos, 1934, pp. 298-299, fig. 32.

Type locality — Villány Kalkberg (= Vi3), Hungary.

Studied localities — Villány 3, Osztramos 3/2, Tegelen.

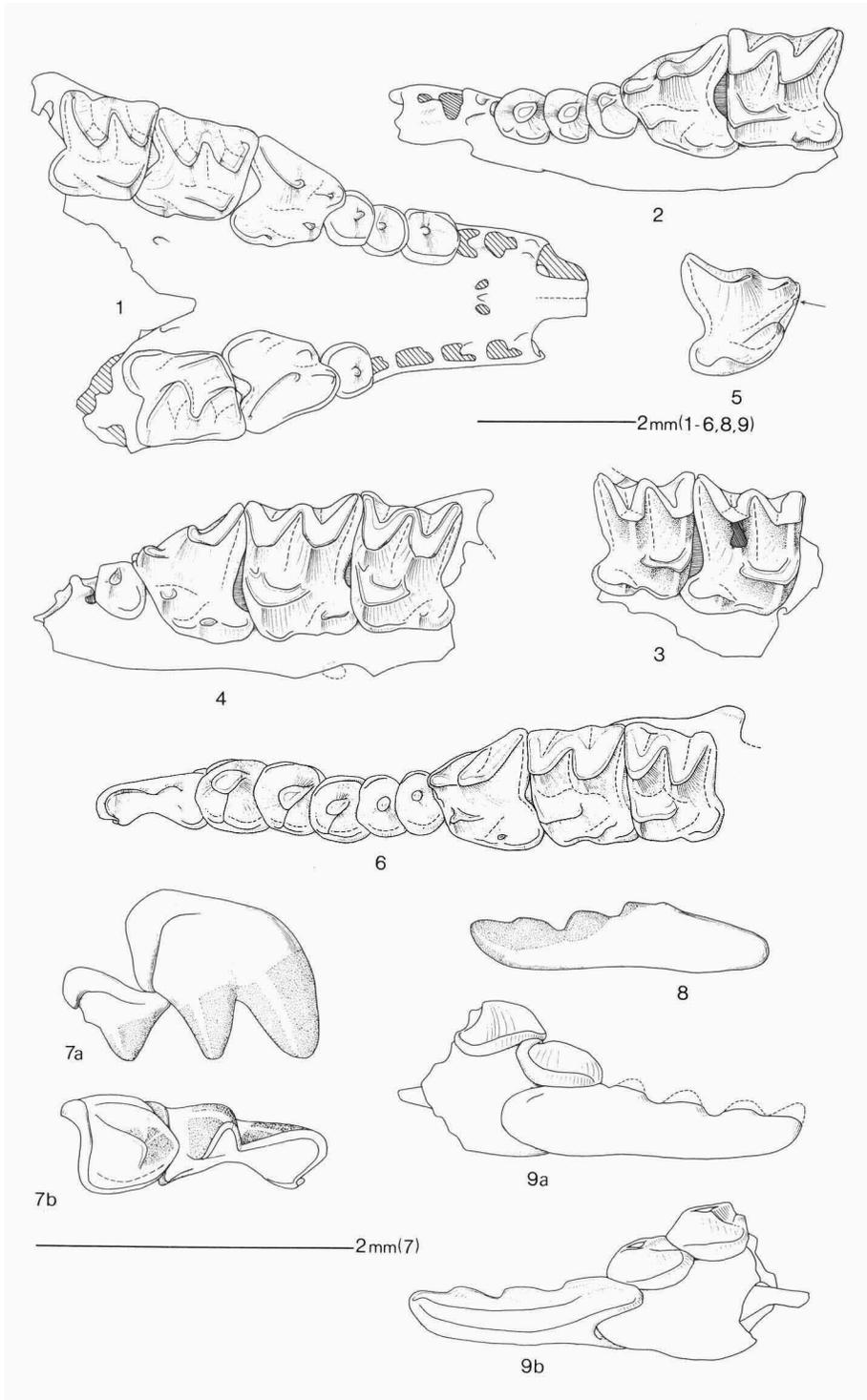
Age — Tiglian = late Villányian (MN 17).

Plate 9

Drepanosorex praeareneus (Kormos, 1934)

1. Holotype, Villány Kalkberg (= Vi3), coll. MÁFI no. Ob.3681.
2. Left A³-M¹, Te, RGM 257 044.
3. Right M¹-M², Te, RGM 257 329.
4. Left A⁵-M², Te, RGM 257 127 (largest specimen).
5. Right P⁴ with small accessory cuspule, see arrow, Te, RGM 257 355.
6. Left upper dentition (except M³), Osz3/2.
7. Right I sup.-A¹, Osz 3/2; a: buccal view; b: occlusal view.
8. Left I inf., Osz3/2.
9. Right I inf.-P₄, Te, RGM 257 019; a: buccal view; b: lingual view.

Plate 9



Synonymy (only concerning the studied localities)

Sorex praeearaneus, in: Kormos, 1934, p. 298 (Vi3).

Sorex praeearaneus Kormos, in: Kormos, 1937b, p. 1090 (Vi3).

Sorex runtonensis Hinton (= *S. praeearaneus* Kormos), in: Kretzoi, 1956, pp. 61 and 184 (Vi3).

Sorex praeearaneus Kormos, 1934, in: Repenning, 1967, p. 32.

Sorex cf. *praeearaneus* Kormos, 1934, in: Freudenthal et al., 1976, p. 14 (Te).

Sorex sp. (*araneus* group), in: Jánosy & Kordos, 1977, p. 44; and in: Jánosy, 1979, p. 36 (Osz3).

Sorex runtonensis Hinton, in: Jánosy, 1979, p. 34 (Vi3).

Original description — Kormos (1934) did not give a formal diagnosis, but only a description, from which the following items may be used as diagnostic features: A⁵ somewhat smaller than A⁴; mental foramen below posterior edge of P₄; external temporal fossa reaches downwards to the upper condylar facet; internal temporal fossa reaches to half-way up the coronoid process and not to the very tip of the coronoid.

Emended diagnosis — A small species of *Drepanosorex*; upper incisor fissident; dentition slightly exoedaenodont; 5 upper antemolars, A¹ and A² large, A³, A⁴ and A⁵ smaller, with A⁴ slightly smaller than A³ and A⁵; hypocones in P⁴ and upper molars poorly developed; lower incisor as a rule tricuspluate with bulbous cuspules; M₃ with well-developed talonid.

Differential diagnosis — *D. praeearaneus* is easily distinguishable from other *Drepanosorex* species by its smaller size and the lesser degree of exoedaenodonty of the dentition. It differs from *Sorex runtonensis*, with which it is often confused, by having more swollen antemolars, a fissident I sup., a rounded apex of the coronoid process, and a generally more robust ramus.

Studied material

Villány felső: : a left fragmentary mandible with P₄ and M₁ (Pl. 11, fig. 2).

Osztramos 3/2: 2 specimens with complete articulated upper and lower dentition, one upper incisor missing only. Furthermore 3 I sup., 11 AA sup., 4 P⁴, 5 M¹, 5 M², 2 M³, 2 I inf., 1 A₁, 2 P₄, 2 M₁, 2 M₂, 1 M₃.

Tegelen: 30 I sup.: RGM 257 026, 120, 138, 139, 140, 169, 202, 221, 222, 223, 256, 257, 258, 311, 312, 314, 316, 363, 364, 365, 366, 367, 368, 388, 389, 390, 391, 392, 420.

4 AA sup.: RGM 257 027 and 044 (3x).

27 P⁴: RGM 257 027, 030, 044, 088, 108, 123, 127, 132, 133, 155, 156, 157, 158, 159, 184, 206, 213, 241, 244, 245, 355, 356, 357, 358, 359, 360, 386.

42 M¹: RGM 257 001, 002, 022, 027, 028, 029, 044, 051, 064, 067, 072, 076, 089, 110, 111, 112, 113, 114, 115, 123, 127, 182, 205, 207, 208, 210, 229, 230, 234, 236, 238, 276, 277, 278, 323, 329, 340, 341, 348, 351, 353, 385.

19M²: RGM 257 001, 049, 056, 064, 091, 127, 131, 161, 209, 239, 281, 282, 329, 342, 350, 352, 354, 419.

31 I inf.: RGM 257 008, 019, 024, 025, 046, 052, 069, 070, 073, 084, 087, 116, 117, 124, 141 (2x), 142, 143, 171, 172, 200, 261, 319, 321, 346, 378, 379, 407, 409, 411, 412.

1 A₁: RGM 257 019.

4 P₄: RGM 179 051, 257 019, 062, 186.

50 M₁: RGM 179 051, 257 003, 006, 016, 017, 018, 020, 021, 062, 063, 103, 104, 105, 106, 107, 118, 119, 130, 152, 165, 166, 186, 187, 195, 196, 214, 215, 216, 218, 247, 250, 252, 273, 285, 288, 290, 296, 322, 334, 337, 343, 344, 370, 371, 372, 374, 376, 396, 397, 398.

29 M₂: RGM 179 051, 257 005, 015, 018, 061, 062, 068, 075, 080, 081, 103, 128, 152, 163, 167, 186, 187, 193, 217, 246, 251, 254, 273, 298, 300, 338, 373, 375, 377.

11 M₃: RGM 179 051, 257 103, 152, 187, 246, 255, 273, 304, 345, 401, 410.

15 measurable condyles: RGM 257 015, 016, 018, 061, 062, 102, 152, 153, 187, 188, 189, 203, 246, 273, 339.

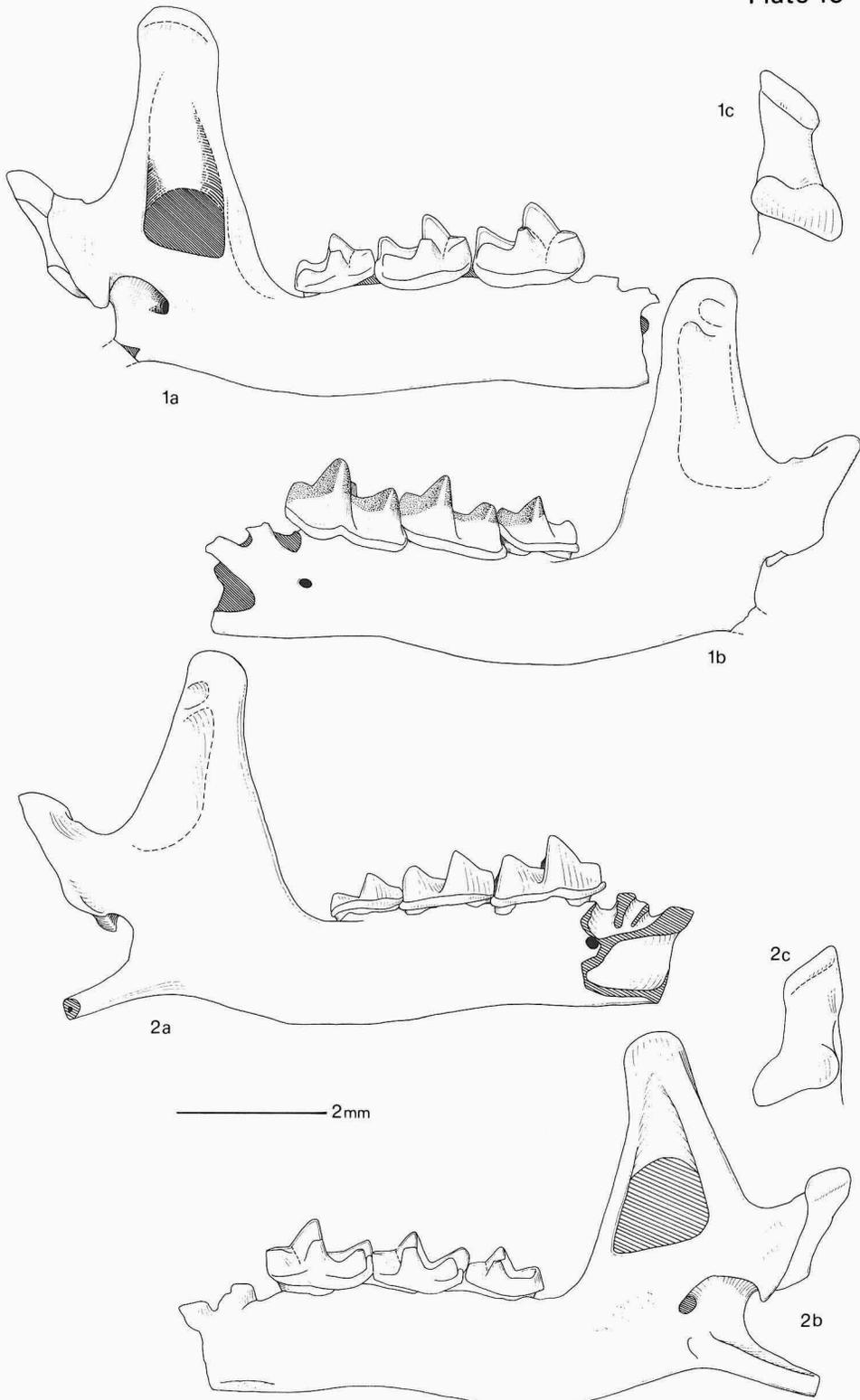
Plate 10

Drepanosorex praeearaneus (Kormos, 1934)

1. Left ramus with M₁-M₃, Osz3/2; a: lingual view; b: buccal view; c: caudal view of condyle.

2. Right ramus with M₁-M₃, Te, RGM 257 187; a: buccal view; b: lingual view; c: caudal view of condyle.

Plate 10



Measurements — See Tables 13-15.

Description — The dental elements are stained.

I sup. — Fissident; the talon is well developed and sharply pointed, it extends far downwards in unworn specimens. The buccal margin is strongly convex ($Os3/2$) and may be undulated (Te); a broad cingulum is present along the buccal posterior margin.

AA sup. — Five upper antemolars are present. The A^1 and A^2 are the largest, they are strongly exoedaenodont. A^3 , A^4 and A^5 are smaller and less bulbous; the elements appear somewhat compressed in antero-posterior direction. A^4 is slightly smaller than A^3 and A^5 . The lingual cingulum is well developed, forming a small postero-lingual flange. A small ridge may run from the lingual cingulum to the main cusp.

P^4 — The hypocone is only poorly developed and separated from the protocone by a wide valley which is usually bordered lingually by a small cingulum. A cingulum runs from the protocone to the parastyle and in most specimens continues underneath this cusp to the buccal side of the tooth. In one specimen (Tegelen, RGM 257 355, see Pl. 9, fig. 5) a small cusplet is present between protocone and parastyle. The posterior emargination is moderate.

M^1 and M^2 — The most characteristic features of M^1 and M^2 are the poor development of the hypocone and of the hypoconal flange. The metaloph is only weakly developed. A wide valley is present between protocone and hypocone, there is a cingulum on the lingual side of this valley. The posterior emargination is moderate.

M^3 — Relatively long and narrow; the postero-lingual corner is formed by two ridges placed at right angles to each other.

I inf. — Tricuspluate, sometimes a slightly tetracuspluate situation can be found, caused by the presence of a small cusplule behind the last normal cusplule. The apex and the cusplules are separated by deep valleys, the central one being the deepest. The cusplules are well developed and somewhat bulbous. As a rule, no cingulum is present on the buccal side, but in some specimens a faint cingulum can be seen. The posterior extension of I inf. reaches to underneath the middle of P_4 , slightly beyond A_1 .

A_1 — A very small part of A_1 is hidden underneath P_4 . A_1 is clearly exoedaenodont; a broad cingulum is present on both sides of the tooth.

P_4 — The postero-lingual basin is bordered posteriorly by a well-developed ridge. The tooth is bulbous and provided with a cingulum on both sides.

M_1 and M_2 — Most characteristic of the large lower molars is the convexity of the sides of the trigonid basin as a first stage towards the exoedaenodonty observed in later *Drepanosorex* species. The entoconid is situated far posteriorly, the entoconid crest is of moderate height. A cingulum is present on both sides, but lingually sometimes only weakly. In M_1 the buccal cingulum is usually undulate underneath the protoconid.

M_3 — The last molar is characterized by a well-developed talonid, in which both hypoconid and entoconid are discernible. The lingual cingulum is weak, the buccal one strong.

Plate 11

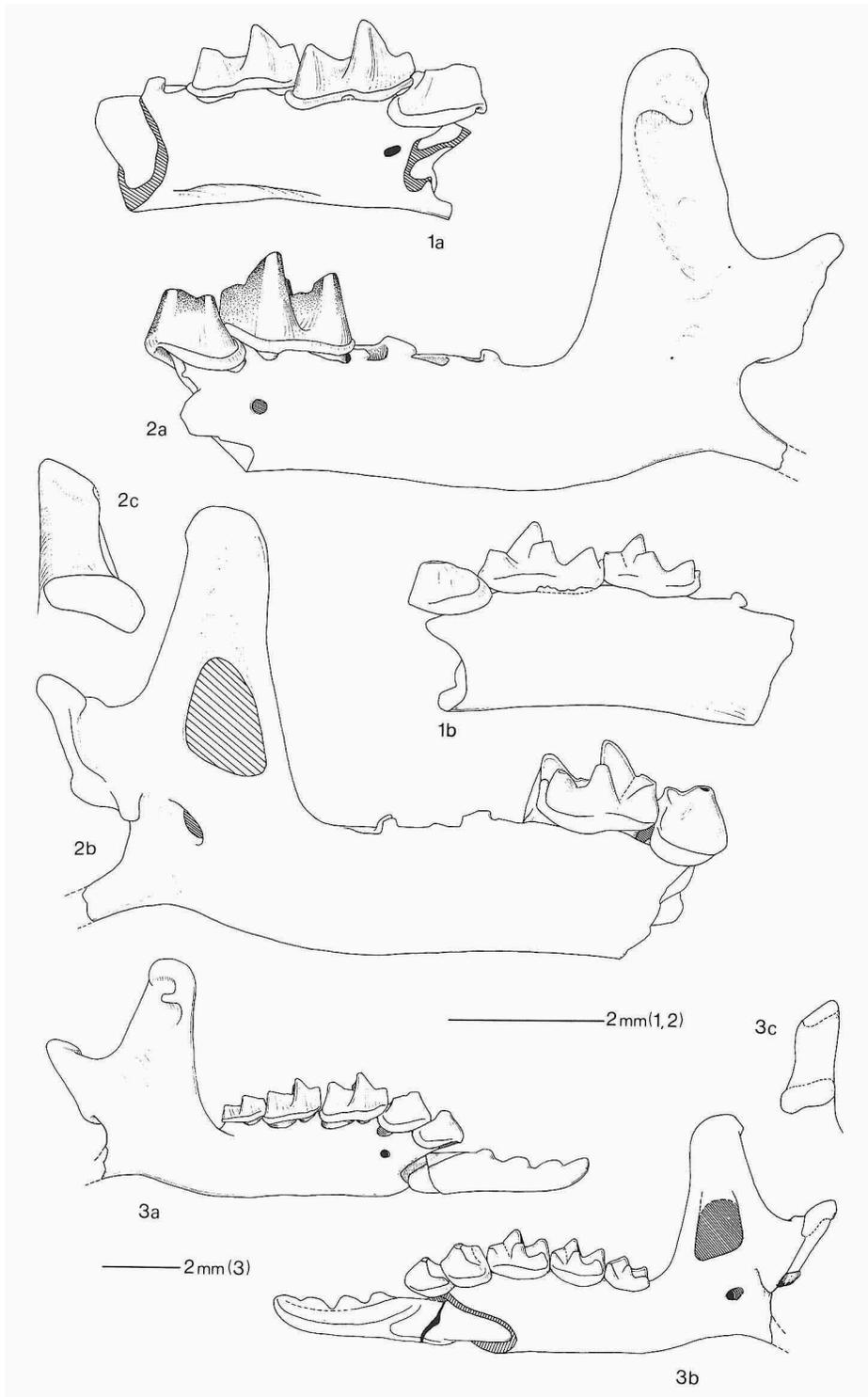
Drepanosorex praeearaneus (Kormos, 1934)

1. Right P_4 - M_2 , Te, RGM 257 186; a: buccal view; b: lingual view.
2. Left ramus with P_4 - M_1 , Vi3 felsb; a: buccal view; b: lingual view; c: caudal view of condyle.

Drepanosorex austriacus (Kormos, 1937)

3. Lectotype, Hundsheim, Austria, coll. TTM no. V.61.1590, same views as fig. 2.

Plate 11



Mandible — The anterior margin of the coronoid process leans backwards; a coronoid spicule is weakly developed and situated close to the apex of the process. The rounded apex of the coronoid process leans a little towards the lingual side. The external temporal fossa is shallow, only vaguely bordered and extending downwards to a level half-way along the condylar process. A pterygoid boss is discernible as a rough spot only. The condyle is relatively small for a *Drepanosorex*; upper and lower facets are almost parallel. When seen from the buccal side, the lower facet is completely visible behind the lower sigmoid notch. The internal temporal fossa extends far upwards, to halfway along the coronoid, and may sometimes continue into a groove that runs to the apex of the coronoid process. The mental foramen is situated below the trigonid of M_1 , sometimes below the edge of P_4 .

Remarks — The attribution of *D. praeareneus* to the genus *Drepanosorex* is based on the exoedaenodonty of the dentition and on the fissident upper incisor. We consider *D. praeareneus* to be the most primitive *Drepanosorex*; it shows many similarities to *Sorex* in general shape and morphology. Therefore, *D. praeareneus* could be close to the origin of *Drepanosorex* from an ancestral *Sorex* stock.

References to *S.* (cf.) *praeareneus* from pre-Villányian ages (e.g. Podlesice, Kowalski, 1956 and Weże, Sulimski, 1962) are probably incorrect. *D. praeareneus* is the oldest known representative of the genus, being the only Villányian species.

The following species also belong to the genus *Drepanosorex*:

D. austriacus (Kormos, 1937) from Hundsheim, Austria. Kormos (1937c) did not designate a holotype. Rabeder (1972b) mentions this species in his description of the Insectivora and Chiroptera of Hundsheim, but he was unable to retrace the type material. Rabeder suggested that the specimen illustrated by Kormos (1937c, fig. 2) should be considered as the lectotype, if found again. The illustrated specimen is indeed present in the collections of the TTM (coll. no. V.61.1590); it is the lectotype (Pl. 11, fig. 3). *D. margaritodon* Kormos, 1935 (holotype coll. TTM no. V.61.1589) from Püspökfürdő (= Betfia, now in Rumania).

D. pachyodon (Pasa, 1947) from the Cava Sud, Soave, Italy. Generic attribution according to Repenning, 1967.

D. savini (Hinton, 1911) from the Upper Freshwater Bed, West Runton, England (holotype coll. BM(NH) no. M 18242); synonym *D. tasnadii* Kretzoi, 1941 from Gombaszög, Czechoslovakia.

To some extent these species form a morphological sequence. Three major trends (morphoclines) may be observed within this sequence, i.e. exoedaenodonty, size increase and enlargement of the condyle. The oldest known species, *D. praeareneus*, has only a slight exoedaenodonty in the antemolars and is smaller than the other known species. The youngest representative, *D. savini* from the Cromerian is the largest known species, while all post-Villányian taxa are more exoedaenodont than *D. praeareneus*.

Genus *Deinsdorfia* Heller, 1963

Type species — *D. franconica* Heller, 1963 (= *D. hibbaridi* (Sulimski, 1962))

Original diagnosis (translated) — A smaller form of Soricidae in which the anterior margin of the coronoid process has an extremely tilted position; condyle placed high; large internal temporal fossa divided by a muscle-attachment bar.

Heller had only one specimen, an edentulous right ramus, which he described as *Deinsdorfia franconica* from Deinsdorf, Germany. This ramus appears identical to the rami from Osztramos 7, as

can be decided by the short and tilted coronoid process, the presence of the horizontal bar in the internal temporal fossa and the large condyle. This type of ramus was described already from Węże 1 by Sulimski (1962) as *Sorex hibbardi*. Therefore, *D. franconica* Heller, 1963 is now considered to be a junior synonym of *D. hibbardi* (Sulimski, 1962).

As abundant material is available of *D. hibbardi* and of two more (new) species, an emended diagnosis can be given for this genus.

Emended diagnosis — Medium-sized Soricini; upper incisor not fissident; five upper antemolars, the A⁵ of which is placed lingually of the parastyle of P⁴; P⁴ with extremely elongate parastyle and high parastylar crest; hypocones and hypoconal flanges in the upper molars reduced and small; lower incisor tricuspluate and reaching as far backwards on the buccal side of the mandible as P₄; A₁ small; P₄ large; M₁ and M₂ with short talonids, M₃ with a small, usually single-cusped talonid. The teeth are stained red. Ramus short and stout with a low coronoid process; coronoid spicule well developed; condyle comparatively large; mental foramen below talonid of M₁.

Differential diagnosis — *Deinsdorfia* differs from *Sorex* by having an M₃ with reduced talonid, by the elongate parastyle in P⁴, by the position of the mental foramen, and by having a short horizontal ramus. It differs from *Petenya* by having a considerably stronger posterior emargination in P⁴, M¹ and M², by having one more upper antemolar and by having less quadrate lower molars. It differs from *Blarinella* by the same characters as it differs from *Petenya*, except for the number of upper antemolars, which is five in both genera. It differs from *Drepanosorex* by having a non-fissident upper incisor, by having an extremely small A⁵, by the elongate parastyle in P⁴, by having a small coronoid process, and by the position of the mental foramen.

Remarks — Repenning (1967) already indicated the necessity of establishing a new genus for *Sorex hibbardi*, but as he had not seen the material he refrained from doing so. Heller (1963) however, had already erected this genus for the single ramus from Deinsdorf: *Deinsdorfia*.

The abundance of *D. hibbardi* and of two related species in the studied Hungarian localities now allows us to refer the three species to the correct genus, *Deinsdorfia*.

The combination of the following characters clearly indicates the attribution of the genus to the tribe Soricini: pigmented dentition; a tricuspluate lower incisor; the presence of entoconid crests in the lower molars; a P₄ with a postero-lingual basin; a non-fissident upper incisor; and a broad interarticular area in the condyle.

Deinsdorfia janossyi sp. nov.

Pl. 12.

Holotype — A right horizontal ramus with complete dentition, coll. TTM no. V.83.11 (Pl. 12, fig. 5).

Etymology — The species is named in honour of Dr Dénes Jánossy, Budapest.

Type locality — Osztramos 9.

Stratigraphic occurrence — Early Ruscinian.

Diagnosis — A *Deinsdorfia* species with upper antemolars diminishing in size from A¹ to A⁵, A¹ and A² not inflated; M² nearly quadrate to sub-trapezoidal in outline (PW/AW = 0.95); lower incisor with three, non-inflated cuspules and a distinct buccal cingulum.

Differential diagnosis — *D. janossyi* sp. nov. differs from *D. hibbardi* (Sulimski, 1962) by not having inflated (exoedaenodont) A¹ and A² and by having no inflated cuspules on the lower incisor; by having a slender coronoid process and by lacking a high internal temporal fossa with a bar. It differs from *D. kordosi* sp. nov. in the same characters except for the bar, and additionally in a slightly smaller size, a less extreme reduction of the talonid of M₃, no reduction of the M², and the presence of a distinct buccal cingulum on the lower incisor.

Available material — 7 I sup., 8 AA sup., 6 P⁴, 4 M¹, 3 M², 1 M³, 5 I inf., 2 A₁, 6 P₄, 7 M₁, 5 M₂, 3 M₃, 2 condyles.

Measurements — See Table 16 and Figs. 9-11.

Description — The dental elements are stained dark red to sometimes even black at the tips of the cusps.

I sup. — Large and *Sorex*-like; the angle between apex and talon is sharp; the buccal cingulum runs along $\frac{2}{3}$ of the posterior margin and then fades away. The buccal posterior margin may vary from slightly convex to slightly concave.

AA sup. — An A⁴ has not been found among the five antemolars that the species possessed. A¹ and A² are the largest of the five; A³ and presumably A⁴ are much smaller; A⁵ is still smaller and hidden at the lingual side of the parastyle of P⁴. A³ and A⁵ are unicuspid; A¹ and A² have a central cusp which is divided in two, thereby giving a Z-shape to the central crest.

P⁴ — Most characteristic is the parastyle, which is placed far towards the anterior and connected to the paracone by a high parastylar crest. The whole tooth thus acquires an elongate shape. The protocone is not very high. A hypocone is not developed as a cusp, but only as a ridge or cingulum, which is separated from the protocone by a wide valley. The hypoconal flange is small and flat.

M¹ and M² — The hypoconal flange is small and flat and surrounded by a very low ridge without a hypocone. The protocone on the other hand is well developed and connected by ridges with both paracone and metacone. In M¹ the postero-buccal corner is protruding; in M² this is not the case. In one unworn M¹ the mesostyle is split.

M³ — One detached M³ was found; its hypocone is poorly developed, as is the protocone, which is only a small single cuspule. In fact only the paracone is large.

I inf. — Tricuspluate; the central depression is the deepest; the central cuspule is the largest. The apex is slightly upturned. A cingulum is present on the buccal posterior part. The lower incisor reaches backwards on the buccal side of the mandible to the posterior end of P₄, below the paraconid of M₁.

A₁ — Small and hidden below P₄ for a large part. A cingulum is present on both sides, but the lingual one is weak. The element is single-cusped.

P₄ — The postero-lingual basin is triangular and reaches the corner of the tooth; the buccal overhang over the root is large; the buccal cingulum is broad but not very pronounced; the lingual cingulum is weak.

M₁ and M₂ — The short talonid is conspicuous, particularly when looked at from the lingual side. The entoconid is close to the metaconid; the entoconid crest is not very high. There is a relatively wide furrow between the entoconid and the hypolophid. The buccal cingulum is well developed; it is sometimes a little undulate. The lingual cingulum is well developed only below the trigonid valleys and nearly lacking below the cusps. The trigonid valley opens low.

Plate 12

Deinsdorfia janossyi sp. nov., all from Osz9

1. Right M³.

2. Right A⁵-M².

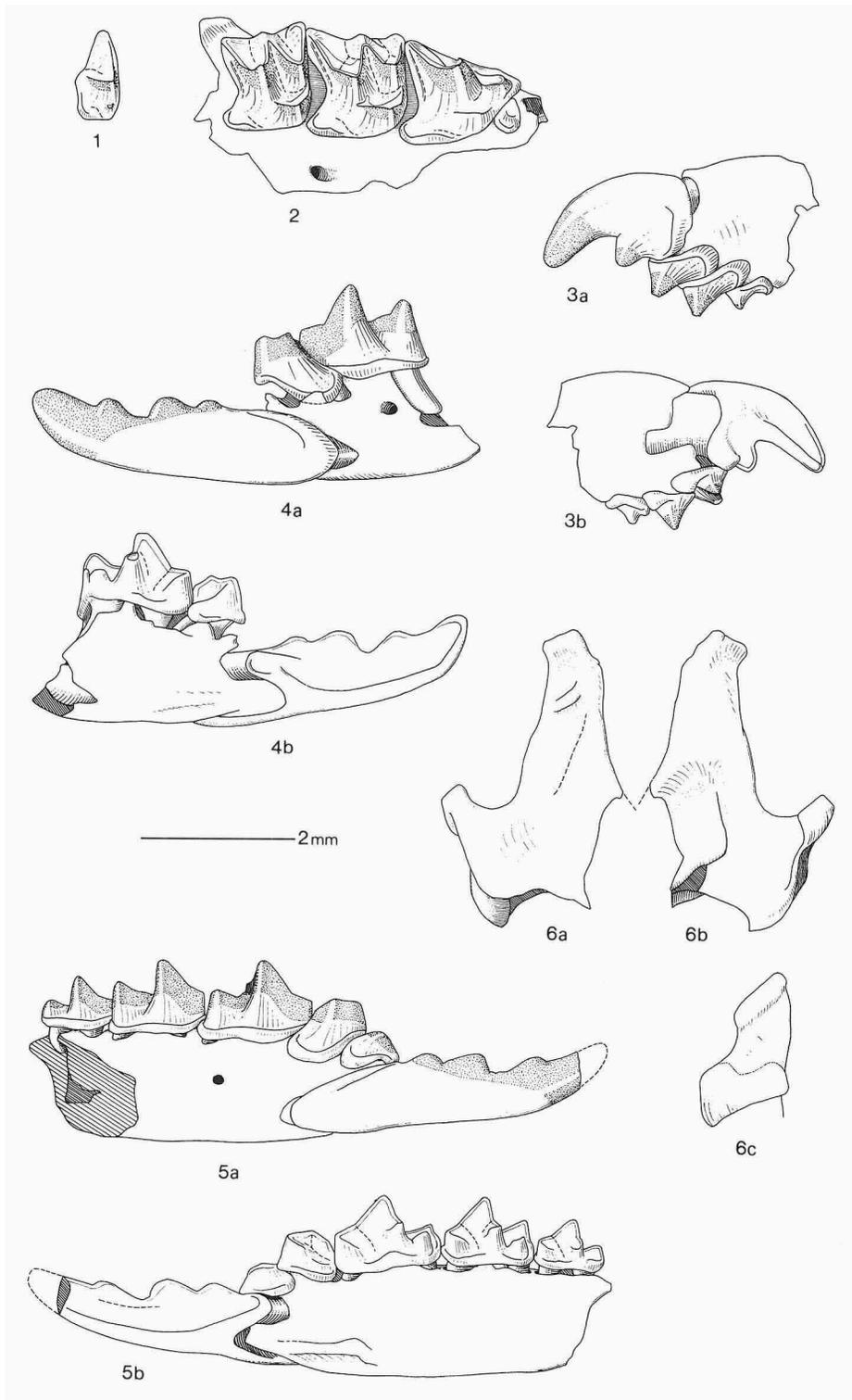
3. Left I sup.-A³; a: buccal view; b: lingual/medial view.

4. Left I inf. and P₄-M₁; a: buccal view; b: lingual/symphysial view.

5. Right I inf.-M₃, holotype, coll. TTM no. V.83.11, same views as fig. 4.

6. Fragmentary right ascending ramus; a: internal view; b: external view; c: caudal view of condyle.

Plate 12



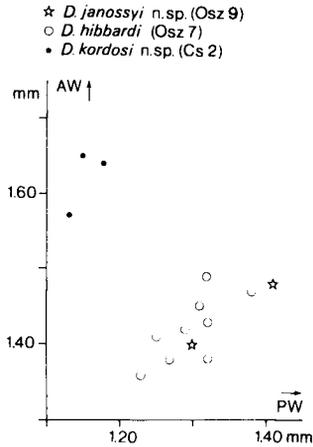


Fig. 9. Scatter diagram of the relation between anterior width (AW) and posterior width (PW) of M₂ in the studied species of *Deinsdorfia*.

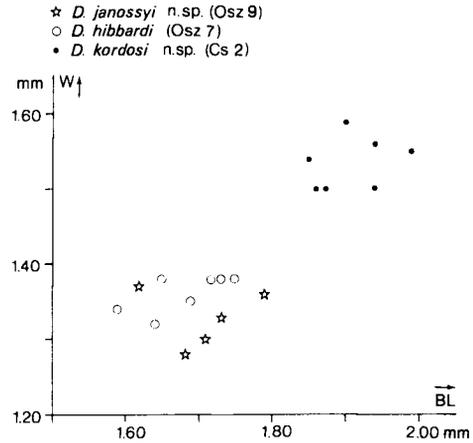


Fig. 10. Scatter diagram of the relation between width (W) and buccal length (BL) of P₄ in the studied samples of *Deinsdorfia*.

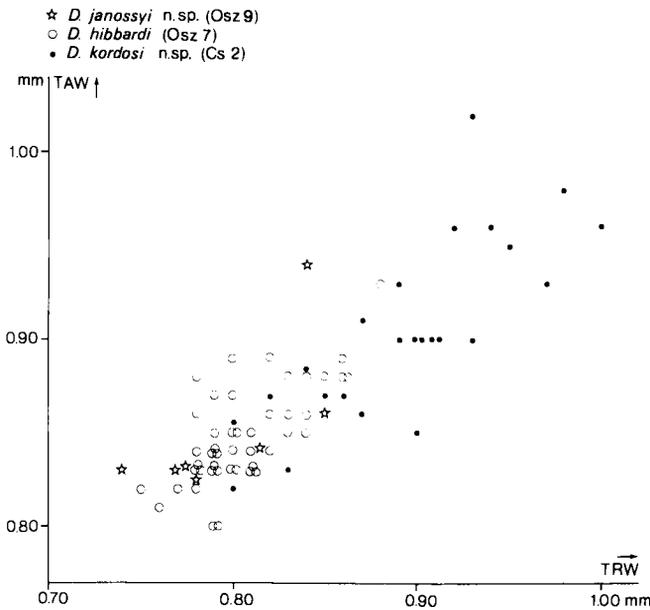


Fig. 11. Scatter diagram of the relation between talonid width (TAW) and trigonid width (TRW) of M₁ in the studied species of *Deinsdorfia*. For *D. hibbaridi* (Osz7) a random sample has been used in order to enhance the clarity of the figure.

M₃ — The talonid is small and reduced and as a rule single-cusped with a tiny basin. In one specimen a trace of two cusps can be seen. The buccal cingulum is narrow but clearly developed; the lingual cingulum is almost completely absent.

Mandible — The anterior margin of the coronoid process is concave. The tip of the coronoid appears rather slender. The posterior margin is almost straight. The external

temporal fossa extends to the upper sigmoid notch and bears a distinct coronoid spicule at $\frac{2}{3}$ of its height. The internal temporal fossa does not continue to the tip of the coronoid. The upper facet of the rather large condyle is narrow, long and cylindrical; it is placed almost parallel to the lower facet. The interarticular area is broad and short. The lower facet has a dented upper margin; it is wider lingually than it is at the buccal side. The foramen mentale is situated below the talonid of M_1 .

Deinsdorfia hibbardi (Sulimski, 1962)

Pl. 13, figs. 1-6; Pl. 14, fig. 1.

Type locality — Węże, Poland.

Studied locality — Osztramos 7.

Other known localities — Deutsch-Altenburg 21 (Austria, Rabeder, pers. comm.), Deinsdorf (Germany, Heller, 1963) and possibly Ivanovce (Czechoslovakia, Fejfar, 1966).

Stratigraphic occurrence — Late Ruscinian (Csarnótanian) - Villányian.

Synonymy (complete)

Sorex hibbardi n. sp., in: Sulimski, 1962, p. 467.

Deinsdorfia franconica n. g. n. sp., in: Heller, 1963, p. 5.

Deinsdorfia cf. *franconica* Heller, in: Fejfar, 1966a, p. 242.

'*Sorex*' *hibbardi* Sulimski, 1962, in: Repenning, 1967, p. 36.

Deinsdorfia franconia Heller, 1963 (misprint), in: Repenning, 1967, p. 57.

Original diagnosis — See Sulimski, 1962 (only concerning mandibular material) and Heller, 1963 (only concerning the ramus).

Emended diagnosis — I sup. with slightly inflated talon; A^1 and A^2 large and inflated; A^3 - A^5 small and compressed; M^2 nearly quadrate to sub-trapezoidal in outline ($PW/AW = 0.92$); lower incisor with three bulbous cuspules and a small but distinct buccal cingulum; mental foramen situated in a shallow depression on the buccal side of the mandible; internal temporal fossa with a horizontal bar.

Differential diagnosis — *D. hibbardi* differs from *D. janosyi* sp. nov. by having inflated elements in the anterior dentition (talon of the upper incisor, A^1 , A^2 , and the cuspules on the lower incisor); by having a less slender coronoid process and a high internal temporal fossa with a bar. *D. hibbardi* differs from *D. kordosi* sp. nov. by having a bar in the internal temporal fossa, by having a distinct buccal cingulum on the lower incisor, by not having an extremely reduced M^2 , and by being slightly smaller.

Available material — 41 I sup., 16 AA sup., 14 P^4 , 29 M^1 , 18 M^2 , 2 M^3 , 32 I inf., 6 A_1 , 13 P_4 , 79 M_1 , 66 M_2 , 38 M_3 , 19 condyles.

Measurements — See Table 17 and Figs. 9-11.

Description — The dental elements are stained a dark orange to dark red, I inf. even blackish.

I sup. — The appearance of I sup. is much like that in *Sorex*, with a convex upper margin and a rather strongly down-turned apex. The buccal posterior margin is undulate and provided with a cingulum along most of its length. Between apex and talon there is a shallow groove on the buccal side.

AA sup. — Five upper antemolars are present, the two anterior ones being relatively large and somewhat inflated (exoedaenodont). Usually, A^2 is a trifle larger

than A¹. A³, A⁴ and A⁵ are much smaller, with A⁵ being the smallest and compressed between A⁴ and P⁴. All antemolars are unicuspid.

P⁴ — P⁴ is characterized by the strongly developed and far anteriorly placed parastyle. The parastylar crest is moderately high; the protocone is well developed. The hypocone is virtually or completely absent as a cusp. The hypoconal flange is not bordered posteriorly by a cingular ridge.

M¹ and M² — Also in the upper molars there is virtually no hypocone and no cingular ridge along the posterior margin of the narrow hypoconal flanges. The protocone, on the contrary, is well developed and U-shaped due to connections to both paracone and metacone. Between the protocone and the hypoconal vestige there is a wide valley.

M³ — The protocone is relatively well developed. Behind it is a small valley separating the protocone from the posterior crest.

I inf. — Tricuspluate; the central depression is the deepest one. The cuspules as well as the upturned apex are rather bulbous. A cingulum is present along the dorsal buccal posterior margin, but it is not very pronounced. I inf. reaches buccally to underneath the posterior edge of P₄ or slightly further, i.e. below the paraconid of M₁.

A₁ — Small, for its larger part pinched in between I inf. and P₄. Cingula are present on both sides of the unicuspid element.

P₄ — The P₄ is relatively large and inflated buccally, causing considerable overhang over the root. The element is double-cusped, both cusps being of the same height. The postero-lingual basin does not reach all the way down to the postero-lingual corner. On both sides of the tooth the cingula are moderately developed; the buccal cingulum is wide.

M₁ and M₂ — The metaconid is close to the entoconid in the lower molars, hence the trigonid valley is wide and open. The entoconid crest is not very high. The lingual cingulum is either weak or absent; as a rule there is only a tiny bit of it underneath the trigonid valley. The buccal cingulum is well developed, sometimes a little undulate.

M₃ — The talonid is small and reduced and as a rule single-cusped with a tiny basin usually discernible.

Mandible — The coronoid process is low and short, having its narrowest part below the top at the level of the coronoid spicule. Hence both anterior and posterior margins are concave. The coronoid spicule is strongly pronounced, but the external temporal fossa is hardly excavated. This fossa extends to below the upper sigmoid notch. The internal temporal fossa extends to close to the tip of the coronoid and is provided with a horizontal bar separating the shallow dorsal part from the deep ventral part of the

Plate 13

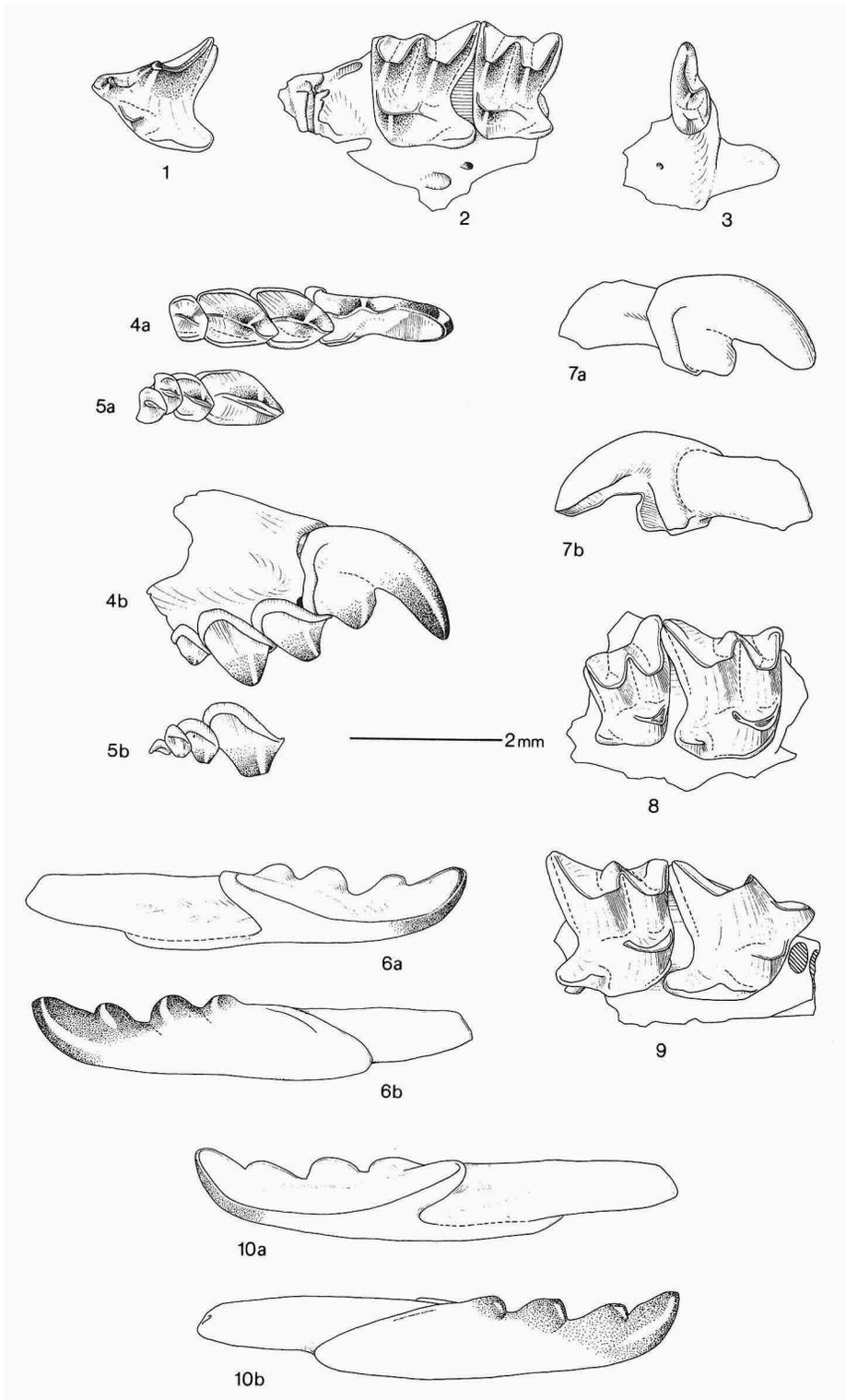
Deinsdorfia hibbardi (Sulimski, 1962), all from Osz7

1. Left P⁴.
2. Left M¹-M².
3. Left M³.
4. Right I sup.-A³; a: occlusal view; b: buccal view.
5. Right A²-A⁵, same views as fig. 4.
6. Left I inf.; a: symphysial view; b: buccal view.

Deinsdorfia kordosi sp. nov., all from Cs2

7. Right I sup., Cs2/12; a: buccal view; b: medial view.
8. Right M¹-M², Cs2/22.
9. Right P⁴-M¹, Cs2/20.
10. Right I inf., Cs2/20; a: symphysial view; b: buccal view.

Plate 13



fossa. the condyle is large, protruding far backwards. The upper facet is long and cylindrical, the lower facet is broad and provided with a dented upper margin. The two facets are not parallel. The interarticular area is broad and high and centrally excavated. The mandibular foramen is situated below the posterior half of M_1 , in a shallow depression.

Remarks — The material from Osztramos 7 is attributed to the species *hibbardi*, originally described from Węże, on the basis of the following characters: I inf. with conspicuous cingulum; mental foramen in a depression; buccal cingulum in M_1 not very undulate; interarticular area high and broad; internal temporal fossa with a transverse bar. The ramus described by Heller (1963) as *Deinsdorfia franconica* agrees well with the description presented here.

Deinsdorfia kordosi sp. nov.
Pl. 13, figs. 7-10; Pl. 14, fig. 2.

Holotype — A right ramus with M_1 - M_3 , coll. MÁFI no. V.12704, Vt.98 (Pl. 14, fig. 2).

Etymology — This species is named in honour of Dr László Kordos, Budapest.

Type locality — Csarnóta 2.

Stratigraphic occurrence — Late Ruscinian (Csarnótian).

Diagnosis — I sup. with slightly inflated talon; M^2 strongly trapezoidal due to reduction of the posterior part ($PW/AW = 0.71$); lower incisor with three bulbous cuspules and only a faint and hardly individualized buccal cingulum or none at all; M_1 with a strongly undulate buccal cingulum; M_3 with a strongly reduced talonid; mental foramen situated in a depression of the mandible; internal temporal fossa oval and low, not reaching the tip of the coronoid.

Differential diagnosis — *D. kordosi* sp. nov. differs from *D. janossyi* sp. nov. by having inflated elements in the anterior dentition, by having a reduced M^2 and a more reduced talonid in M_3 , by the absence of a distinct cingulum in the lower incisor, by having a less slender coronoid process, and by being generally larger. *D. kordosi* sp. nov. differs from *D. hibbardi* by having an extremely reduced M^2 , by being generally larger, by not having a bar in the internal temporal fossa, and by not having a distinct buccal cingulum on the lower incisor.

Available material — 50 I sup., 8 P^4 , 11 M^1 , 3 M^2 , 40 I inf., 1 P_4 , 28 M_1 , 21 M_2 , 9 M_3 , 42 condyles.

Measurements — See Table 18 and Figs. 9-11.

Description — The dental elements are stained red.

Plate 14

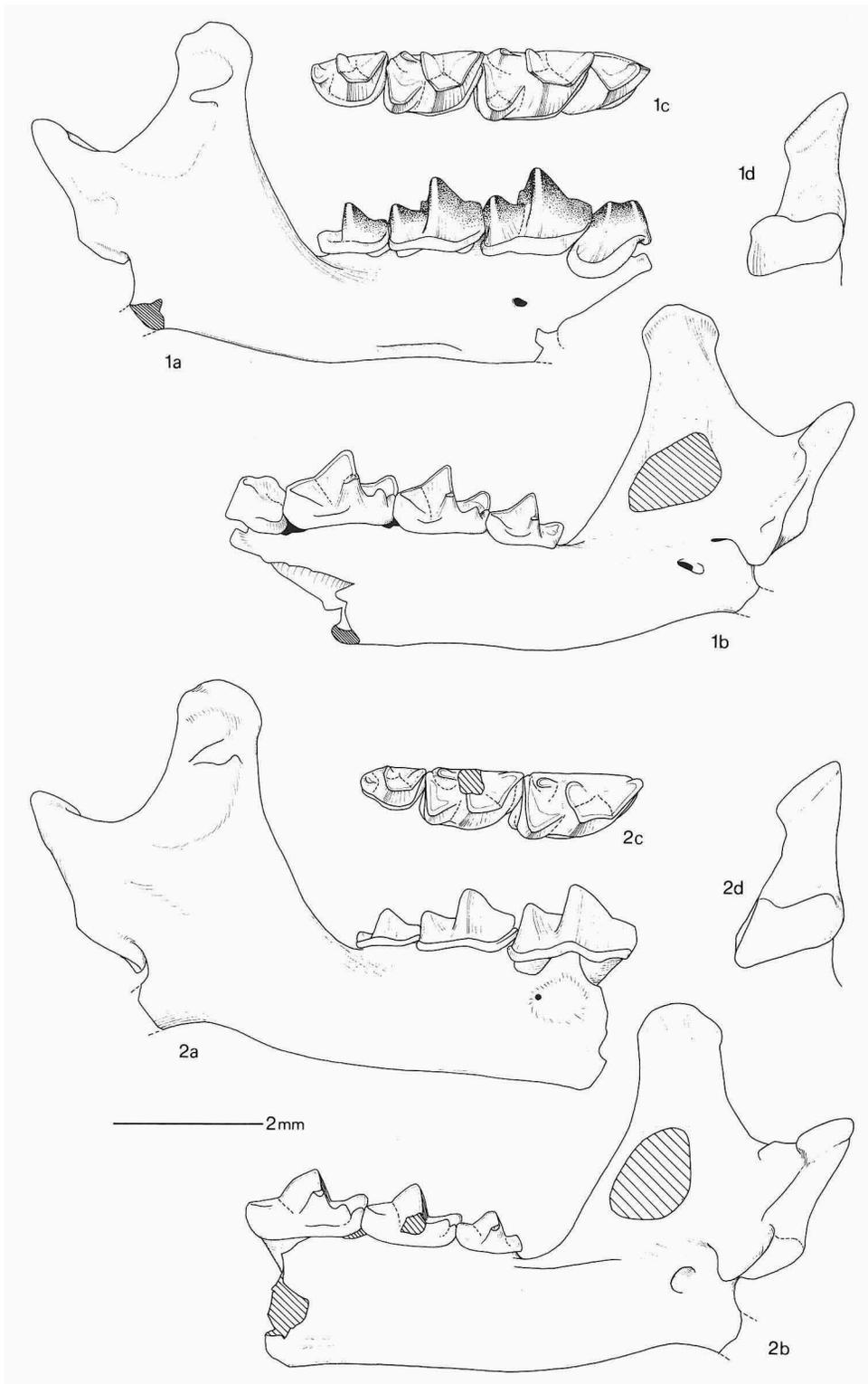
Deinsdorfia hibbardi (Sulimski, 1962), Osz7

1. Right ramus with P_4 - M_3 ; a: buccal view; b: lingual view; c: occlusal view; d: caudal view of condyle.

Deinsdorfia kordosi sp. nov., Cs2

2. Right ramus with M_1 - M_3 , holotype, coll. MÁFI no. V.12704, Vt.98, same views as fig. 1.

Plate 14



I sup. — Not fissident, there is a sharp angle between apex and talon; the posterior buccal cingulum is rather broad, reaching up to $\frac{3}{4}$ of the height of the tooth; the posterior margin is either straight or slightly concave.

P⁴ — P⁴ is characterized by the anterior position of the parastyle; the paracone is situated nearly half-way along the buccal side. The protocone has a rather buccal position, about half-way between parastyle and the poorly developed hypocone. From the protocone a loph runs posteriad to the paracone. Protocone and hypocone are separated by a wide and deep furrow. The hypocone is hardly individualized as a cusp, the hypoconal flange is narrow and flat and not surrounded by a ridge.

M¹ — The shape of M¹ is characterized by the relatively robust postero-buccal corner and the reduced talon. The protocone is U-shaped but the metaloph does not reach the metacone; hence a narrow groove is present between protocone and metacone. The metacone is higher than the paracone. The hypocone is strongly reduced and hardly individualized. A hypoconal flange is present but short and flat and low when compared to the other cusps. As a rule, a small but distinct cingulum is present underneath the protocone.

M² — The M² is more reduced than in any other type of shrew known from Europe (except for the dimyloid genera *Amblycoptus* and *Dimylosorex*). The reduction is most conspicuous in the posterior half. Hence the general shape of M² is trapezoidal. The development of the cusps and lochs in the trigon is comparable to the situation in M¹, although the metacone is relatively lower. The hypocone is strongly reduced, the whole talon is a mere flat appendix situated half-way between the protocone and the metacone.

I inf. — Tricuspluate, with the cuspules rather bulbous at the buccal side. The central cuspule is the largest; the deepest depression is the central one. The dorsal surface is rather broad and extends on the symphyisial side; it gives the tooth a slightly spatulate appearance when seen from the symphyisial side. There is no buccal cingulum or only a trace of one. Buccally, the I inf. reaches to the paraconid of M₁.

M₁ and M₂ — The trigonid basin is low and open on the lingual side, particularly in M₁. The paraconid is placed far forwards, while the protoconid and metaconid are close together. The entoconid and metaconid are also rather close, with a moderately high entoconid crest in between. If present, the lingual cingulum is broad but hardly pronounced. The buccal cingulum is broad and well pronounced, strongly undulate and sometimes also varying in width.

M₃ — The talonid is strongly reduced, even more so than in genera like *Petenyia* or *Crocidura*; only a single comma-shaped or straight cusplet is present.

Mandible — The coronoid process is low and wide; the tip bends somewhat towards the median and has a little undulation at its posterior corner. The anterior edge of the coronoid process is strongly concave because of the forward bending of the tip of the coronoid. The coronoid spicule is large, placed at two-thirds of the height of the external temporal fossa and pointing towards the upper condylar facet. The external temporal fossa extends downwards to underneath the level of the upper sigmoid notch. The condyle is large; the upper facet is cylindrical. The interarticular area is broad and high and slightly excavated. The lower facet is high, with the upper margin slightly dented. As a rule, the entire lower facet is visible behind the lower sigmoid notch when looked at from the side. A pterygoid boss is present. The internal temporal fossa is relatively small, triangular/oval and not extending upwards to the tip of the coronoid process. The mandibular foramen is placed underneath the posterior corner of the internal temporal fossa; it is large and open. The mental foramen is situated underneath the talonid of M₁, at the rear of a shallow depression of the mandible.

Remarks — The three named species are all clearly separable on morphological grounds, most notably by the lack of exoedaenodonty in the early Ruscinian *D. janossyi* sp. nov. and the strong reduction of M^2 in the late Ruscinian *D. kordosi* sp. nov. Two evolutionary lineages are possible: *janossyi* → *hibbardi* → *kordosi*, or: *janossyi* → *hibbardi* and *kordosi*. Trends in these lineages are: 1) slight general enlargement; 2) enlargement of the condyle; 3) shortening and widening of the coronoid process; 4) exoedaenodonty of the anterior dentition; 5) reduction of the posterior dentition.

The trends 1, 2, 4, and 5 can also be observed in the Pleistocene lineage *Drepanosorex praeareneus* → *Drepanosorex* (other species) → *Dimylosorex tholodus* (see also Rabeder, 1972a).

Although there are important differences between *Deinsdorfia* and *Drepanosorex* (e.g. in the structure of the upper incisor and the development of A^3 - A^5), it is clear that both genera show a parallel evolution.

Deinsdorfia is older than *Drepanosorex*. *Deinsdorfia* occurs from MN 14 up till MN 17; *Drepanosorex* first appears in MN 17; there is an overlap in ranges in MN 17 (the late Villányian).

It is likely that *Drepanosorex* took over the ecological niche of *Deinsdorfia* during this period. It is generally accepted (see for example Rabeder, 1972a) that exoedaenodont insectivores ate a diet consisting mainly of molluscs.

Genus *Petenyia* Kormos, 1934

Type species — *P. hungarica* Kormos, 1934.

Remarks — Several species of this genus have been named or mentioned in the literature: *P. hungarica*, *P. neglecta*, *P. stehlini*, *P. dubia*, and ?*P. cf. dehneli*. Of all these, we retain only *P. hungarica*, the genus thus becomes monospecific. For remarks see the section after the description of this single species.

Petenyia hungarica Kormos, 1934 Pls 15-19.

Holotype — A skull with nearly complete dentition, coll. MÁFI no. Ob.3684 (Pl. 15, fig. 1).

Type locality — Villány Kalkberg (Nord), Hungary (= Villány 3).

Studied localities — Osztramos 1, 3/2, 7, Csarnóta 2, Villány 3, and Tegelen.

Selected other localities — Podlesice (Kowalski, 1956), Kadzielnia (Kowalski, 1958), Węże (Sulimski, 1959, 1962), Mała Cave (Sulimski et al., 1979), Plešivec (Fejfar, 1961), Hajnáčka (Fejfar, 1964), Ivanovce A and B (Fejfar, 1966a), Weissenburg 7 (von Koenigswald, 1971), Püspökfürdő (= Betfia, as *P. neglecta*, Kretzoi, 1943, Terzea, 1973), Beremend 5 and 11 (Jánossy, 1979), Villány 5, Nagyarsányhegy 2, Osztramos 2, 8 and 14, Kövesvarad (Jánossy, 1979), Csarnóta 1 (Kretzoi, 1956).

Stratigraphic range — Early Ruscinian to early Biharian (Templomhegy phase).

Original description — Kormos (1934) did not give a formal diagnosis but only a description, from which the following items may be used as a set of diagnostic features: rostral part of the skull (above the antemolars) excavated; I sup. with strong talon; four upper antemolars, diminishing in size towards the back; P^4 , M^1 and M^2 with nearly straight posterior margins. Mandible short and massive; mental foramen between paraconid and protoconid of M_1 (note: this is probably a mistake as in all

studied specimens the mental foramen is situated between protoconid and hypoconid of M_1). Coronoid process with concave anterior edge; tip of the coronoid process undulate; coronoid spicule highly pronounced. I inf. bicuspluate, without a buccal cingulum; M_3 with a single-cusped talonid.

To these features, the following are here added as being diagnostic: upper incisor not fissident; upper molars with a small but distinct metaloph and without a hypocone. Lower molars with entoconids close to metaconids and usually high entoconid crests; lower incisor reaching buccally to the end of P_4 ; anterior edge of the coronoid process with a small spicule, giving it a slight 3-shape in side view; the coronoid spicule divides the external temporal fossa into two parts roughly equal in size. Lower condylar facet high; interarticular area broad and low. The teeth are pigmented with a dark red stain.

Synonymy (only concerning the studied localities):

Petényia hungarica in: Kormos, 1934, p. 301 (Vi3).

Petényia hungarica Korm., in: Kormos, 1937b, p. 1089 (Cs2) and p. 1090 (Vi3).

Petényia hungarica Kormos, in: Kretzoi, 1956, pp. 47 and 170 (Cs2) and pp. 61 and 184 (Vi3).

Petényia hungarica Kormos, in: Kretzoi, 1959a, pp. 238 and 245 (Cs2).

Petényia hungarica Kormos, in: Kretzoi, 1962, pp. 301 and 349 (Cs2).

Petényia hungarica Kormos, 1934, in Repenning, 1967.

Petényia sp. (non *Petényia* cf. *hungarica* Kormos), in: Jánossy, 1972 (Osz1).

Petényia hungarica Kormos, in: Jánossy, 1973a (Osz7).

Petényia cf. *hungarica* Kormos, 1934, in: Freudenthal et al., 1976 (Te).

Petényia sp. (non *Petényia* cf. *hungarica* Kormos), in: Jánossy & Kordos, 1977, p. 41 (Osz1).

Petényia hungarica Kormos, in: Jánossy & Kordos, 1977, p. 44 (Osz3) and p. 47 (Osz7).

Petényia hungarica Kormos, in: Jánossy, 1978 (Osz7).

Petényia hungarica Kormos, in: Jánossy, 1979, p. 23 (Cs2), p. 27 (Osz7), p. 34 (Vi3) and p. 36 (Osz3).

Studied material

Osztramos 1B: 4 I sup., 2 P^4 , 1 M^1 , 1 M^2 , coll. TTM no. V.73.16.

Osztramos 1C: 2 I sup., 2 M^1 , 3 I inf., 2 P_4 , 3 M_1 , 3 M_2 , 1 M_3 , coll. TTM no. V.73.16.

Osztramos 1E: 1 I inf., coll. TTM.

Osztramos 7: 25 I sup., 11 AA sup., 12 P^4 , 22 M^1 , 13 M^2 , 4 M^3 , 25 I inf., 8 A_1 , 13 P_4 , 42 M_1 , 57 M_2 , 46 M_3 , 28 condyles.

Csarnóta 2: 6 I sup., 3 AA sup., 1 M^1 , 7 I inf., 3 M_1 , 7 M_2 , 5 M_3 , 21 condyles.

Villány 3: 1 M^1 , 2 I inf., 1 P_4 , 5 M_1 , 5 M_2 , 3 M_3 , 5 condyles.

Villány 3 alsó: 1 I sup., 2 AA sup., 2 P^4 , 1 M^1 , 1 M^2 , 2 I inf., 1 A_1 , 2 P_4 , 4 M_1 , 4 M_2 , 4 M_3 , 5 condyles.

Villány 3 felső: I sup., 9 AA sup., 4 P^4 , 6 M^1 , 5 M^2 , 4 M^3 , 4 I inf., 3 A_1 , 4 P_4 , 7 M_1 , 7 M_2 , 8 M_3 , 5 condyles.

In addition, the holotype from Villány Kalkberg (= Vi3) has been seen.

Tegelen: 13 I sup.: RGM 257 004, 007, 010, 013, 053, 090, 099, 224, 259, 270, 271, 272, 324.

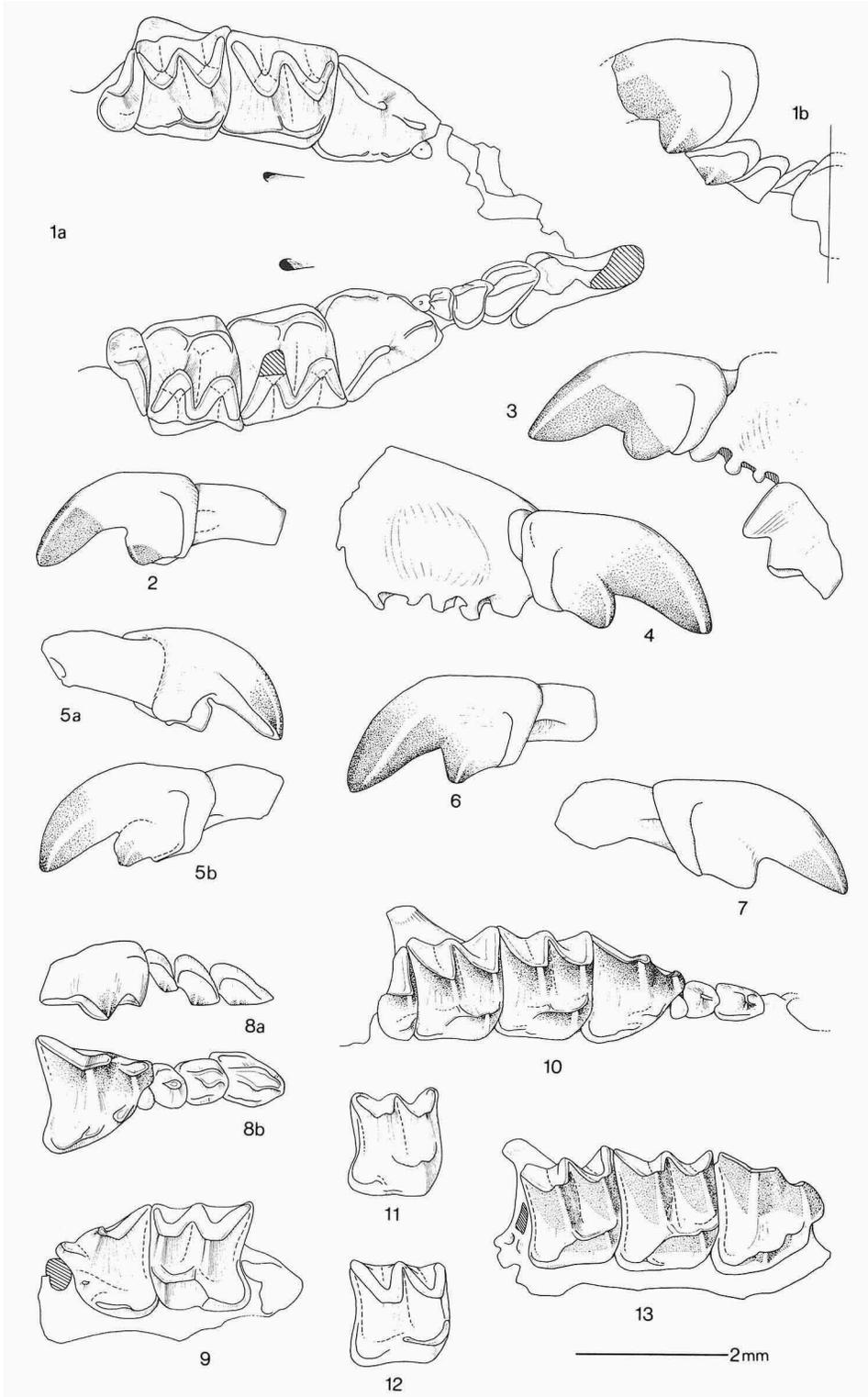
4 P^4 : RGM 257 011, 083, 160, 384.

Plate 15

Petényia hungarica Kormos, 1934

- Holotype, Villány Kalkberg (= Vi3), coll. MÁFI no. Ob.3684; a: whole specimen, occlusal view; b: left I sup.-AA sup., buccal view.
- Left I sup., Osz1C.
- Left I sup. and P^4 , Osz3/2, buccal view.
- Right I sup., Vi3 felső.
- Left I sup., Cs2/14; a: medial view; b: buccal view.
- Left I sup., Osz7.
- Right I sup., Te, RGM 257 010.
- Right A^1 - P^4 , Vi3 felső; a: buccal view; b: occlusal view.
- Left P^4 - M^1 , Osz1B.
- Right A^2 - M^3 , Osz7.
- Right M^2 , Osz1B.
- Right M^1 , Cs2/15.
- Right P^4 - M^2 , Osz3/2.

Plate 15



6 M¹: RGM 257 048, 066, 177, 181, 267, 381.
 9 M²: RGM 257 012, 048, 059, 060, 178, 233, 240, 279, 349.
 1 M³: RGM 257 279.
 2 I inf.: RGM 257 320, 408.
 9 M₁: RGM 179 052, 257 023, 058, 086, 100, 192, 269, 301, 394.
 14 M₂: RGM 179 052, 257 058, 074, 085, 086, 101, 162, 194, 286, 294, 295, 297, 299, 399.
 6 M₃: RGM 179 052, 257 058, 074, 086, 101, 302.
 3 rami: RGM 179 052, 257 101, 327.
 Osztramos 3/2: 3 I sup., 2 AA sup., 6 P⁴, 5 M¹, 3 M², 1 M³, 7 I inf., 3 A₁, 6 P₄, 10 M₁, 11 M₂, 9 M₃, 9 condyles.

Measurements — See Tables 19-24.

Description — The dental elements are (usually intensely) stained a dark red.

I sup. — I sup. is rather elongate, with a pointed, non-fissident apex. The dorsal and buccal posterior edges make a sharp angle; the dorsal outline is usually straight in side-view. Apex and talon are separated by a shallow groove. A buccal cingulum is present, but it does not reach the dorsal edge: at about $\frac{1}{2}$ to $\frac{3}{4}$ of its height it bends anteriorly and then fades away.

AA sup. — Four unicusped upper antemolars are present. As a rule, they diminish in size from A¹ to A⁴. When seen from the buccal, A⁴ is completely hidden behind the parastyle of P⁴.

P⁴ — Most characteristic of P⁴ (as well as of M¹ and M²) is the nearly straight posterior margin. The parastyle is well developed and as a rule connected to the paracone by a high parastylar crest. Both protocone and hypocone are poorly developed, usually separated but sometimes connected to each other. The hypoconal flange is rather deeply concave.

M¹ and M² — Hardly any posterior emargination is present. Paracone and metacone are much better developed than the protocone; the hypocone is usually not developed. Protocone and hypocone are usually separated, but in some specimens (e.g. the holotype, Pl. 15, fig. 1a) both cusps are connected, thus forming a continuous endoloph. A metaloph is always present, albeit sometimes very weakly. The outlines of both M¹ and M² do not differ much.

M³ — The M³ usually has a large and well-developed paracone and a lingual part consisting of a basin surrounded by a U-shaped ridge on which no cusps can usually be discerned. In the type from Vi3 a small protocone can be seen (see Pl. 15, fig. 1a).

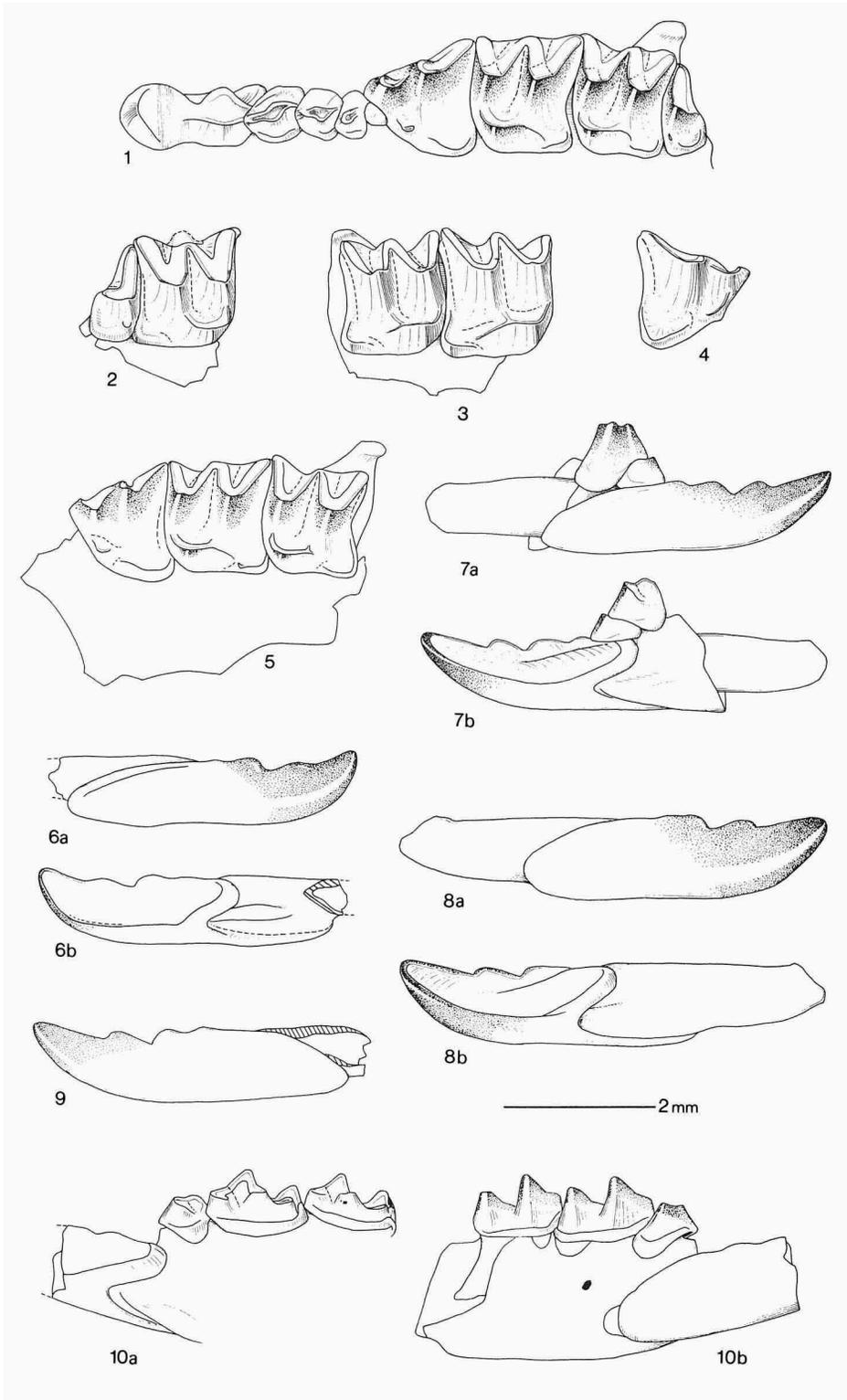
I inf. — Bicuspluate, a tendency towards a tricuspluate state can often be noted due to the presence of a minute third posterior cuspule (e.g. Pl. 16, figs. 7, 9). The cuspules are not very prominent when compared to other genera within the tribe Soricini.

Plate 16

Petenya hungarica Kormos, 1934

1. Left upper dentition, Vi3 felső.
2. Right M²-M³, Te, RGM 257 279.
3. Right M¹-M², Te, RGM 257 048.
4. Right P⁴, Te, RGM 257 011.
5. Left P⁴-M², Püspökfürdő, originally designated as *Petenya neglecta*, coll. TTM no. V.61.1593.
6. Right I inf., Cs2/1; a: buccal view; b: symphysial view.
7. Right I inf.-P₄, Osz7, same views as fig. 6.
8. Right I inf., Vi3 alsó, same views as fig. 6.
9. Left I inf., Te, RGM 257 408.
10. Right I inf. and P₄-M₂, Osz1C, coll. TTM no. V.73.16; a: lingual view; b: buccal view.

Plate 16



A buccal cingulum is either absent or weakly developed along the dorsal edge. At the buccal side of the mandible, I inf. reaches back as far as the posterior end of P₄, sometimes (e.g. in Osz7, Pl. 16, fig. 7) a bit further.

A₁ — The first lower antemolar is very small, of tetrahedric shape and lacking a postero-lingual basin. The larger part of the element is squeezed in between I inf. and P₄; only the very tip is free. Cingula are weak.

P₄ — The P₄ is rather large, two-cusped and sometimes somewhat bulbous. The postero-lingual basin is well developed, but it does not reach the postero-lingual corner of the tooth. The buccal overhang over the root is not extreme; the buccal cingulum however, is broad and well developed. The lingual cingulum is weak.

M₁ and M₂ — In occlusal view the lower molars are rather quadrate in outline (i.e. relatively wide and short), though not as extremely 'bat-like' as in *Blarinella*. The entoconid is in a rather anterior position and separated from the hypolophid by a wide valley. The entoconid crest is high (Pl. 18, fig. 3), but in some specimens (Pl. 18, fig. 2b) it may be quite low. The oblique crest may bear a small mesoconid in unworn specimens (see e.g. the M₁ in Pl. 18, fig. 2a). The buccal re-entrant valley opens low, directly above the broad, well-pronounced and sometimes slightly undulate buccal cingulum. The lingual cingulum is less well developed than the buccal one.

M₃ — Characteristic for M₃ is the reduced talonid, which bears only a comma-shaped hypoconid and lacks an entoconid and a talonid basin. Cingula are developed on both sides, but the lingual cingulum is weak or sometimes even absent.

Mandible — The horizontal ramus is short and high, its lower margin is convex. The anterior margin of the coronoid process is concave, with usually a small spicule situated just below the middle. The tip of the coronoid is broad, slightly divergent with a strongly undulating outline. The posterior margin is almost straight. The coronoid spicule is very large and strongly pronounced; it points towards the upper condylar facet and it divides the external temporal fossa into two almost equally parts. This deep fossa does not reach much below the level of the upper sigmoid notch. The internal temporal fossa is usually high and triangular; it may extend to the tip of the coronoid. The upper facet of the condyle is small and cylindrical to elongate ovoid; the lower facet is not very long and higher linguallly than laterally. The interarticular area is broad and low and centrally somewhat depressed. On the lateral side the condyle may bulge somewhat. In Csarnóta 2 the condyle is slightly more slender than in the situation described here; an extreme example is shown in Pl. 18, fig. 1. The mandibular foramen is below the posterior corner of the internal temporal fossa. The mental foramen is below M₁, between protoconid and hypoconid.

Remarks — Although slight variations and differences between the various samples of *P. hungarica* can be noted (e.g. in the development of an endoloph, the degree of pigmentation, the sizes, the height of the entoconid crests), it is neither possible nor useful to express this variation in different species names.

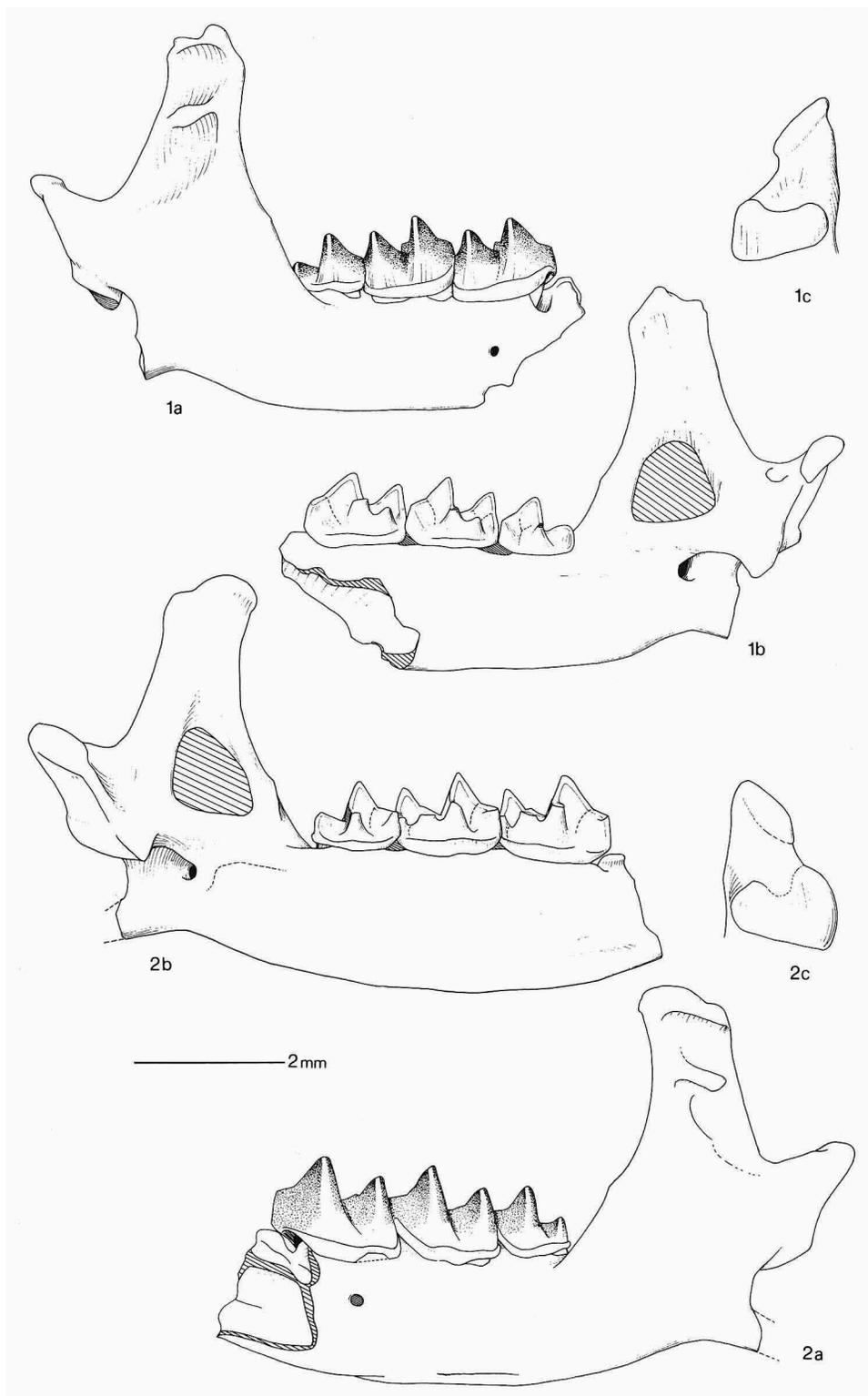
It appears that the variation found between the samples has the same range within samples; see e.g. the difference in height of the entoconid crests in Osz 3/2 (Pl. 18, figs. 2, 3). Therefore, all *Petenyia* material is here referred to as *P. hungarica*.

Plate 17

Petenyia hungarica Kormos, 1934

1. Right ramus with M₁-M₃, Osz7; a: buccal view; b: lingual view; c: caudal view of condyle.
2. Left ramus with M₁-M₃, Vi3 felső, same views as fig. 1.

Plate 17



The following species of *Petenyia* are known from the literature: *P. hungarica* Kormos, 1934 (many localities, see above); *P. neglecta* Kretzoi, 1943 (Püspökfürdő = Betfia, Rumania); *P. stehlini* Kretzoi, 1943 (Cotencher Cave, Switzerland); *P. suavensis* Pasa, 1948 (Soave, Italy); *P. dubia* Bachmayer & Wilson, 1970 (Kohfidisch, Austria); and ?*P. cf. dehneli* (Kowalski) in: Jánossy, 1974 (Osztramos 9).

P. neglecta is here considered to be a synonym of *P. hungarica*. The holotype of *P. neglecta* is a mandible with extremely worn dentition (Pl. 19, fig. 2). There is no morphological difference at all between the Püspökfürdő material and other *hungarica* samples of the same age; Kretzoi's only clearly diagnostic feature of *P. neglecta* (the type of cusplation of I inf.) is the result of the worn state of this tooth in the type specimen. The conclusion of synonymy was reached already by Sulimski, 1959.

P. stehlini is not a *Petenyia*, but a *Sorex*, as originally stated by Stehlin, 1932. This is evident when one compares *Petenyia* with the illustrations given by Stehlin (1932) for the Cotencher material. The shape of I sup., the stronger posterior emargination of the upper molars and the tricuspluate I inf. all rule out the assignment to the genus *Petenyia* and are suggestive of *Sorex*. This conclusion relieves us of this strangely young *Petenyia*: the Cotencher material is of 'Mousterian' = Weichselian age, while the supposed age of extinction of *Petenyia* is early Biharian. The youngest known locality with *Petenyia* remains is Kövesvarad.

P. suavensis is here referred to *Sorex minutus*, judging from Pasa's (1947) illustrations and descriptions. The shape as well as the size (e.g. length M_1 - M_3 of 2.95-3 mm) agree exactly with the morphology and the size of *S. minutus*. Among the morphological similarities between *S. minutus* and the Soave material are: an elongate 2-cusplated P_4 ; far posteriorly placed entoconids in the lower molars; a basined talonid in M_3 ; the rounded tip of the slender coronoid process; a longitudinal external temporal fossa with a central crest; a long, slender horizontal ramus with a concave ventral edge; the mental foramen, which is situated below the protoconid of M_1 .

P. dubia from Kohfidisch is referred to the genus *Blarinella*, a possibility already stated by Bachmayer & Wilson (1970), see below.

The mentioning of ?*P. cf. dehneli* (Kowalski) by Jánossy (1974) from Osztramos 9 is based on a misinterpretation. Jánossy compared his material from Osz9 to *Sorex dehneli* from Podlesice. However, *Sorex dehneli* (originally described from Podlesice by Kowalski, 1956) belongs to the tribe Blarinini, genus *Mafia* gen. nov., and not to the tribe Soricini to which *Petenyia* belongs. The material from Osztramos 9 that Jánossy referred to is here described as *Blarinella dubia* (see below).

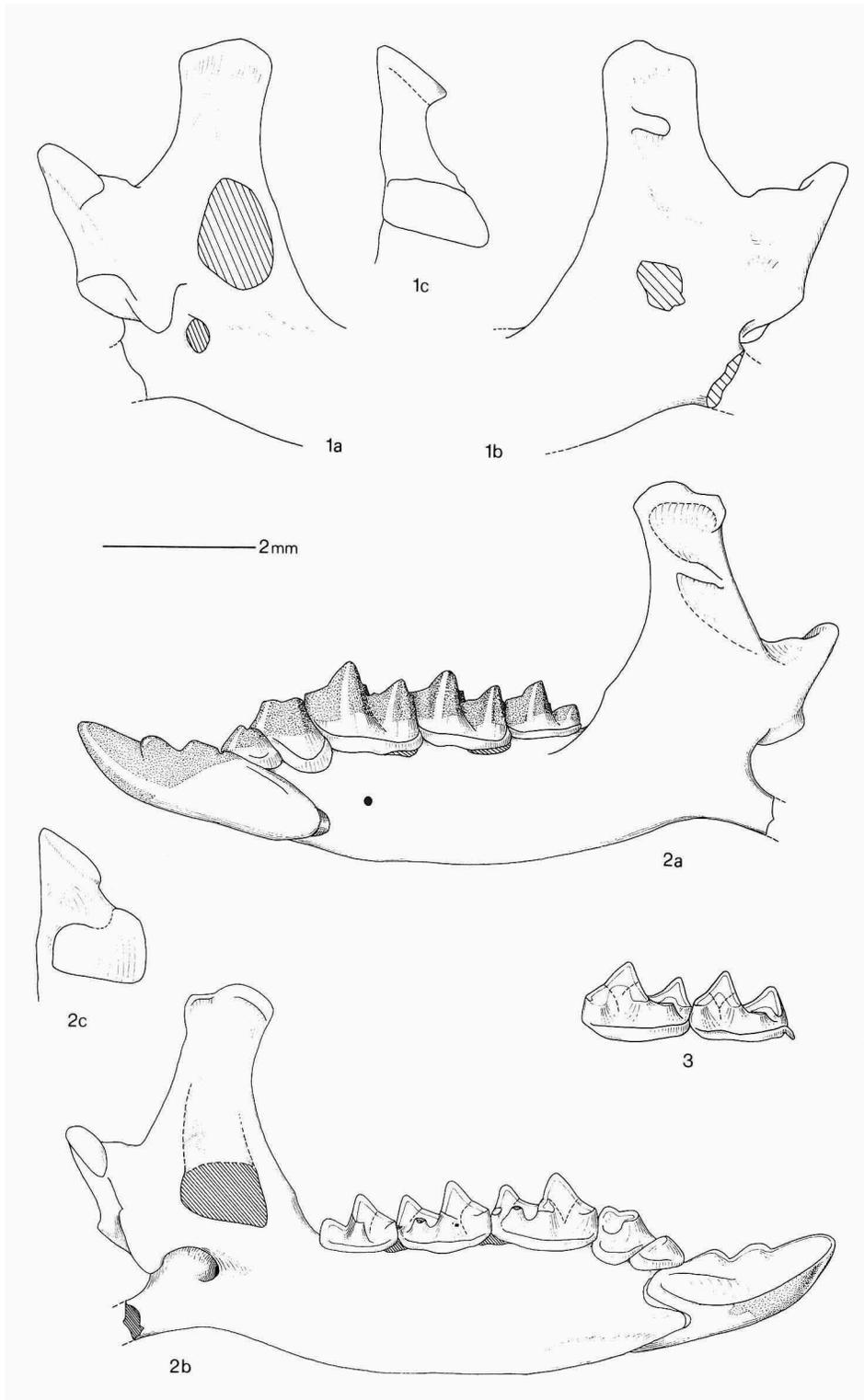
Summarizing, the only valid species of *Petenyia* that remains, is *P. hungarica*; this species shows a remarkably long stratigraphic range for a soricid.

Plate 18

Petenyia hungarica Kormos, 1934

1. Left ascending ramus, Cs2/1; a: internal view; b: external view; c: caudal view of condyle.
2. Left ramus with complete dentition, Osz3/2; a: buccal view; b: lingual view (note low entoconid crests); c: caudal view of condyle.
3. Right M_1 - M_2 , Osz3/2 (note high entoconid crests).

Plate 18



Petenyia aff. *hungarica* Kormos, 1934
Pl. 20, figs. 1-4.

Locality — Osztramos 9.

Synonymy

Petényia cf. *hungarica* Kormos, in: Jánosy, 1974, p. 18.

Petényia cf. *hungarica* Kormos, in: Jánosy & Kordos, 1977, p. 50.

Studied material — 1 I sup., 2 AA sup., 3 P⁴, 4 M¹, 1 M², 1 I inf., 1 P₄, 2 M₁, 4 M₂, 6 M₃.

Measurements — See Table 25.

Description

I sup. — Not as elongate as is normal for *P. hungarica*; it does not reach as far back on the side of the rostrum as it does in *P. hungarica* (compare Pl. 15, fig. 1b with Pl. 20, fig. 1). The dorsal edge is straight and almost perpendicular to the buccal posterior edge. A cingulum is present along most of the posterior edge.

AA sup. — Only A¹ and A² are known, they are quite large. Especially the A² is larger than it is in *P. hungarica*. Cingula are well developed.

P⁴ — The posterior emargination is slight. The parastyle is connected to the paracone by a high parastylar crest. Protocone and hypocone are weakly developed but discernible as cusps.

M¹ and M² — A hypocone is hardly present, in fact there is only a cingular ridge surrounding the hypoconal flange. The protocone has a U-shape and is hence connected to both the paracone and the metacone. The posterior emargination is slight.

I inf. — Primitive tricuspluate; in the single preserved specimen no buccal cingulum can be seen. The incisor extends backward to a point below the protoconid of M₁.

P₄ — The postero-lingual basin is rather shallow. On both sides cingula are present, but they are very weak.

M₁ and M₂ — The lower molars are not extremely quadrate in outline; in both M₁ and M₂ the trigonid is narrower than the talonid. The entoconids are situated anteriorly and are connected to the metaconids by high entoconid crests. Cingula are narrow on both sides; they are more pronounced buccally than lingually.

M₃ — The talonid is reduced to a comma-shaped single cusp.

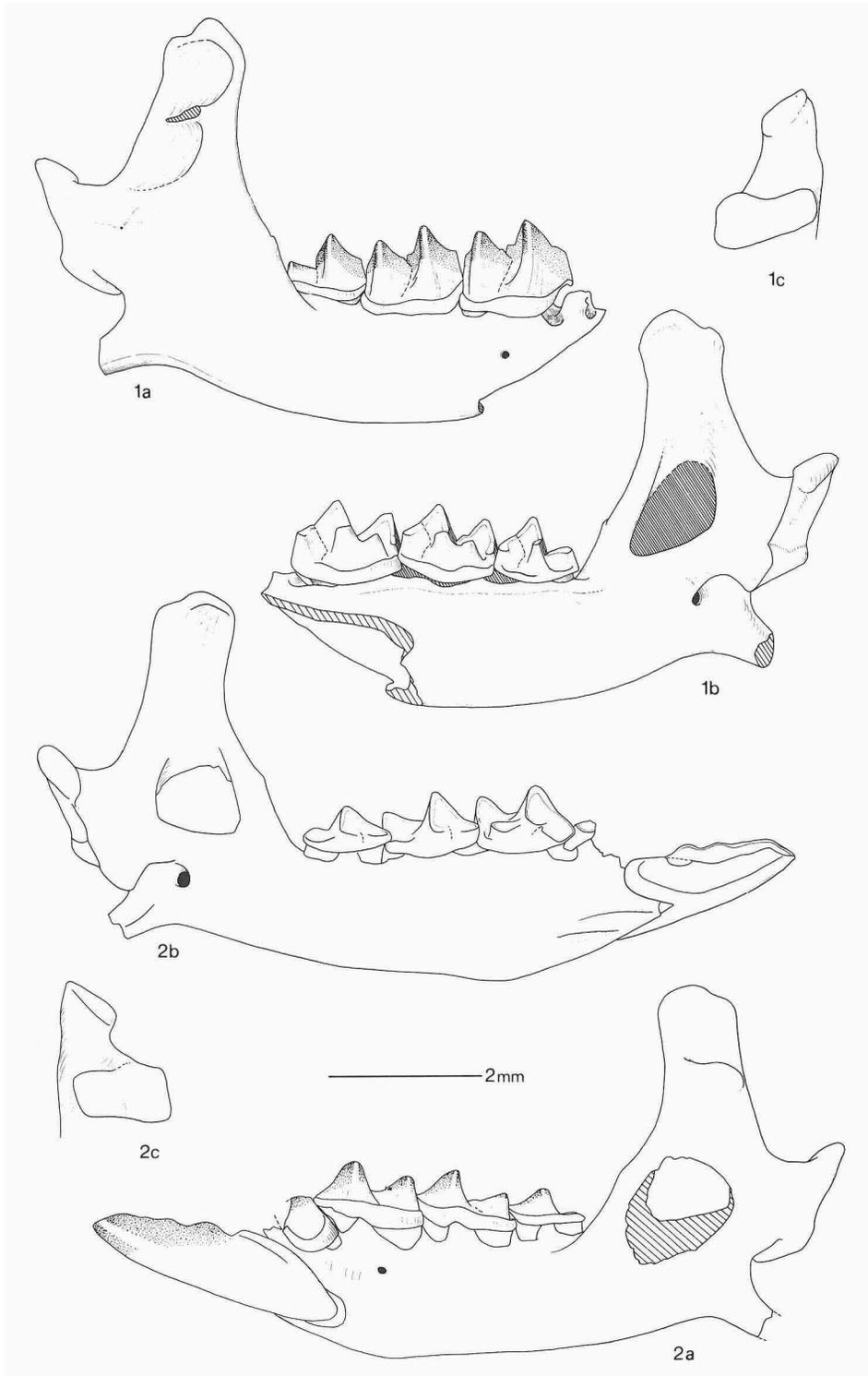
Remarks — The material from Osztramos 9 is quite different from other *P. hungarica* samples in the smaller size of the anterior dentition and in the slightly smaller overall size. Since further significant morphological differences in the dentition cannot be found, and since no ascending ramus has been preserved, this sample is here referred to as *P. aff. hungarica* and no new name has been given.

Plate 19

Petenyia hungarica Kormos, 1934

1. Right ramus with M₁-M₃, Te, RGM 179 052; a: buccal view; b: lingual view; c: caudal view of condyle.
2. Left ramus with nearly complete dentition, holotype of *Petenyia neglecta* Kretzoi, 1943, Püspökfürdő, coll. TTM no. V.61.1593, same views.

Plate 19



Genus *Blarinella* Thomas, 1911

Type species — *Sorex quadraticauda* Milne-Edwards, 1872.

Remarks — *Blarinella* is still living in part of South China; the only living species (*B. quadraticauda*) is apparently a relict.

The presence of five upper antemolars is the criterion for separating *Blarinella* from *Petenyia* (Repenning, 1967). Moreover, characters like the prominent entoconid crest and the more intense pigmentation also point towards *Blarinella*. It will not always be easy to separate *Petenyia* and *Blarinella* in single samples from Europe. On the average, *Blarinella* is somewhat larger.

Morphological differences between the two genera in Europe may be summarized as follows:

Petenyia

pigmentation moderate to strong
I sup. and I inf. with pointed apex
I sup. with nearly straight ventral border of the apex (Pl. 15, figs. 5-7)
4 upper antemolars
coronoid spicule in centre of external temporal fossa (e.g. Pl. 17, fig. 1a)
internal temporal fossa without a horizontal bar
lower molars less quadrate (less 'bat-like')
lower molars with elongate W-pattern (less sharp angles between the lophids)
entoconid crests moderately high

Blarinella

pigmentation extremely strong
I sup. and I inf. with spatulate apex
I sup. with S-curved ventral border in unworn specimens (Pl. 21, figs. 1, 2)
5 upper antemolars
coronoid spicule above centre of external temporal fossa (e.g. Pl. 22, fig. 3a)
internal temporal fossa with a horizontal bar (e.g. Pl. 22, fig. 2a)
lower molars more quadrate (more 'bat-like')
lower molars with compressed W-pattern (sharp angles between the lophids)
entoconid crests extremely high

Blarinella dubia (Bachmayer & Wilson, 1970)

Pl. 20, figs. 5-8.

Original diagnosis — 'Lower incisor relatively smooth in dorsal profile. Pigmentation present, but not as intense as now preserved. Coronoid spicule not especially prominent. Size as in *Petényia hungarica*'.

Emended diagnosis — P⁴ with normally developed protocone; M¹ and M² with protocone and talon and not having an endoloph; hypocones not present. Lower molars with a very strong cingulum on both sides; high entoconid crests. There is a horizontal bar in the internal temporal fossa.

 Plate 20

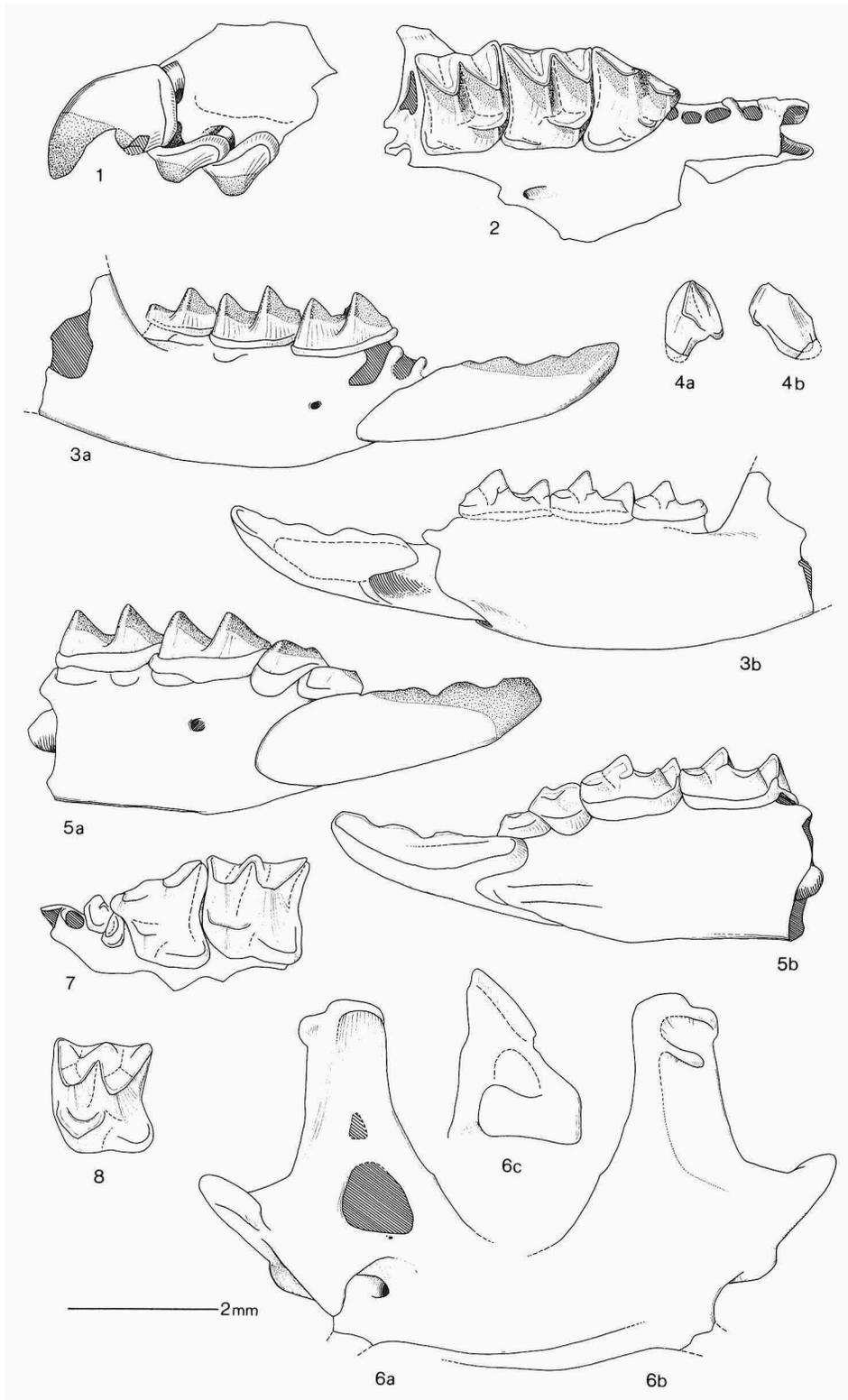
Petenyia aff. *hungarica* Kormos, 1934, Osz9

1. Left I sup.-A².
2. Right P⁴-M².
3. Right horizontal ramus with I inf. and M₁-M₃; a: buccal view; b: lingual view.
4. Left P₄; a: occlusal view; b: buccal view.

Blarinella dubia (Bachmayer & Wilson, 1970), Osz9

5. Right I inf.-M₂; a: buccal view; b: lingual view.
6. Left ascending ramus; a: internal view; b: external view; c: caudal view of condyle.
7. Left A⁴-M¹.
8. Left M².

Plate 20



Differential diagnosis — *B. dubia* differs from the extant Asiatic *B. quadraticauda* by having a less quadrate P⁴ and no cingulum lingually of the protocone of P⁴, by lacking hypocones and by having a horizontal bar in the eternal temporal fossa. *B. dubia* differs from *B. europea* sp. nov. by having a well-developed protocone in P⁴ and by not having a continuous endoloph in M¹-M².

Type locality — Kohfidisch, Austria.

Studied locality — Osztramos 9.

Other locality — Maritsa (Rhodes, Greece, as *Blarinella* sp., in de Bruijn et al., 1970).

Stratigraphic occurrence — Turolian - early Ruscinian (MN 11 - MN 14).

Original reference — *Petényia dubia*, in: Bachmayer & Wilson, 1970.

Synonymy (only concerning Osz9)

? *Petényia* cf. *dehneli* (Kowalski), in: Jánossy, 1974, p. 18.

Petényia (?) cf. *dehneli* (Kowalski), in: Jánossy & Kordos, 1977, p. 50.

Available material — 2 AA sup., 2 P⁴, 2 M¹, 1 M², 2 I inf., 1 A₁, 2 P₄, 2 M₁, 3 M₂, 2 M₃, 1 condyle.

Measurements — See Table 26.

Description — The pigmentation of the dentition is intense: in M₁ and M₂ even the bottoms of the talonid basins are pigmented.

AA sup. — It is here assumed that five were originally present, although definite proof of this assumption is not available. Only A⁴ and A⁵ have been found. A⁴ is a small element, consisting of a single cusp, surrounded by a strong cingulum. A⁵ is smaller and hidden when seen from the buccal side behind A⁴ and the parastyle of P⁴.

P⁴ — The posterior emargination in P⁴ (and also in M¹ and M²) is very slight. The protocone forms an antero-lingual corner in the outline of the tooth; the cusp is well developed and separated from the hypocone by a valley. The hypocone is hardly developed on the ridge surrounding the hypoconal flange.

M¹ and M² — There is a metaloph; between the protocone and the talon there is a valley. The hypocones are not developed; the hypoconal flanges are deeply excavated. Both M¹ and M² are roughly quadrate in occlusal view.

I inf. — Two distinct cuspules are present on the dorsal edge. A cingulum is not discernible on the buccal side, but on the symphyseal side it is broad and well-developed. Seen from the buccal side the I inf. goes back to underneath the posterior half of P₄, more or less underneath the paraconid of M₁.

A₁ — This element is relatively small and it lies wedged in between I and P₄. A cingulum is present on both sides, but buccally only faintly so.

P₄ — The buccal shearing blade is relatively long and the tooth appears two-cusped in side-view. The postero-lingual basin is shallow. A cingulum is present on both sides; it is well developed buccally.

M₁ and M₂ — The lower molars are *Petényia*-like. The entoconid is placed relatively close to the metaconid and the entoconid crest is high. The oblique crest runs strongly linguad, to near the metaconid. The antero-buccal corner of the molars is very sharp, due to a conspicuous bend in the cingulum. The buccal cingulum is broad, and is at its broadest underneath the re-entrant valley, which begins directly above the cingulum. The lingual cingulum is less broad.

M₃ — The M₃ has a reduced talonid, although a talonid basin is still distinguishable.

Mandible — The coronoid process is broad; the anterior and the posterior edges of the upper part are almost parallel; the upper edge is undulated. The internal temporal

fossa is divided into two parts by a horizontal bar. No pterygoid boss or spicule is present; the pterygoid fossa is clearly depressed. On the buccal side a small but sharply protruding coronoid spicule is present; it is placed at about three-quarters of the height of the external temporal fossa. The external temporal fossa extends ventrally to about the level of the centre of the condyle. The upper facet of the condyle is narrow and cylinder-shaped and it makes an angle of about 45° with the lower facet. The lower facet has a concave upper edge. The interarticular area is low and broad and centrally depressed. A slight lingual offset of the lower facet from the lower sigmoid notch can be observed, but this feature is not as strong as in the Soriculini. The mental foramen is placed underneath the buccal re-entrant valley of M₁.

Remarks — Although the *B. dubia* material cannot be shown to have five antemolars in the maxillary, it has been attributed with certainty to *Blarinella* on the basis of several other characters, the most important of which is the position of the coronoid spicule. Therefore, the conclusion of Sulimski et al. (1979) that *P. dubia* is a synonym of *Petenyia hungarica* is not followed.

The material from Kohfidisch (*Petenyia dubia* Bachmayer & Wilson, 1970) has been attributed to *Blarinella* because of the clearly developed spatulate I sup. with an S-curved ventral margin, the strongly quadrate lower molars, the position of the coronoid spicule, the presence of a horizontal bar in the internal temporal fossa, and because of the nearly certain presence of five upper antemolars.

The material from Osztramos 9 has been given the same specific name (*B. dubia*) because of the similarities between this material and the Kohfidisch material. The most notable similarity is the absence of a continuous endoloph in the upper molars.

The *Blarinella* material from Maritsa, Greece (de Bruijn et al., 1970) does not possess a continuous endoloph either and is here referred to *B. dubia* too.

Blarinella europaea sp. nov.
Pls 21, 22.

Holotype — A maxillary fragment with M¹ and M², coll. MÁFI no. V.12705, Vt.99 (Pl. 21, fig. 6).

Etymology — This species is named after Europe.

Type locality — Csarnóta 2.

Stratigraphic occurrence — Ruscinian.

Studied localities — Osztramos 1 and 7, Csarnóta 2.

Probable other locality — Apolakkia (Rhodes, Greece), as *Blarinella* sp. in: van de Weerd et al., 1982.

Synonymy

Petényia hungarica Kormos (partim!), in Kretzoi, 1962, e.g. p. 389, pl. II, fig. 2 (Cs2)

Petenyia cf. *hungarica* Kormos (non *Petenyia* sp.), in: Jánossy, 1972 (Osz1)

Petenyia cf. *hungarica* Kormos (non *Petenyia* sp.), in: Jánossy & Kordos, 1977 (Osz1).

Diagnosis — Large *Blarinella* with heavily pigmented teeth; both upper and lower incisors with a strongly spatulate apex; P⁴ with hardly developed protocone; upper molars with strongly developed paracone and metacone and a continuous endoloph; lower molars quadrate, with sharp buccal edges of protoconids and hypoconids due to sharp angles of the lophids and with extremely high entoconid crests.

Differential diagnosis — *B. europaea* sp. nov. differs from the extant Asiatic *B. quadraticauda* (Milne-Edwards) by having a triangular P⁴ without well-developed protocone and by having a continuous endoloph in M¹ and M². *B. europaea* sp. nov. differs from *B. dubia* (Bachmayer & Wilson) by having a P⁴ without a well-developed protocone and by having a continuous endoloph in M¹ and M².

Available material

Osztramos 1C: a maxillary fragment with M¹-M³, coll.

Osztramos 1B: 1 condyle.

TTM no. V.73.17 (originally labelled V.73.16), 2 I sup.

Osztramos 1E: 1 M¹, 1 ascending ramus, coll. TTM no. V.75.11.

Csarnóta 2: 14 I sup., 3 AA sup., 4 P⁴, 5 M¹, 8 M², 9 I inf., 1 P₄, 10 M₁, 11 M₂, 10 M₃, 17 condyles.

Osztramos 7: 2 I sup., 3 AA sup., 1 I inf., 2 M₁, 2 M₂, 1 M₃.

Measurements — See Tables 27-29.

Description — All dental elements are intensely stained dark red to nearly black.

I sup. — The apex is broad and spatulate, but not fissident; it protrudes far forwards. The ventral edge of the apex is S-shaped in unworn specimens due to the spatulate broadening of the apex. The talon is relatively small. The buccal posterior margin makes a sharp angle with the dorsal margin. A buccal cingulum is present only along the ventral half of the posterior edge.

AA sup. — Five upper antemolars are present; A¹ and A² are large, A³ is much smaller, and A⁴ and A⁵ are still smaller. All antemolars seen are unicuspid.

P⁴ — There is hardly any posterior emargination, neither are there distinct protocones and hypocones. Instead, a ridge (endoloph) runs from the position of the protocone and continues into the cingulum which surrounds the hypoconal flange. The parastyle is placed well towards the anterior; it is connected to the paracone by a high and long parastylar crest.

M¹ and M² — There is a continuous endoloph which connects the protocone to the postero-lingual cingulum. There is no hypocone on this endoloph. The bases of the paracone and the metacone reach far towards the lingual side, coming close to the endoloph. In the oldest sample (Osz1) a vestige of the metaloph can be distinguished (see Pl. 21, fig. 5: the M²). The posterior emargination is slight. M¹ is sub-trapezoidal to quadrate in occlusal view, M² is quadrate.

M³ — The only known M³ is from Osztramos 1 (Pl. 21, fig. 5). It is quite large; the only well-developed cusp is the paracone. The lingual part of M³ is a basin, surrounded by a semi-circular ridge without cusps.

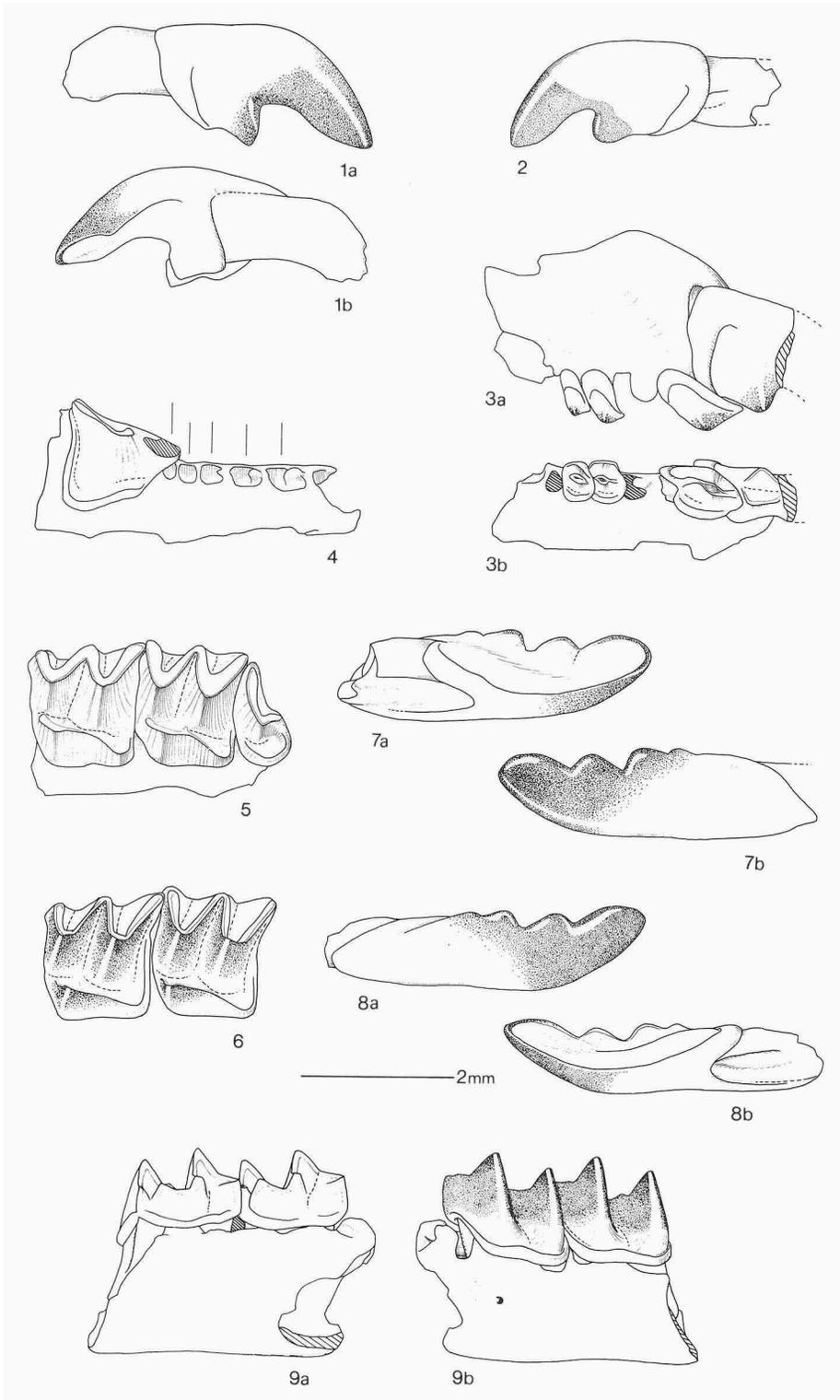
I inf. — Bicusperate or slightly tricusperate; the apex is extremely spatulate. A buccal cingulum is present, but it is hardly individualized and only detectable as a weak little ridge. I inf. extends buccally to underneath P₄, viz. below the paraconid of M₁.

Plate 21

Blarinella europaea sp. nov.

1. Right I sup., Cs2/19; a: buccal view; b: medial view.
2. Left I sup., Osz1C.
3. Right I sup., A¹, A³ and A⁴, note alveoles for A² and A⁵, Osz7; a: buccal view; b: occlusal view.
4. Right P⁴ with five antemolar alveoles, Cs2/12.
5. Left M¹-M³, Osz1C, coll. TTM no. V.73.17 (originally labeled as V.73.16).
6. Left M¹-M², holotype, coll. MÁFI no. V.12705, Vt 99, Cs2/3.
7. Left I inf., Cs2/25; a: buccal view; b: symphyseal view.
8. Right I inf., Osz7, same views as fig. 7.
9. Left M₁-M₂, Osz7; a: lingual view; b: buccal view.

Plate 21



P_4 — P_4 is slightly elongate, 2-cusped and somewhat compressed laterally when seen in occlusal view. The postero-lingual basin is very narrow and shallow. Cingula are present on both sides, but lingually only weakly.

M_1 and M_2 — The lower molars are bat-like, i.e. they have a subquadrate and sharply crested appearance. The protoconids and hypoconids are all of about the same height and sharply pointed. The angles formed by their arms (the lophids) are sharp. The buccal re-entrant valley is deep and wide. The compressed W-pattern is enhanced by the oblique crests that run to near the metaconids. The entoconids are placed far forwards; the entoconid crests are extremely high and form a solid wall when seen from the lingual side. Cingula are strong on the buccal sides of the molars, lingually they are weak.

M_3 — The talonid is reduced to a comma-shaped hypoconid; lingually there is hardly a cingulum. The antero-buccal corner is sharp and nearly square in occlusal view.

Mandible — The horizontal ramus is short and high. The coronoid process has a slightly divergent tip, which has a slight undulation. Both anterior and posterior edges are concave; a small spicule may be present on the anterior edge. The coronoid spicule is well developed, and situated at about three-quarters of the height of the external temporal fossa. This fossa extends downwards to the level of the upper sigmoid notch. The internal temporal fossa has a more or less pronounced horizontal bar. The condyle resembles that of *Petenya*, but generally it is a bit larger. The upper facet is cylindrical and obliquely placed. The lower facet is high and has a concave upper margin. The interarticular area is broad and centrally depressed. The mandibular foramen is rather large and located centrally underneath the internal temporal fossa. The mental foramen is placed below the buccal re-entrant valley of M_1 , sometimes in a slight depression of the mandibular ramus.

Remarks — *B. europaea* differs from *B. dubia* not only by the absence of a protocone in the P^4 and the presence of an endoloph, but also by a generally more bat-like appearance (strongly quadrate teeth with sharply edged cusps).

The living *B. quadraticauda* has a metaloph and no endoloph (see Repenning, 1967). Superficially *B. quadraticauda* shows a better resemblance to *B. dubia*.

Apparently, the development of the endoloph and the related reduction of the metaloph is a trend within the European branch of the genus. The oldest material of *B. europaea* (from Osz1) still has a small metaloph (Pl. 21, fig. 5), but in later samples (Cs2) even this vestige has disappeared (Pl. 21, fig. 6).

It is possible that during the Pliocene *Blarinella* had a Eurasiatic distribution, of which the Recent population in China is a relict. It is therefore not necessarily true that *Blarinella* is an Asiatic element in Europe, as stated by van de Weerd et al., 1982. *Blarinella* sp. from the Upper Ruscinian of Apolakkia (van de Weerd et al., 1982) may belong to *B. europaea*, but this cannot be confirmed due to the scarcity of the material.

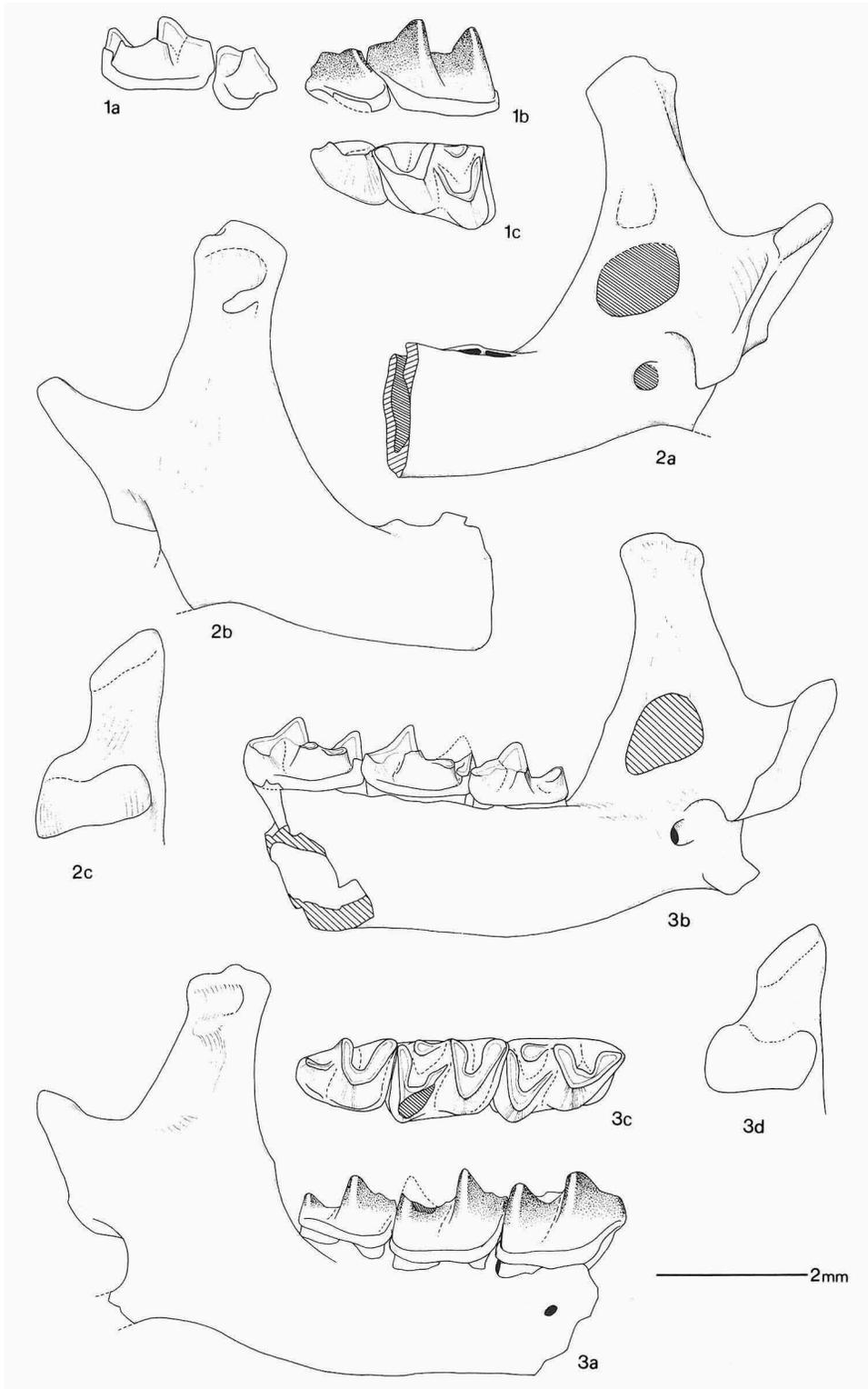
The only other fossil *Blarinella* species mentioned in the literature is *B. kormosi* (Schlosser, 1924) from Ertemte, Mongolia, described by Schlosser as *Crocidura kormosi*

Plate 22

Blarinella europaea sp. nov.

1. Left P_4 - M_1 , Cs2/25; a: lingual view; b: buccal view; c: occlusal view.
2. Right ascending ramus, Osz1E, coll. TTM no. V.75.11; a: internal view; b: external view; c: caudal view of condyle.
3. Right ramus with M_1 - M_3 , Cs2/24; a: buccal view; b: lingual view; c: occlusal view; d: caudal view of condyle.

Plate 22



(see Miller, 1927). Repenning (1967) suggested that this species does not belong to the Soricini, but to the Blarinini, as no entoconid crests seem to be present. Repenning nevertheless retained *kormosi* as a *Blarinella* species. This assignment to the Soricini must be considered doubtful.

Genus *Zelceina* Sulimski, 1962

Type species — *Neomys soriculoides* Sulimski, 1959.

Remarks — At first sight the tribal attribution of *Zelceina* seems rather problematical. The Blarinini can be excluded due to the presence of an entoconid crest on the lower molars. Sulimski (1959) described the species as a *Neomys* (our tribe Soriculini). Repenning (1967) listed *Zelceina* as a Soricini Incertae Sedis.

Indeed, the genus has several characters that are suggestive of either the Soriculini or the Soricini. The rather narrow interarticular area, the slight lingual offset of the lower condylar facet, the shape of the lower incisor and the presence of four upper antemolars (Sulimski, 1959, 1962) may indicate a position within the Soriculini. At first glance, the lower incisor may be mistaken for an *Episoriculus* incisor, due to the two cuspules. The *Zelceina* tooth differs from *Episoriculus* by having (1) a stronger pigmentation, (2) the cuspules more anteriorly placed, (3) no distinct corner between the ascending and the ventral branch of the symphyseal cingulum.

Other characters however, the most important of which are the reduced talonid of M_3 and the non-fissident I sup. (Sulimski, 1962), firmly indicate attribution to the Soricini. A slight lingual offset of the lower condyle can be observed in several genera of the Soricini, e.g. in *Petenya*, also in *Petenya* there is a bicusperate I inf., and in some specimens the interarticular area can become quite narrow (see Pl. 18, fig. 1c).

In many respects *Zelceina* resembles *Petenya*: the reduced talonid in M_3 , the slight posterior emargination of the upper molars, the presence of four upper antemolars, the bicusperate lower incisor. Also, the typical tetrahedral hypocone of *Zelceina* can be found in some *Petenya* specimens (see Pl. 15, fig. 9, *P. hungarica* from Osz1). Differences can be found mainly in the morphology of the ramus and the lower molars.

Zelceina is restricted to the Csarnótian of Central Europe; its origin is not known.

Zelceina soriculoides (Sulimski, 1959)
Pl. 23.

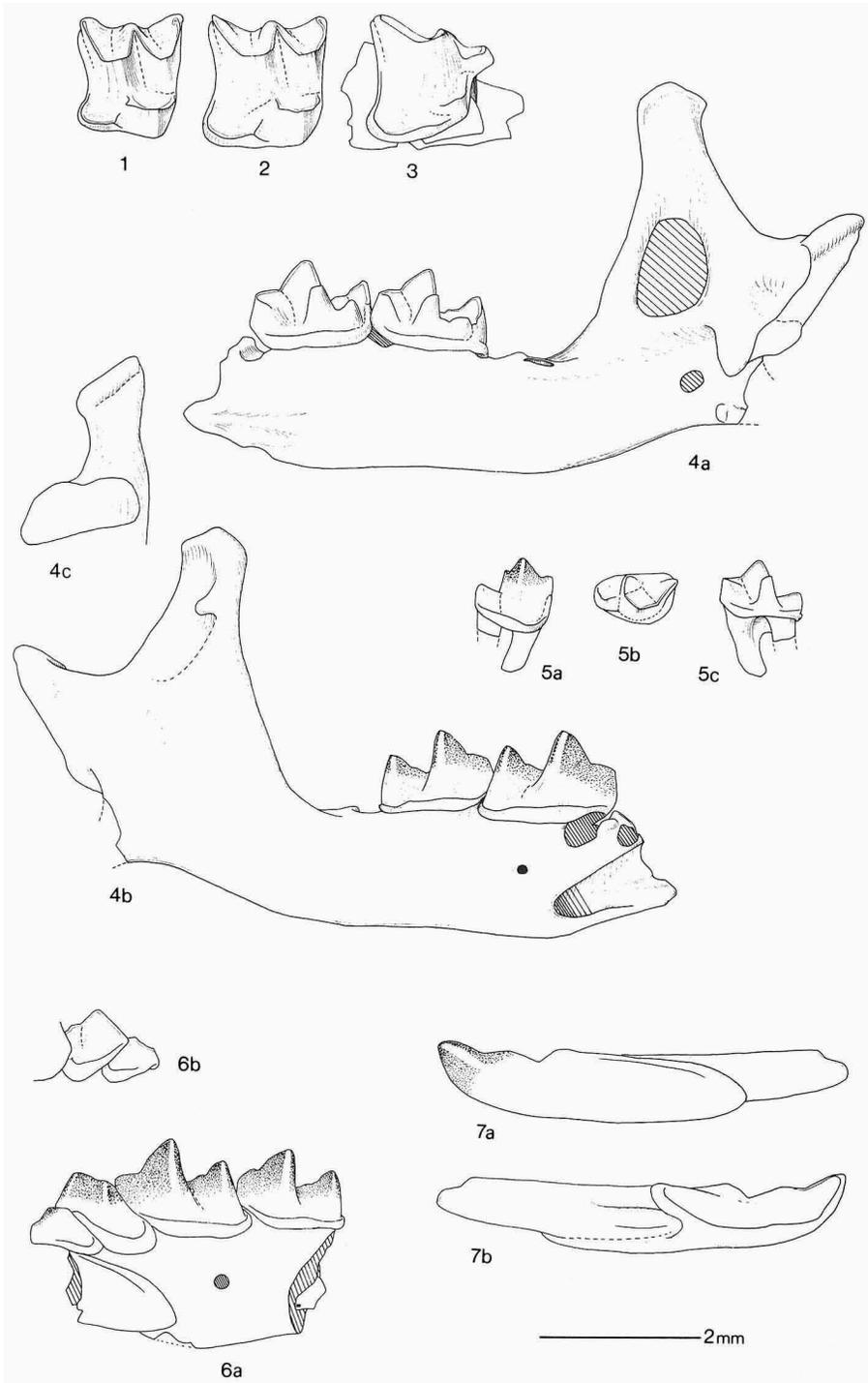
Type locality — Węże 1 (Poland).

Plate 23

Zelceina soriculoides, Sulimski, 1959, all from Cs2

1. Right M^2 , Cs2/18.
2. Right M^1 , Cs2/18.
3. Right P^4 , Cs2/18.
4. Right ramus with M_1 - M_2 , Cs2/16; a: lingual view; b: buccal view; c: caudal view of condyle.
5. Right M_3 , Cs2/1; a: buccal view; b: occlusal view; c: lingual view.
6. Left I inf. (broken)- M_2 , Cs2/2; a: buccal view; b: lingual view of antemolars.
7. Left I inf., Cs2/23; a: buccal view; b: symphyseal view.

Plate 23



Studied locality — Csarnóta 2.

Other locality — Ivanovce A (Czechoslovakia, Fejfar, 1966a).

Stratigraphic occurrence — Ruscinian (Csarnótanian).

Synonymy

Neomys soriculoides n. sp., in: Sulimski, 1959, p. 149.

Zelceina soriculoides (Sulimski, 1959), in: Sulimski, 1962, p. 478.

Zelceina soriculoides (Sulimski), in: Fejfar, 1966a, p. 223.

Zelceina soriculoides (Sulimski), in: Repenning, 1967, p. 36.

Available material

Csarnóta 2: 7 P⁴, 19 M¹, 13 M², 32 I inf., 1 A₁, 1 P₄, 29 M₁, 19 M₂, 4 M₃, 48 condyles.

Measurements — See Table 30.

Description — The teeth are stained.

P⁴ — The parastyle protrudes anteriorly; the parastylar crest is high. The protocone is placed relatively far buccally; it is L-shaped and separated from the hypocone by a deep trough. The hypocone is poorly developed on the ridge surrounding the hypoconal flange. This flange is deeply concave. The posterior emargination is rather slight, hence the tooth has a trapezoidal shape in occlusal view.

M¹ and M² — The large upper molars are characterized by a tetrahedric hypocone; from this cusp three ridges originate: one backwards, surrounding the hypoconal flange; one in antero-lingual direction to the edge of the tooth, giving rise to a small cingulum underneath the valley between protocone and hypocone; and one in antero-buccal direction, pointing towards the paracone and ending against the metaloph. A low metaloph is present. Both M¹ and M² are more or less quadrate in outline, without any corner protruding extremely. The zygomatic process is situated at the level of the metastyle of M².

I inf. — Bicuspulate, both cuspules are placed relatively far anteriorly; the posterior part of the tooth is elongate. The first cuspule is less conspicuous than the second one, the posterior valley is the deepest. A cingulum is present along the dorsal edge of the buccal posterior part, but it does not surround the posterior corner. At the symphyseal side, the ascending branch of the cingulum emerges smoothly from the ventral part. The I inf. reaches to underneath the protoconid of M₁, slightly beyond P₄ (Pl. 23, fig. 6a).

A¹ — Only one specimen is preserved. A₁ is nearly entirely hidden underneath P₄, to such a degree that the anterior edges of both elements are almost in line. Cingula are present on both sides.

P₄ — Rather short, with a well-developed postero-lingual basin and broad and pronounced cingula. When seen from the buccal side, the element appears 2-tipped.

M₁ and M₂ — The lower molars are rather uncharacteristic elements. The entoconid and metaconid are not far apart; the entoconid crest is low to moderately high. There are cingula on both sides, lingually less well developed than buccally. Small mesoconids can be seen on the oblique crests.

M₃ — The M₃ is characterized by a reduced talonid: the hypoconid is comma-shaped and quite low. The lingual cingulum is hardly developed.

Mandible — The coronoid process is relatively sharply pointed and provided with concave posterior and anterior edges; the upper edge (tip) is serrate or slightly undulate. The coronoid spicule is short and small and placed at two-thirds of the height of the

process. The external temporal fossa does not extend far downwards, and reaches only to the level of the upper sigmoid notch. The internal temporal fossa is rather small and does not extend upwards. A pterygoid boss is present as a rough patch. The condyle is relatively large; most of the lower facet is hidden behind the lower sigmoid notch in lateral view. The upper facet is cylindrical; the lower facet has a slight dorsal undulation.

The interarticular area is narrow, but not as narrow as in Soriculini and not as wide as is usual in Soricini. There is a very slight lingual offset of the lower facet from the lower sigmoid notch. The mandibular foramen is small; the mental foramen is placed underneath the re-entrant valley of M_1 .

Remark — This species was not mentioned before from Csarnóta 2.

Soricini gen. et sp. indet.

Pl. 24, figs. 1-6.

Locality — Osztramos 1.

Available material

Osztramos 1: 1 M_1 , 1 M_2 .

Osztramos 1B: 2 I sup., 1 M^1 , 1 M^2 , 1 I inf., 4 M_1 , 4 M_2 , 2 M_3 , 1 condyle.

Osztramos 1C: 5 I sup., 8 I inf., 1 A_1 , 2 P_4 , 5 M_1 .

Measurements — See Table 31.

Description — The dental elements are stained.

I sup. — Not fissident, rather small; the posterior buccal edge is slightly undulate and provided with a broad cingulum.

M^1 and M^2 (one specimen of each) — M^1 has a strongly protruding metastyle; in M^2 this is not so, M^2 is therefore trapezoidal in occlusal outline. On both teeth there are small parastyles. The hypocones and hypoconal flanges are small and reduced, especially in M^2 there is no hypocone. Between the protocones and the hypocones there are wide valleys.

I inf. — Tricuspluate, the last cuspule is small and insignificant. The buccal cingulum is narrow and hardly pronounced; the symphyseal cingulum shows a slight undulation in the posterior part. I inf. reaches to below the trigonid of M_1 , slightly beyond P_4 .

A_1 — A_1 lies for half its length below P_4 ; a shallow postero-lingual basin is developed. Both sides possess a well-developed cingulum.

P_4 — The postero-lingual basin is shallow and only faintly bordered. The worn surface of the tip of the element has the shape of an elongate figure of eight (8-shaped). The cingula are well developed, particularly on the lingual side.

M_1 and M_2 — The lower M_1 and M_2 are rather uncharacteristic. The entoconid crest is quite high; the cingula are well developed. The buccal cingulum is often undulate. Metaconid and protoconid are close together.

M_3 — The talonid is reduced to a comma-shaped unicuspid crest. The lingual cingulum is weak.

Mandible (only one specimen) — The tip of the coronoid process is slender, bent slightly lingually and its anterior margin is concave. The coronoid spicule is small and high. The external temporal fossa is hardly excavated and short. The internal temporal fossa is large and high. There is no pterygoid spicule or boss. The condyle is rather large;

its upper facet is placed far towards the posterior. This facet is small and cylindrical, the lower facet has a downward directed lingual end and a slight lingual offset from the lower sigmoid notch. The interarticular area is wide and slightly depressed. The mandibular foramen is large and open, the mental foramen is situated below the buccal re-entrant valley of the M_1 .

Remarks — The material described above is referable to the tribe Soricini because of the combination of a tricusplute I inf., entoconid crests, a reduced talonid in M_3 , pigmentation, and a broad interarticular area.

A relation to *Sorex* seems unlikely due to the reduced talonid in M_3 . This feature is known from *Petenya*, *Blarinella*, *Deinsdorfia*, and *Zelceina*. The moderate posterior emargination in the upper molars seems to exclude a relationship to *Petenya* or *Blarinella*. If the lumping of the mandibular and maxillary material is correct, then the material is unlikely to be an early *Zelceina*, in which genus the hypocones are well developed.

The material seems to be closest to *Deinsdorfia*, and especially to *D. janossyi* sp. nov. from Osztramos 9. However, as the characteristic P^4 is not available in our scanty material, we refrain from a closer generic assignment.

Tribe Blarinini Kretzoi, 1965

Genus *Mafia* gen. nov.

Type species — *M. csarnotensis* sp. nov.

Diagnosis — Medium-sized, rather unspecialized representative of the Blarinini with a relatively posteriorly placed condyle; robust lower molars with strong cingula; a normal soricine P_4 ; upper molars without hypocones; upper incisor not fissident; last upper antemolar small and reduced, shifted to the lingual side. All dental elements are strongly pigmented.

Differential diagnosis — *Mafia* gen. nov. differs from *Blarinoides* Sulimski, 1959 by having a posteriorly placed condyle, a small coronoid spicule and by virtually lacking hypocones in the upper molars. In addition, *Mafia* has a normal soricine P_4 with a postero-lingual basin. *Mafia* differs from *Sulimskia* gen. nov. by having a less squeezed-in A_1 , better developed cingula in the lower molars and by having a much stronger pigmentation. Also, *Mafia* has no extensively developed buccal cingulum in I inf.; the internal temporal fossa is considerably smaller in *Mafia* than in *Sulimskia*.

Plate 24

Soricini gen. et sp. indet., Osz1

1. Left I sup., Osz1C.
2. Left M^1 - M^2 , Osz1B.
3. Left ramus, Osz1B; a: external view; b: internal view; c: caudal view of condyle.
4. Right I inf.- M_1 , Osz1C; a: buccal view; b: lingual view.
5. Right M_2 , Osz1C, same views as fig. 4.
6. Left M_2 - M_3 , Osz1C, same views as fig. 4.

Soricinae gen. et sp. indet. 2

7. Right M^1 , Cs2/20.

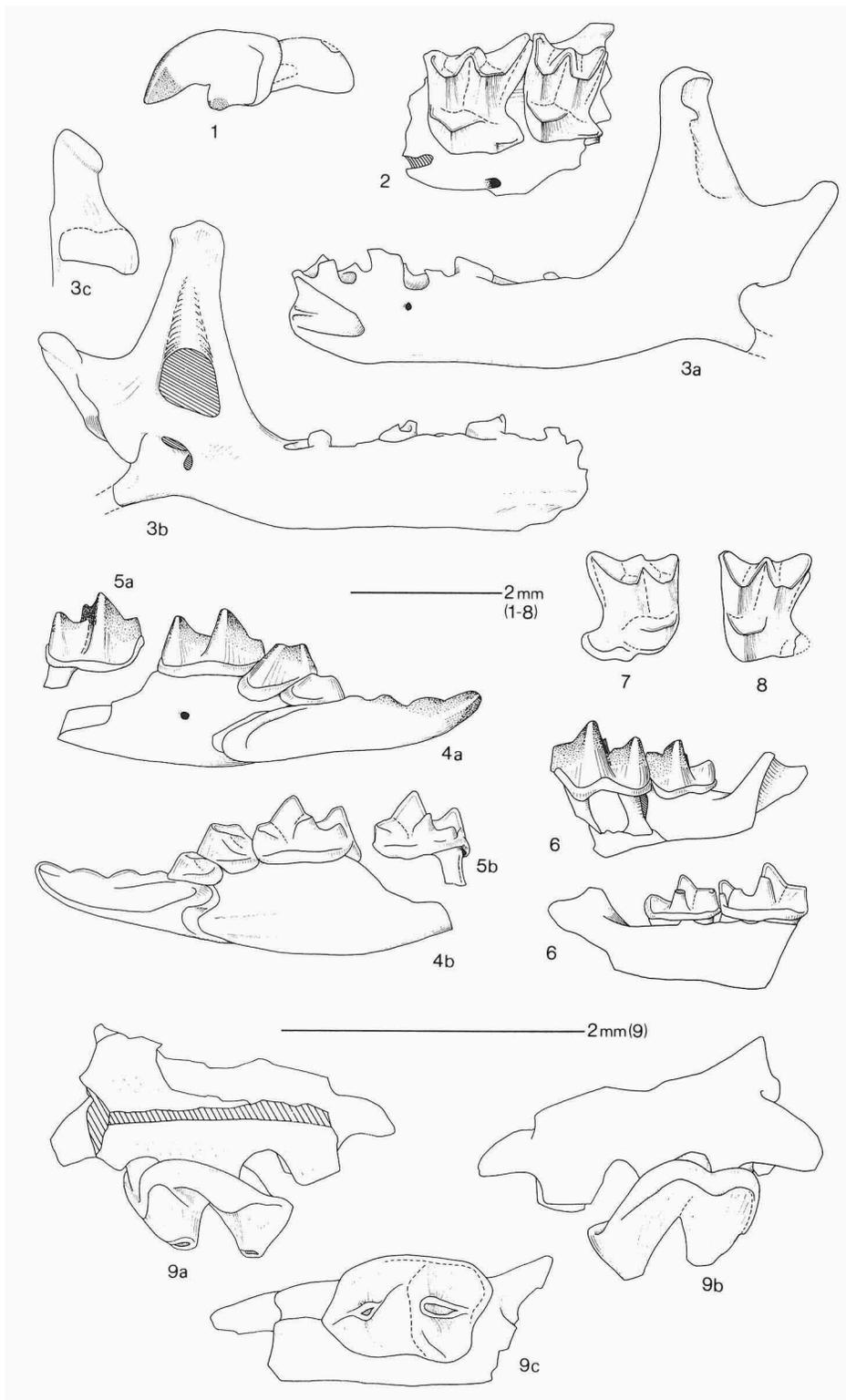
Soricinae gen. et sp. indet. 3

8. Left M^2 , Osz7.

Soricinae gen. et sp. indet.

9. Nearly divided left upper antemolar, Cs2/22; a: lingual view; b: buccal view; c: occlusal view.

Plate 24



Etymology — The genus is named after the Magyar Állami Földtani Intézet (MÁFI), the Hungarian State Geological Survey, where the Csarnóta 2 material is stored.

Remarks — A new genus has been erected for the following reasons. The only Blarinini genus so far described from Europe is *Blarinoides* Sulimski, 1959. This genus is extremely specialized in several respects; these include the P₄ without a postero-lingual basin; the presence of small extra conules in the upper molars; extremely strong cingula around the lower molars; anteriorly placed lower condylar facet; a spatulate coronoid process. The material found in the Csarnóta 2 sample, to be described hereafter, is not nearly as specialized.

It has been suggested by Kowalski (1960) that *Sorex dehneli* from Podlesice (Kowalski, 1956) might belong to *Blarinoides*. However, this species too lacks the specialization of *Blarinoides*. Therefore, as will be explained below, *Mafia* gen. nov. is considered to contain two species: *M. csarnotensis* sp. nov. and *M. dehneli* (Kowalski, 1956).

For practical reasons (viz. the author has not actually studied material of *M. dehneli*), *M. csarnotensis* is chosen as the type species.

Mafia csarnotensis sp. nov.

Pl. 25.

Holotype — Fragmentary right mandible with M₂, coll. MÁFI, no. V.12706, Vt.100 (Pl.25, fig. 1).

Etymology — The species is named after the village of Csarnóta.

Type locality — Csarnóta 2.

Stratigraphic occurrence — Late Ruscinian.

Diagnosis — A *Mafia* species with a well-developed coronoid spicule; a blunt, but non-spatulate coronoid process; weak lingual cingula in the lower molars.

Differential diagnosis — *M. csarnotensis* sp. nov. differs from *M. dehneli* (Kowalski, 1956) by having weak lingual cingula in the lower molars; by having an internal temporal fossa that does not continue upwards as a groove; by having a coronoid spicule (judging by Kowalski's pl. I, fig. 6a, 1956, *M. dehneli* lacks a coronoid spicule); by having the condylar facets almost parallel; by not having a spatulate coronoid process.

Available material

Csarnóta 2: 9 I sup., 4 AA sup., 4 P⁴, 5 M¹, 1 M², 4 I inf., 2 A₁, 2 P₄, 5 M₁, 9 M₂, 6 condyles.

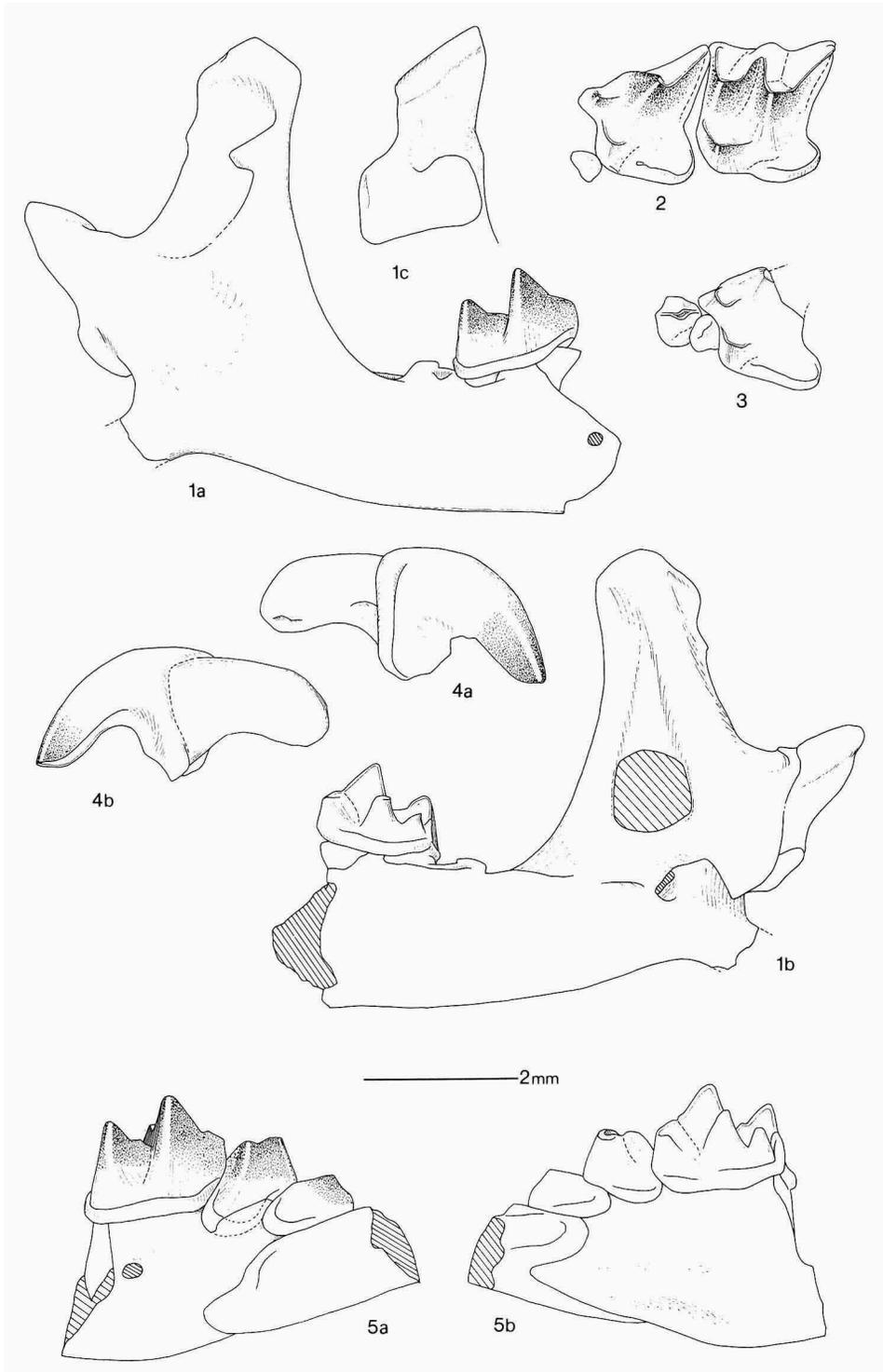
Measurements — See Table 32.

Plate 25

Mafia csarnotensis gen. et sp. nov., Cs2

1. Right fragmentary ramus with M₂, holotype, Cs2/2, coll. MÁFI no. V.12706, Vt.100; a: buccal view; b: lingual view; c: caudal view of condyle.
2. Left A⁵-M¹, Cs2/3.
3. Left A⁴-P⁴, Cs2/3.
4. Right I sup., Cs2/2; a: buccal view; b: medial view.
5. Right I inf. (broken)-M₁, Cs2/1; a: buccal view; b: lingual view.

Plate 25



Description — The teeth are stained.

I sup. — Not fissident, rather generalized. The buccal cingulum runs along the posterior edge almost to the upper edge; the posterior edge is straight.

AA sup. — The number of upper antemolars is unknown. The last one (A^{5?}) is small and lies compressed between A⁴ (?) and P⁴; it is shifted lingually, sometimes even extremely so, see Pl. 25, fig. 2. A⁴ (?) and P⁴ are touching.

P⁴ — The parastyle is well developed, the parastylar crest is high. The L-shaped protocone at the antero-lingual corner of the tooth is separated from the hypocone by a valley. There is hardly any hypocone on the ridge surrounding the flange. The paracone is situated in the middle of the buccal edge as a result of the strong development of the parastyle.

M¹ and M² — There is no metaloph. The hypocone is not present as a distinct cusp.

I inf. — Probably tricuspluate, but it might have been bicuspluate. I inf. reaches as far back as P₄ does, i.e. to underneath the trigonid of M₁. A cingulum is present along part of the posterior upper edge, which in one specimen (Pl. 25, fig. 5) is undulate. The symphyseal cingulum has no corner.

A₁ — Elongate, 'lying' on top of I inf.; for less than half of its length it lies underneath P₄. A cingulum is present on both sides.

P₄ — Relatively high and short, the postero-lingual basin is well developed as a gully. P₄ is 2-cusped in side-view; it has cingula on both sides, the buccal one being well developed.

M₁ and M₂ — The entoconid is close to the metaconid; the entoconid crest is virtually absent, hence the entoconid is conical. The valley between the entoconid and the hypolophid is relatively broad. The trigonid basin is narrow and V-shaped in lingual view. The elements make a rather sturdy, compact impression. Cingula are well developed buccally, but lingually they are weaker.

Mandible — Rather stout, the horizontal ramus is high and short. The coronoid process is high and broad, with a concave anterior edge. The coronoid spicule is little developed and placed at about two-thirds of the height of the process. The external temporal fossa reaches to slightly underneath the upper sigmoid notch. The internal temporal fossa is small and it continues upwards as a furrow. The condyle has a broad interarticular area; the upper facet is cylindrical; the lower facet is short and high and slightly set off from the lower sigmoid notch. Both facets are nearly parallel (see Pl. 25, fig. 1c). The mental foramen lies underneath the hypoconid of M₁.

Remarks — In size, *Mafia csarnotensis* is intermediate between *Sulimskia kretzoi* and *Blarinoides*.

Our material shows many resemblances with *Sorex dehneli* from Podlesice (Kowalski, 1956) and therefore this species is here included in the new genus: *Mafia dehneli*. Among the resemblances are: the position of the mental foramen; general size and position of the condyle; stoutness of the ramus and the lower molars; V-shaped trigonid basins; strong cingula on the lower molars; the buccal backward extension of the lower incisor; and the strong pigmentation.

Differences between *M. csarnotensis* and *M. dehneli* are mentioned above.

The material from Mala Cave referred to by Sulimski et al., 1979, as *Sorex dehneli* looks quite different from *M. dehneli* from Podlesice: the I inf. is shorter, the mental foramen is more anteriorly placed, the trigonid valleys are more open and the cingula are considerably weaker in the Mala material. Therefore, the attribution of this material to the species *dehneli*, and in fact to the genus *Mafia* is here doubted.

Genus *Blarinoides* Sulimski, 1959

Type species — *B. mariae* Sulimski, 1959.

Remarks — The genus *Blarinoides* is monospecific; therefore the diagnosis and description given by Sulimski (1959) and Rzebik-Kowalska (1976) apply both to the genus *Blarinoides* and to the species *mariae*. Sulimski's (1959) diagnosis is rather descriptive and long, but the following features can be regarded as diagnostic: five upper antemolars, A¹ and A² large, A³ and A⁴ about half as large, A⁵ minute and not visible from the side. Upper molars with slight posterior emargination. I inf. massive, tricuspluate; A₁ small, P₄ with two indistinct cusps; M₃ with five cusps. Broad interarticular area of the condyle.

To these can be added: I sup. not fissident, P₄ without a postero-lingual basin, coronoid spicule large and pronounced.

Blarinoides mariae Sulimski, 1959

Pl. 26.

Type locality — Węże 1, Poland.

Studied localities — Osztramos 9, 7, Csarnóta 2.

Selected other localities — Podlesice, Rebielice Krolewskie I and II, Zamkowa Dolna, Kadzielnia, and Kamyk (all Poland, Rzebik-Kowalska, 1976); Ivanovce A and B (Czechoslovakia, Fejfar, 1966); Stranzendorf (Austria, Rabeder, 1974); Arondelli (Italy, Berzi et. al., 1969).

Stratigraphic range — Early Ruscinian-early Villányian (Mn 14-16).

Original reference — Sulimski, 1959, p. 144.

Synonymy (only concerning the studied localities)

Blarinoides mariae Sulimski, in: Kretzoi, 1959a, pp. 238, 245 (Cs2).

Shikamainosorex (?*Blarinoides*) *mariae* (Sulimski), in: Kretzoi, 1962, pp. 305, 353 (Cs2).

Blarinoides mariae Sulimski, in: Jánossy, 1973 a, p. 102 (Osz7).

Blarinoides mariae Sulimski, in: Jánossy & Kordos, 1977, p. 47 (Osz7).

Blarinoides mariae Sulimski, in: Jánossy, 1979, p. 23 (Cs2), p. 27 (Osz7).

Available material

Osztramos 9: 3 I sup., 1 A sup., 1 P⁴, 1 M¹, 1 M², 1 I inf., 2 condyles.

Osztramos 7: 21 I sup., 22 AA sup., 31 P⁴, 30 M¹, 22 M², 3 M³, 31 I inf., 18 A₁, 40 P₄, 85 M₁, 77 M₂, 32 M₃, 22 condyles.

Csarnóta 2: 78 I sup., 26 AA sup., 36 P⁴, 57 M¹, 32 M², 1 M³, 72 I inf., 6 A₁, 30 P₄, 67 M₁, 47 M₂, 17 M₃, 55 condyles.

Measurements — See Tables 33-35 and Fig. 16.

Description — All dental elements are intensely stained a dark red; as a rule even the basins of talonids, trigons, hypoconal flanges, etc. are stained.

I sup. — Not fissident, the apex is rather proodont, the talon is 2-cusped and hence has an 8-shaped occlusal surface when worn. The dorsal and posterior buccal margins make a slightly obtuse or perpendicular angle. A buccal posterior cingulum runs from the ventral side to half-way along the posterior margin; it then bends forward and disappears.

AA sup. — Five upper antemolars are present; A¹ and A² are large, A³, A⁴ and A⁵ are successively smaller, A⁴ (partly) and A⁵ (completely) are hidden behind P⁴ when seen

in buccal view. The large upper antemolars possess an S-shaped central ridge and a small extra cusplet on the lingual cingulum.

P⁴ — P⁴ makes a somewhat inflated impression, due to the large paracone and the lack of a strong posterior emargination. The parastyle is large but low and connected to the paracone by a broad and low parastylar crest. The antero-lingual margin of the P⁴ is formed by a ridge, which is provided with 3 or 4 cusps of decreasing size: parastyle, protocone, hypocone, and often an extra cingular cusp. This ridge may be almost straight. Often a short and small cingulum borders the small valley between protocone and hypocone. In one case (Pl. 26, fig. 8) there is an accessory cusplet in the central basin.

M¹ and M² — The molars have a slight posterior emargination. M¹ is nearly quadrate; M² however is strongly trapezoidal in occlusal view. M¹ shows a slight development of a parastyle; both M¹ and M² have a little protoconule on the anterior arm of the U-shaped protocone (Pl. 26, figs. 1, 6). The hypocone is well developed as a small but distinct, usually conical cusp. Lingually of the protocone a small cingulum may be present; in some unworn specimens the mesostyle is split (Pl. 26, fig. 7). In one specimen (Pl. 26, fig. 6) there is an accessory cusplet on the lingual margin.

M³ — The last upper molar is small, consisting of only a paracone and a semi-circular lingual basin.

I inf. — Bicuspluate or weakly tricuspluate (Pl. 26, fig. 4); through wear the cusplules go away quickly. The I inf. has a symphyisial surface which is smooth and not provided with furrows. The apex is slightly upturned. A buccal cingulum is present, but as a rule it is very weakly developed. On the buccal side of the mandible, I inf. reaches beyond the P₄, underneath the protoconid of M₁.

A₁ — This element is small and compressed; for nearly two-thirds of its length it lies pinched in between I inf. and P₄. The cingulum is broad on both sides, but hardly pronounced.

P₄ — The P₄ has a tetrahedral shape, which is quite strange for a member of the Soricinae. The postero-buccal edge of the pyramid is usually sharp. In unworn specimens the top is two-cuspled (see Pl. 26, fig. 9). After some wear the occlusal surface acquires a B- or 8-shape. The buccal overhang over the root is considerable; the cingula are well developed; especially the buccal one looks inflated.

M₁ and M₂ — There are no entoconid crests. The entoconids are high; in M₁ a tiny cusplet may be present on the buccal cingulum below the hypoconid (see Pl. 26, fig. 3b). The lingual cingulum is not as extreme as the buccal one. The hypolophids are short. In one M₁ (Pl. 26, fig. 10) there is an aberrant extra cusplet buccally of the paraconid.

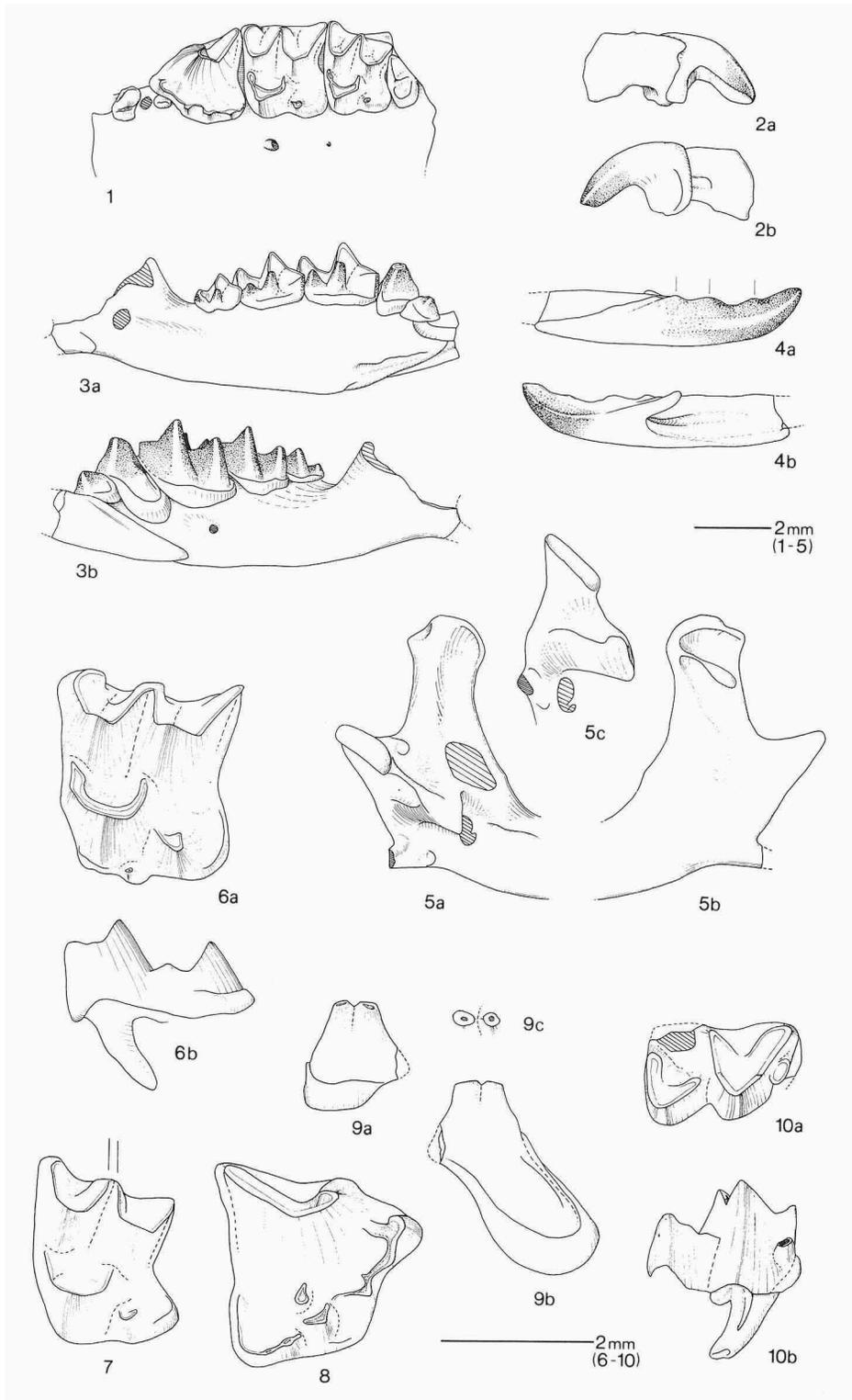
M₃ — M₃ is relatively small. There is always a talonid basin, in some cases even a small entoconid can be seen.

Plate 26

Blarinoides mariae Sulimski, 1959

1. Left A³, A⁵-M³, Osz7.
2. Left I sup., Osz7; a: medial view; b: buccal view.
3. Left I inf. (broken)-M₃, Osz7; a: lingual view; b: buccal view.
4. Right I inf., Osz7; a: buccal view; b: symphyisial view.
5. Left ascending ramus, Osz7; a: internal view; b: external view; c: caudal view of condyle.
6. Left M¹, Osz7; a: occlusal view showing extra lingual cusplet; b: anterior view showing protoconule.
7. Left M², Cs2/3, showing split mesostyle.
8. Right P⁴, Cs2/12, showing extra central cusplet.
9. Left P₄, Osz7, showing the split tip; a: lingual view; b: buccal view; c: occlusal view of the tip.
10. Right M₂, Osz7, showing extra anterior cusplet; a: occlusal view; b: buccal view.

Plate 26



Mandible — The coronoid process is strongly spatulate and has an undulate tip. The coronoid spicule is large, well pronounced and it points towards the upper condylar facet. The external temporal fossa is small, it does not reach below the level of the upper sigmoid notch. There is a shallow depression in the mandibular surface below the external temporal fossa. The internal temporal fossa is small, with a narrow opening and no significant dorsal extension. The pterygoid fossa is strongly excavated, the connection between the upper and the lower condylar facets is therefore only a thin wall. A pterygoid boss is present. The upper condylar facet is narrow and cylindrical; the lower facet is broad and high and provided with a concave upper margin. The lower facet is entirely hidden behind the lower sigmoid notch due to an anterior shift. The interarticular area is broad and depressed. The mandibular foramen is large and situated right below the internal temporal fossa. The mental foramen is placed below the talonid of M_1 , as a rule in a depression of the horizontal ramus.

Remarks — Our material fits in nicely with the clear and detailed description of Polish *B. mariae* given by Rzebik-Kowalska, 1976. She has also pointed out the major differences between this species and — the superficially quite similar — *Beremendia fissidens*.

Repenning (1967) argued against Kretzoi's (1962) attribution of *B. mariae* to the genus *Shikamainosorex* Hasegawa, 1957; his arguments are here accepted.

As Rzebik-Kowalska (1976) already stated, neither the size nor the morphology of *B. mariae* showed any essential change through time.

Because of its presence in Osztramos 9 the range of *B. mariae* is extended downwards into the Earliest Ruscinian.

Genus *Sulimskia* gen. nov.

Type species — *Sorex kretzoi* Sulimski, 1962.

Diagnosis — Relatively small Blarinini; trigonid valleys open and low; lingual cuspids pointed; I inf. tricuspidate with a well-developed buccal cingulum; a normal soricine P_4 . Coronoid process broad and spatulate, with a well-pronounced coronoid spicule. Condyle large and low, with a broad interarticular area. I sup. not fissident; five upper antemolars.

Plate 27

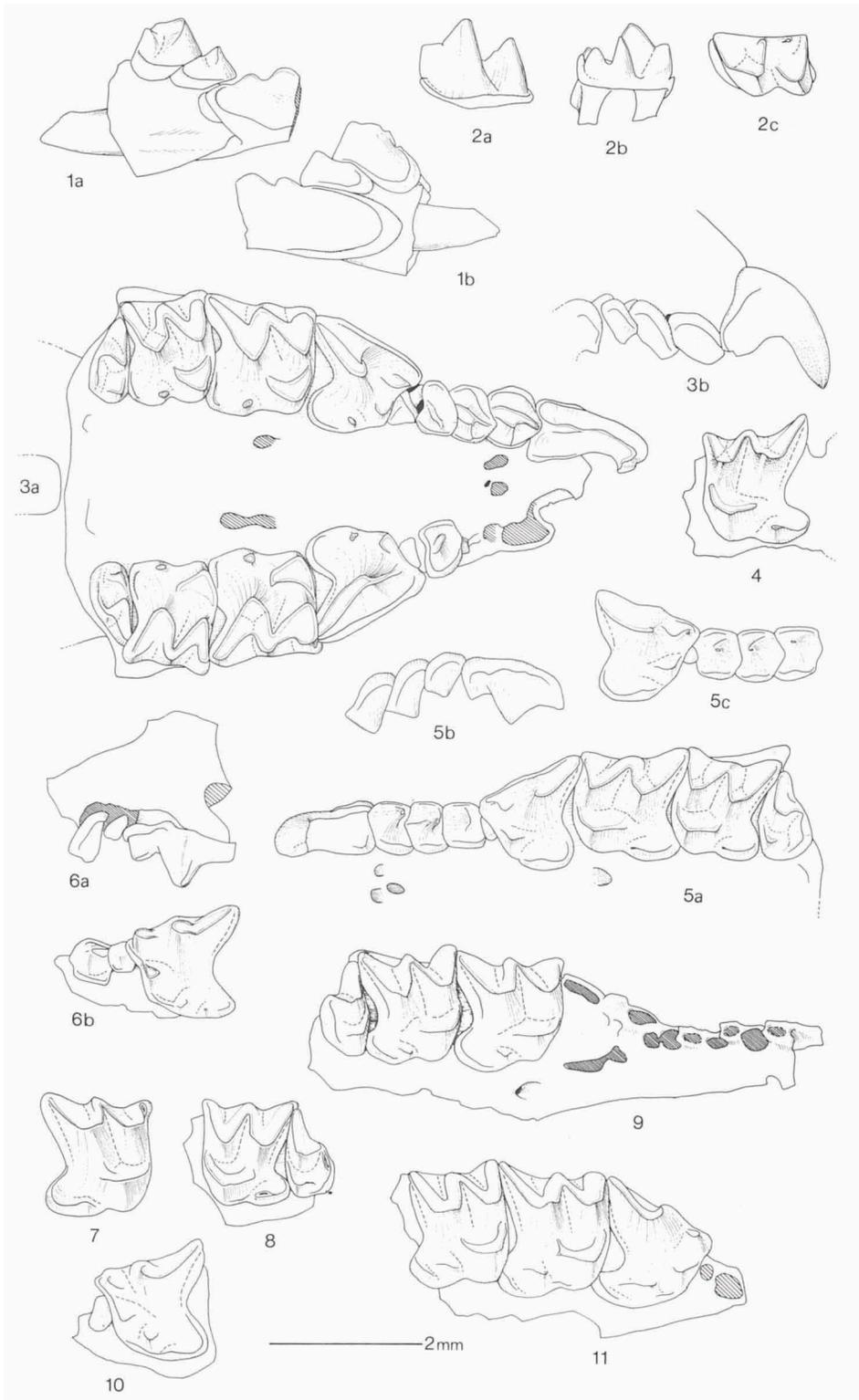
Sulimskia kretzoi (Sulimski, 1962), Osz7

1. Left I inf. (broken)- P_4 ; a: lingual view; b: buccal view.
2. Left M_2 ; a: buccal view; b: lingual view; c: occlusal view.

Episoriculus gibberodon (Petényi, 1864)

3. Holotype of *Soriculus kubinyii* Kormos, 1934, Villány Kalkberg (= Vi3), coll. MÁFI no. Ob.3685; a: occlusal view of whole specimen; b: buccal view of right anterior dentition.
4. Left M^1 , Vi3 alsó.
5. Details of the holotype of *Episoriculus tornensis* Jánossy, 1973, Osz13, coll. TTM no. V.72.114; a: occlusal view; b: buccal view.
a: left upper dentition, occlusal view; b: left AA sup. and P^4 , buccal view; c: right AA sup. and P^4 , occlusal view.
6. Holotype of *Episoriculus borsodensis* Jánossy, 1973, Osz1, left A^3 - P^4 , coll. TTM no. V.72.115;
7. Right M^1 , Osz1B, coll. TTM no. V.73.20.
8. Left M^2 - M^3 , coll. TTM no. V.73.20.
9. Right M^1 - M^3 and alveoles of other teeth, Osz9.
10. Left A^4 - P^4 , Osz9.
11. Right P^4 - M^2 , Cs2/23.

Plate 27



Etymology — The genus is named after Dr Andrzej Sulimski, Poland, who first described the type species.

Differential diagnosis — *Sulimskia* gen. nov. differs from *Blarinoides* Sulimski, 1959, by having a lower condylar facet which is visible from the buccal side, by having an I inf. with a well-developed buccal cingulum and by having a normal soricine P₄ with a postero-lingual basin. *Sulimskia* gen. nov. differs from *Mafia* gen. nov. by having a more compressed A₁, less developed cingula in the lower molars, less pigmentation, a larger cingulum on I inf., and by having a large and open internal temporal fossa.

Remarks — A few remains of Blarinini from Osztramos 7 could not be assigned to *Blarinoides* nor to *Mafia*. This material shows close resemblance to material from Węże 1 described by Sulimski (1962) as *Sorex kretzoii*. The generic assignment of the Węże material to *Sorex* is here not followed since the material has no entoconid crests (for which reason it is referred to the Blarinini), and since it has a condyle which also excludes attribution to the genus *Sorex*. A new genus has to be erected. As the available material from Osztramos 7 is rather scanty, this new genus is based on the material from Węże 1, described and illustrated by Sulimski (1962).

Sulimskia kretzoii (Sulimski, 1962)

Pl. 27, figs. 1, 2

Type locality — Węże 1, Poland.

Studied locality — Osztramos 7.

Other known localities — Apolakkia (Rhodes, Greece, van de Weerd et al., 1982), Ivanovce A (Czechoslovakia, Fejfar, 1966a).

Stratigraphic age — Late Ruscianian.

Synonymy

Sorex kretzoii n. sp., in: Sulimski, 1962, p. 469.

Sorex kretzoii Sulimski, in: Fejfar, 1966a, p. 223.

'*Sorex*' *kretzoii* Sulimski, 1962, in: Repenning, 1967, p. 44.

Blarinini gen. et sp. indet., in: van de Weerd et al., 1982, p. 93.

Available material — 1 I inf. (broken), 1 A₁, 1 P₄, 2 M₂.

Measurements — M₂: TRW 7.8, 7.6; TAW 7.5, 7.2; L 13.7, 13.4.

Description — All elements (except for one M₂) are stained orange.

I inf. — Only the posterior half has been preserved; it can however be concluded that I inf. is tricuspluate; a clearly developed cingulum is present along the posterior margin on the buccal side; the I inf. reaches to just before the posterior margin of P₄.

A₁ — Most of this element (c. ²/₃) is squeezed in between I inf. and P₄; only one short, single-topped part protrudes in front of P₄. A cingulum is present on both sides.

P₄ — Generalized soricine, rather short and provided with a deep postero-lingual basin; the cingula are well developed.

M₂ — An entoconid crest is absent, the entoconid has a rather anterior position between the hypolophid and the metaconid; it is sharply pointed. The metaconid is sharply pointed too; there is a very weak lingual cingulum; the trigonid valley is deep.

Remarks — The other known European Blarinini, i.e. the two *Mafia* species and *Blarinoides mariae* are much larger than the present material from Osz7, and also quite different in morphology. The lower molars from Osz7 show resemblances with the Węże 1 material ('*Sorex kretzoi*') in morphology and size. Sulimski (1962, text-pl. II, figs. 9, 10) does not indicate any lingual cingula in his illustrations of lower molars and a fairly open and deep trigonid valley. Most of the A₁ in Sulimski's figures appears squeezed in between I inf. and P₄. The I inf. is tricusulate in the Węże material.

Because of these resemblances, one seems justified in concluding that the material from Osztramos 7 and that from Węże 1 belong to the same genus and probably (as no size differences can be found) to the same species. Therefore, the material from Osz7 has been referred to the species *S. kretzoi*.

Our M₂'s show a remarkable resemblance with the material from Apolakkia, in many respects: absence of the entoconid crest; anterior position of the entoconid; deep trigonid valley; narrow and pointed metaconid; and the size. It is here suggested that the scanty material from Apolakkia also belongs to *S. kretzoi*.

These conclusions are supported by the stratigraphical position of the localities, which are all of Late Ruscinian age (Węże 1 and Apolakkia: Mn 15, Osztramos 7: MN16a; see also van de Weerd et al., 1982).

Tribe Soriculini Kretzoi, 1965

Genus *Episoriculus* Ellerman & Morrison-Scott, 1951

Type species — *Sorex caudatus* Horsfield, 1851.

Remarks — The generic delimitation of the genus *Episoriculus* was suggested by Repening (1967); Rzebik-Kowalska (1981) followed this definition.

We have encountered problems concerning the morphological variability of the species *E. gibberodon*. In the sample from Osztramos 7 two types of upper dentition occur, whereas no such distinction occurs in the lower dentition. The two types, to be called morphotypes A and B, can be distinguished as follows:

Morphotype A (Pl. 28, figs. 1, 2) is characterized by an isolated hypocone, separated by a small valley from the ridge that surrounds the hypoconal flange. The PE-index is moderate.

Morphotype B (Pl. 28, fig. 3) has a hypocone which is considerably less well developed and which is connected to the ridge surrounding the flange. The PE-index is moderate to strong; its range does not overlap that of morphotype A in the Osz7 sample (see Table 54 and Fig. 18).

Furthermore, considerable size differences can be observed between the dental elements from various localities (see Fig. 12-14). There are also differences in the relative size of the upper antemolars, particularly the A⁴ (compare e.g. Pl. 27, fig. 5a with fig. 6a); in the buccal extension of the lower incisor (compare e.g. Pl. 28, fig. 12a with Pl. 29, fig. 4); and in several less important characters.

Notwithstanding this wide range of variation, all *Episoriculus* material from Hungary is referred to as *E. gibberodon* (Petényi, 1864). This implies that two species known from the literature: *E. tornensis* Jánossy, 1973 and *E. borsodensis* Jánossy, 1973 are now considered synonyms of *E. gibberodon*.

E. gibberodon was originally described by Petényi (1864) as *Crocidura gibberodon* in a publication written in Old Hungarian. His type material from Beremend has since

been lost. Disregarding Petényi's publication, Kormos (1934) described the same species as *Soriculus kubinyii*.

A paradoxical situation has now arisen: we use the name *gibberodon* of Petényi, with the diagnostic description of Kormos' *kubinyii*.

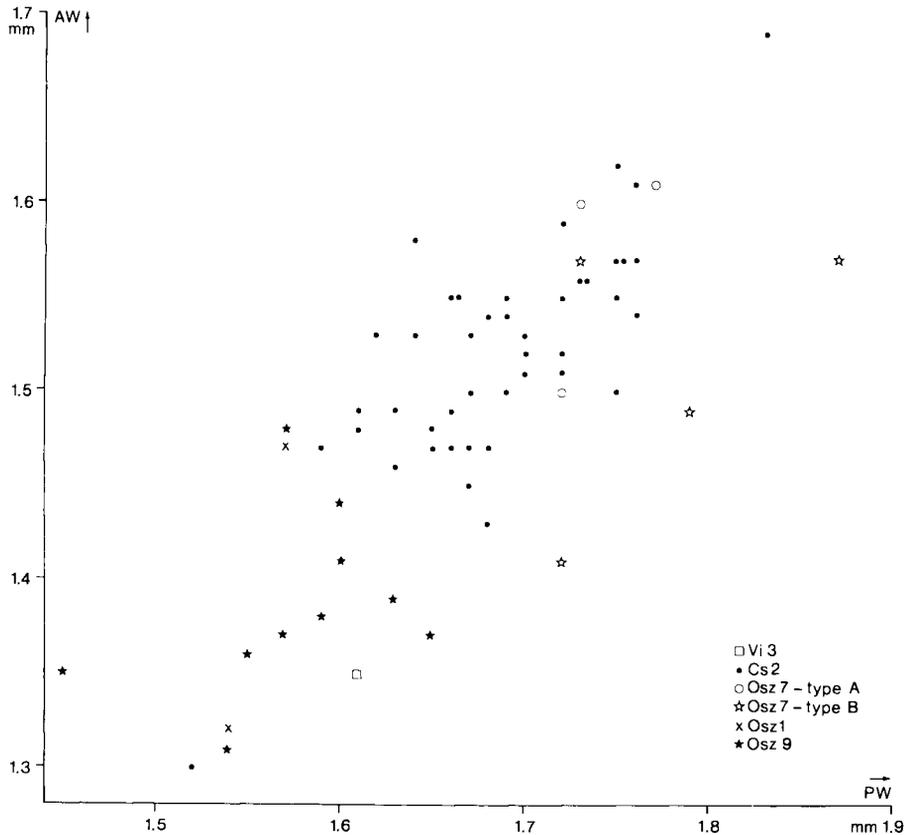


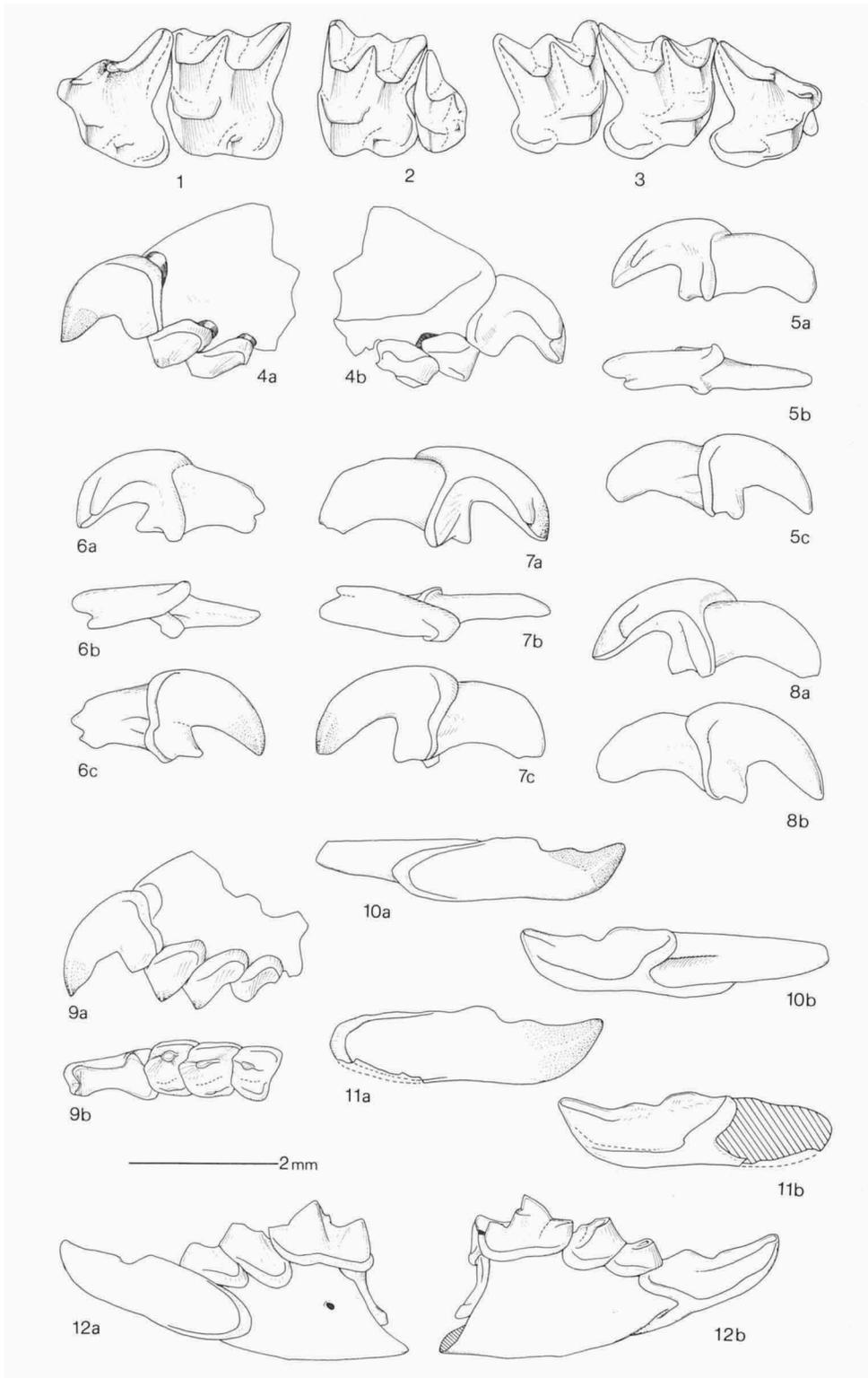
Fig. 12. Scatter diagram of the relation between anterior width (AW) and posterior width (PW) of M^1 in the studied samples of *Episoriculus gibberodon*.

Plate 28

Episoriculus gibberodon (Petényi, 1864)

1. Left P^4-M^1 , Osz7, morphotype A.
2. Left M^2-M^3 , Osz7, morphotype A.
3. Right A^4-M^2 , Osz7, morphotype B.
4. Left I sup.- A^2 , Osz9; a: buccal view; b: lingual view.
5. Right I sup., Osz1C, coll. TTM no. V.73.19; a: medial view; b: dorsal view; c: buccal view.
6. Right I sup., Osz7, same views as fig. 5.
7. Left I sup., Osz7, same views as fig. 5.
8. Right I sup., Cs2/15; a: medial view; b: buccal view.
9. Left I sup.- A^3 , Cs2/1; a: buccal view; b: occlusal view.
10. Right I inf., Osz9; a: buccal view; b: symphyseal view.
11. Right I inf., Osz7, same views as fig. 10.
12. Paratype of *Episoriculus borsodensis* Jánossy, 1973, Osz1, left I inf.- M_1 , coll. TTM no. V.72.123; a: buccal view; b: lingual view.

Plate 28



Episoriculus gibberodon (Petényi, 1864)

Pl. 27, figs. 3-11; Pls 28-30; Pl. 31, figs. 1, 2.

Holotype — (*Soriculus kubinyii*) A skull with nearly complete dentition, coll. MÁFI no. Ob.3685 (Pl. 27, fig. 3).

Type localities — Beremend for *C. gibberodon*; Villány Kalkberg = Vi3 for *S. kubinyii*.

Studied localities — Osztramos 1, 7, 9, 13; Csarnóta 2; Villány 3.

Selected other localities — Podlesice and Węże (Poland, Rzebik-Kowalska, 1981); Maritsa (Rhodes, Greece, de Bruijn et al., 1970); Apolakkia (Rhodes, Greece, van de Weerd et al., 1982); Plešivec (Czechoslovakia, Fejfar, 1961); Beremend 5, Villány 5, Dunaalmás 4, Somssichhegy 1 (all in Hungary, Jánossy, 1979).

Stratigraphic range — Early Ruscinian to early Biharian.

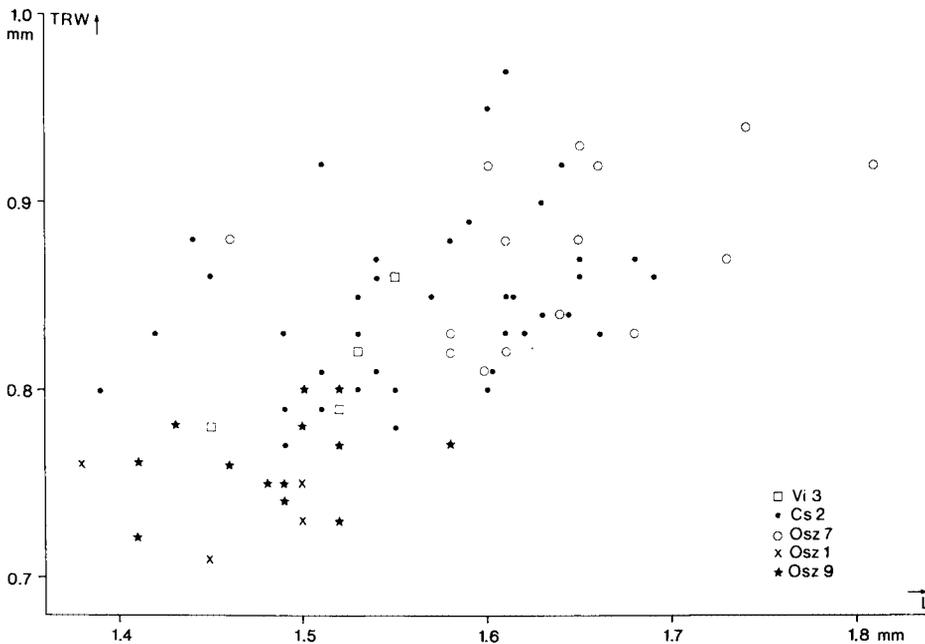


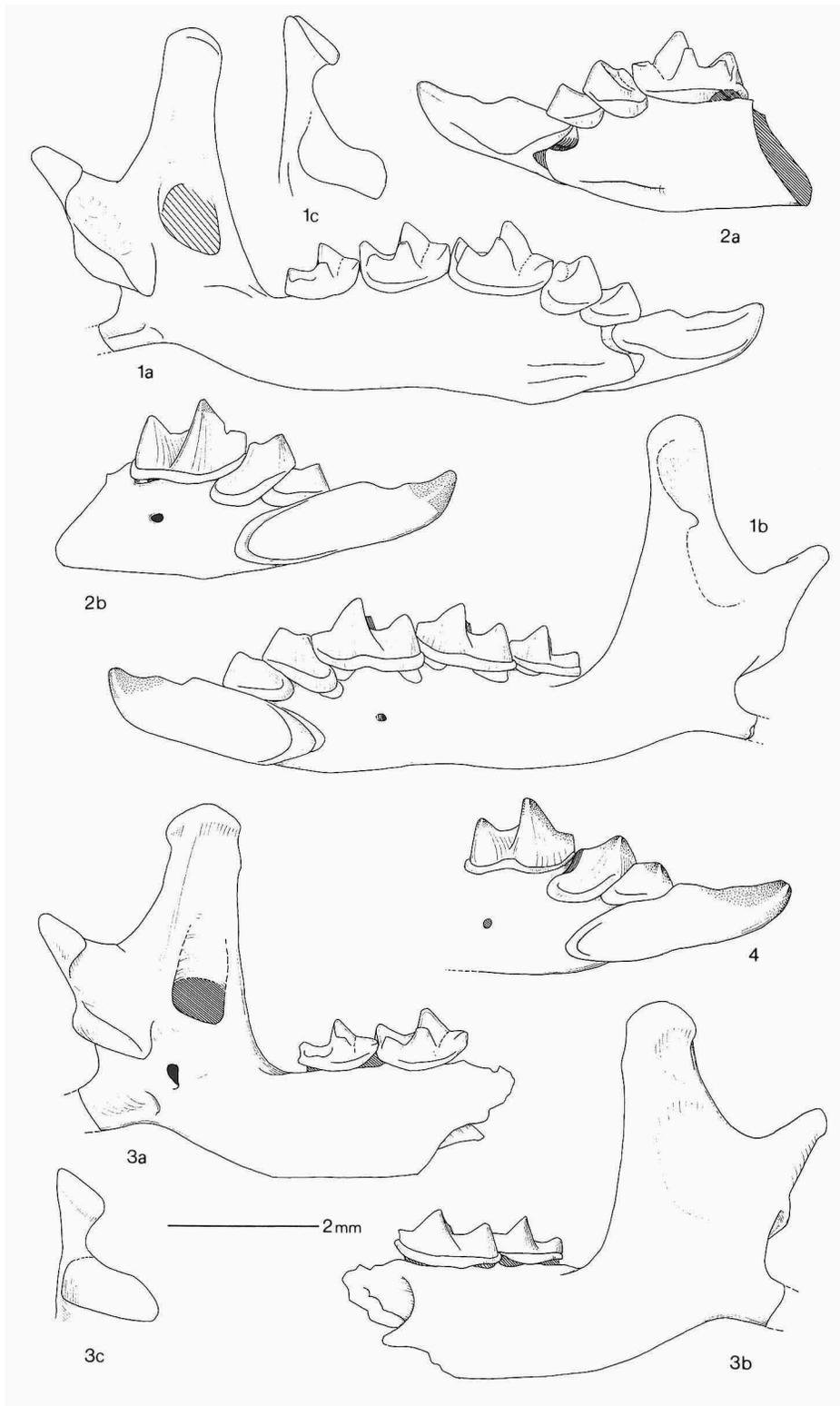
Fig. 13. Scatter diagram of the relation between trigonid width (TRW) and length (L) of M_1 in the studied samples of *Episoriculus gibberodon*.

Plate 29

Episoriculus gibberodon (Petényia, 1864)

1. Paratype of *Episoriculus tornensis* Jánossy, 1973, left ramus with complete dentition, Osz13, coll. TTM no. V.72.122; a: lingual view; b: buccal view; c: caudal view of condyle.
2. Right I inf.- M_1 , Osz9; a: lingual view; b: buccal view.
3. Left ramus with M_2 - M_3 , Osz9, same views as fig. 1.
4. Right I inf.- M_1 , Vi3 alsó.

Plate 29



Original diagnosis — From Kormos' description (1934) the following items can be used as diagnostic features: I sup. fissident; I inf. with weak cusplules; pigmentation present at some tips only.

Emended diagnosis — A rather small member of the Soriculini with only weakly pigmented teeth; four upper antemolars, of which the A⁴ may be variable in its development; upper molars variable in their morphology, with a moderate posterior emargination. I inf. bicusplulate, with a well-developed buccal cingulum; A₁ elongate; lower molars with high entoconid crests; M₃ with a talonid basin. Mental foramen below the posterior half of M₁.

Original descriptions — *Crocidura gibberodon*, in: Petényi, 1864; and *Soriculus kubinyii*, in Kormos, 1934.

Synonymy (only concerning the studied localities)

Soriculus Kubinyii n. sp., in: Kormos, 1934, p. 303 (Vi3).

Soriculus Kubinyii Korm., in: Kormos, 1937b, p. 1090 (Vi3).

Soriculus gibberodon (Petényi) (= *S. kubinyii* Kormos), in: Kretzoi, 1956, pp. 61, 184 (Vi3).

Soriculus (*Asoriculus* n. sg.) *gibberodon* (Petényi), in: Kretzoi, 1959a, pp. 238, 245 (Cs2).

Asoriculus gibberodon (Petényi), in: Kretzoi, 1962, pp. 301, 349 (Cs2).

Episoriculus gibberodon (Petényi), 1864, in: Repening, 1967, p. 48.

? *Episoriculus* group, in: Jánossy, 1972, p. 30 (Osz1).

Episoriculus gibberodon (Petényi), in: Jánossy, 1973a, p. 102 (Osz7).

Episoriculus tornensis sp. n., in: Jánossy, 1973b, p. 50 (Osz13).

Episoriculus borsodensis sp. n., in: Jánossy, 1973b, p. 53 (Osz1).

Episoriculus tornensis Jánossy, in: Jánossy, 1974, p. 18 (Osz9).

Episoriculus borsodensis Jánossy, in: Jánossy & Kordos, 1977, p. 41 (Osz1).

Episoriculus gibberodon (Petényi), in: Jánossy & Kordos, 1977, p. 47 (Osz7).

Episoriculus tornensis Jánossy, in: Jánossy & Kordos, 1977, p. 51 (Osz9), p. 54 (Osz13).

Episoriculus gibberodon (Petényi), in: Jánossy, 1978 (Osz7).

Episoriculus gibberodon (Petényi), in: Jánossy, 1979, p. 23 (Cs2), p. 27 (Osz7), p. 34 (Vi3).

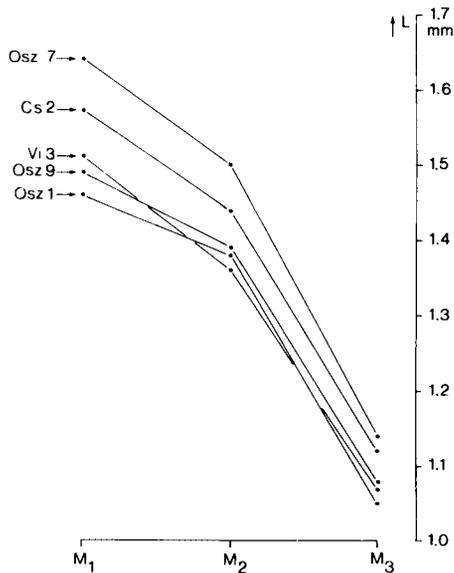


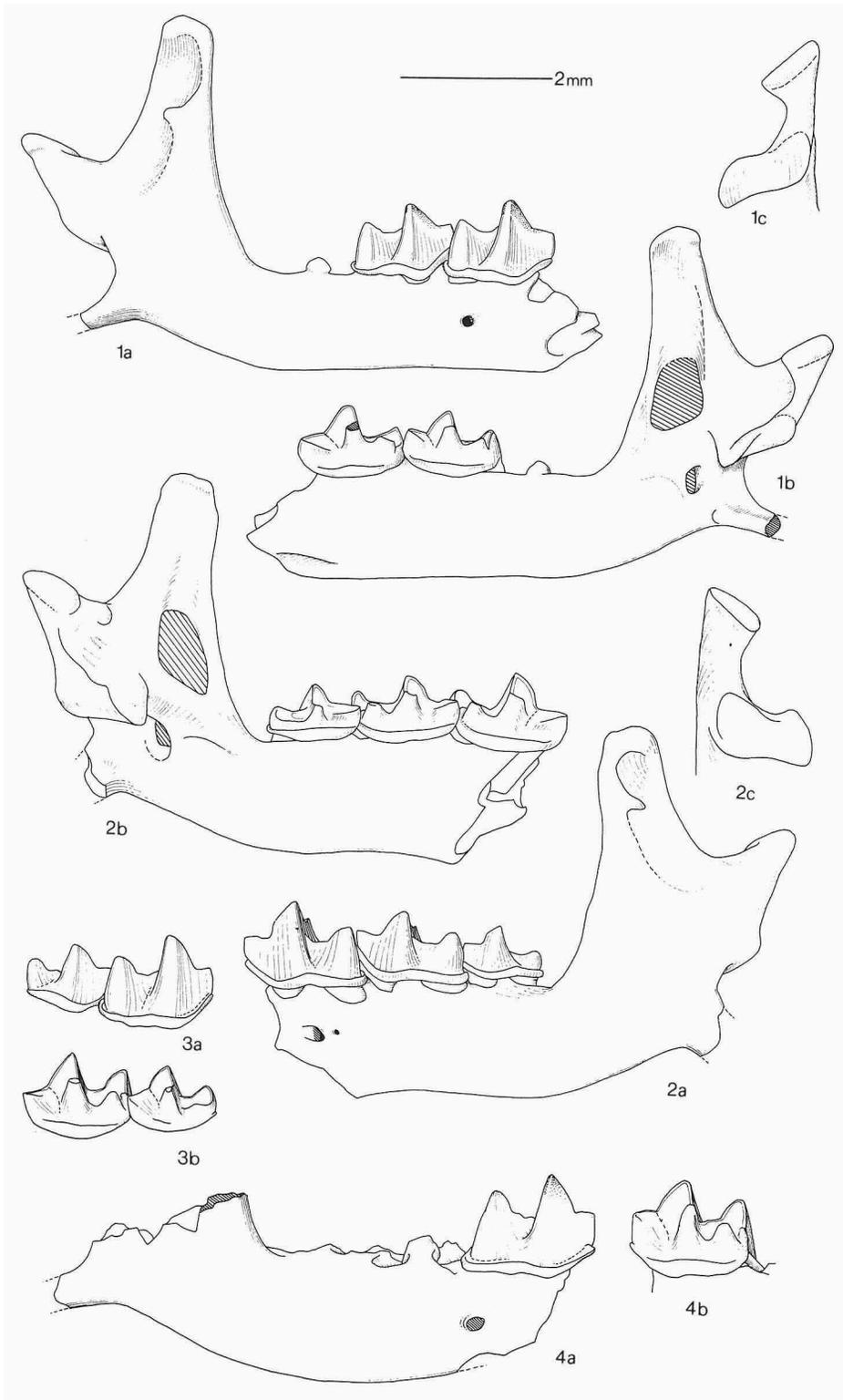
Fig. 14. Diagram showing the mean lengths of M₁, M₂, M₃ of the studied samples of *Episoriculus gibberodon*.

Plate 30

Episoriculus gibberodon (Petényia, 1864)

1. Right ramus with M₁-M₂, Osz1B, coll. TTM no. V.73.20; a: buccal view; b: lingual view; c: caudal view of condyle.
2. Left ramus with M₁-M₃, Cs2/18, same views as fig. 1.
3. Right M₂-M₃, Osz7; a: buccal view; b: lingual view.
4. Right M₁, Osz7, same views as fig. 3.

Plate 30



Studied material

Osztramos 9: 16 I sup., 27 AA sup., 14 P⁴, 13 M¹, 8 M², 3 M³, 12 I inf., 8 A₁, 10 P₄, 16 M₁, 14 M₂, 8 M₃, 5 condyles.

Osztramos 13: the holotype of *E. tornensis*, a skull with complete dentition, coll. TTM no. V.72.114; the paratype of *E. tornensis*, a left mandible with complete dentition, coll. TTM no. V.72.122.

Osztramos 1: 3 I inf., 1 A₁, 1 P₄, 1 M₁, 1 M₂, all coll. TTM no. V. 73.20.

Osztramos 1B: 1 P⁴, 3 M¹, 2 M², 1 M³, 1 I inf., 1 P₄, 3 M₁, 5 M₂, 2 M₃, 2 condyles, all coll. TTM no. V.73.20.

Osztramos 1C: the holotype of *E. borsodensis*, a maxillary fragment with A³, A⁴ and P⁴, coll. TTM no. V.72.115; the paratype of *E. borsodensis*, a mandibular fragment with I-M₁, coll. TTM no. V.72.123; furthermore 1 I sup., 1 I inf., 1 M₂, all coll. TTM no. V.73.19.

Osztramos 1E: 4 I inf., coll. TTM no. V.75.17.

Osztramos 7: 7 I sup., 2 I inf., 1 A₁, 2 P₄, 18 M₁, 20 M₂, 11 M₃, 6 condyles; furthermore 1 A sup., 3 P⁴, 7 M¹, 4 M², and 1 M³ of morphotype A and 1 A sup., 5 P⁴, 4 M¹, and 3 M² of morphotype B.

Csarnóta 2: 124 I sup., 6 AA sup., 33 P⁴, 76 M¹, 54 M², 123 I inf., 1 A₁, 24 P₄, 207 M₁, 219 M₂, 67 M₃, 274 condyles.

Villány 3 alsó: 1 M¹, 1 I inf., 1 A₁, 1 P₄, 1 M₁, 1 M₂, 1 M₃, 2 condyles.

Villány 3 felső: 1 I inf., 1 A₁, 1 P₄, 4 M₁, 4 M₂, 3 M₃, 3 condyles.

In addition, the type material of *S. kubinyii* (coll. MÁFI no. Ob. 3685) has been studied.

Measurements — See Tables 36-42 and Figs. 12-14.

Description — The dental elements are only vaguely stained. As a rule, only the very tips of the teeth have a light orange colour.

I sup. — Fissident; the dorsal margin and the buccal posterior margin make a sharp to perpendicular angle; the posterior margin is provided with an undulation (concave) and a cingulum along its border. This cingulum usually increases its width from ventral to dorsal. A narrow cingulum is also present along the lingual posterior margin.

AA sup. — Of the four upper antemolars, the A¹, A² and A³ usually are of nearly the same size, rather quadrate in occlusal view and provided with a small extra cusplet on their lingual rims. The A⁴ (which is always smaller than A¹-A³) may vary from an element large enough to be seen from the side (e.g. in the *E. borsodensis* holotype, Pl. 27, fig. 6 and in the *Soriculus kubinyii* holotype, Pl. 27, fig. 3) to a minute little peg, hidden by the parastyle of the P⁴ (e.g. in the *E. tornensis* holotype, Pl. 27, fig. 5 and in morphotype B from Osz7, Pl. 28, fig. 3).

P⁴-M² — Amongst these large upper teeth, two morphotypes are distinguished (see the description above). Otherwise, the elements can be described as follows.

Plate 31

Episoriculus gibberodon (Petényi, 1864)

1. Right ramus with M₁-M₃, Vi3 felső; a: buccal view; b: lingual view; c: caudal view of condyle.

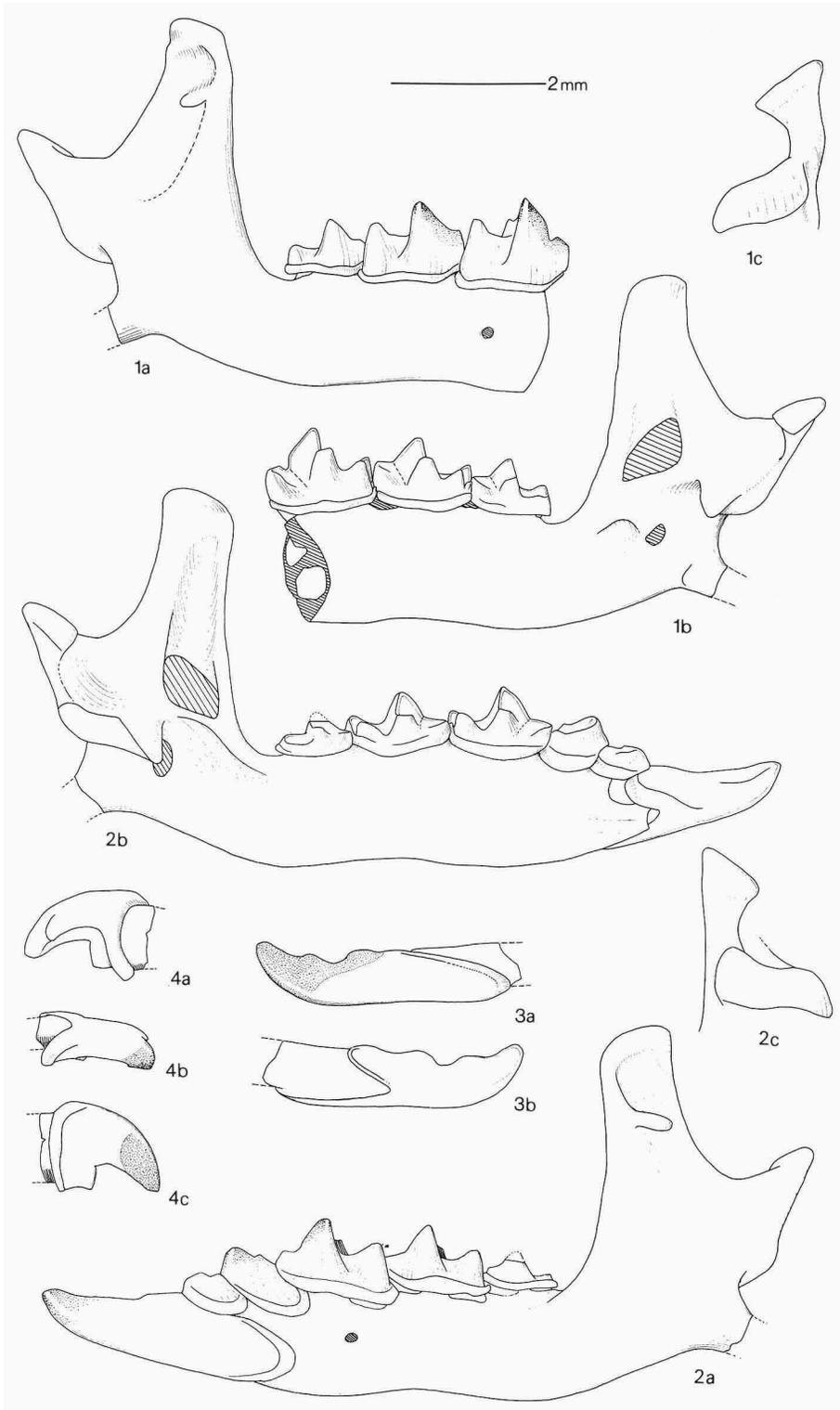
2. Paratype of *Soriculus kubinyii* Kormos, 1934, Villány Kalkberg (= Vi3), coll. MÁFI no. Ob.3685, same views as fig. 1.

Soriculini gen et sp. indet., Osz9

3. Left I inf.; a: buccal view; b: symphysial view.

4. Right I sup.; a: medial view; b: dorsal view; c: buccal view.

Plate 31



P⁴ — The parastyle and the paracone are connected by a high parastylar crest. The protocone is well developed and situated quite close to the parastyle. It is separated from the hypocone by a valley, which is often bordered by a small cingulum. The parastyle may be surrounded by a cingulum, but this is not always the case.

M¹ and M² — A metaloph is present in all samples, except in the morphotype B material from Osz7. The protocone and the hypocone are separated by a wide valley, which in some specimens has a little cingulum at its lingual end. The postero-buccal corner (metastyle) of M¹ protrudes, in M² it protrudes less. The anterior margin bends obliquely beside the protocone. There is quite some variation in the shape of the lingual margin of the molars. The hypocone is placed farther towards the lingual side than the protocone in some samples (e.g. in morphotype B from Osz7, Pl. 28, fig. 3 and in Cs2, Pl. 27, fig. 11), but in other samples both cusps reach lingually to the same extent (e.g. in morphotype A from Osz7, Pl. 28, figs. 1, 2).

M³ — The M³ is not very much reduced, paracone and protocone are both well developed; the metacone is present as a posterior ridge only.

I inf. — The lower incisor is short and bicuspluate. The anterior cuspule (the one between the posterior cuspule and the apex) is only present as a slight undulation of the dorsal margin. The short apex is strongly upturned. A buccal cingulum is present along the posterior part of the tooth, not only dorsally, but also reaching to the ventral margin. The symphyseal cingulum does not show a sharp corner between the horizontal and the ascending parts. The I inf. reaches at the buccal side of the mandible to a varying level: from the end of A₁ (in the *borsodensis* paratype, Pl. 28, fig. 12) to nearly the end of P₄ (in the *Soriculus kubinyii* paratype, Pl. 31, fig. 2 and the Villány 3 material, Pl. 29, fig. 4). In other samples I inf. reaches to half-way along P₄.

A₁ — The size of A₁ is, again, variable, depending on the development of the lower incisor. In samples in which I inf. reaches far backwards (hypsodont situation) the A₁ is small; in samples with a short I inf. the A₁ is larger. A₁ is always elongated, provided with cingula on both sides, with a little postero-lingual basin or none at all and it is pinched in between P₄ and I inf. for about half its length.

P₄ — The lower premolar is two-cusped, the anterior cusp being higher than the posterior one in side view. The postero-lingual basin is shallow, as a rule not reaching the postero-lingual corner but ending somewhat above the cingulum. The basin is triangular in occlusal view. A cingulum is present on both sides of the tooth; the buccal overhang over the root is considerable but not extreme.

M₁ and M₂ — The buccal edge of the hypoconid in the lower molars is somewhat convex; the talonid is wider than the trigonid in both M₁ and M₂. The oblique crest has a central dent; in some unworn specimens a tiny mesoconid may be present. Cingula are developed on both lingual and buccal sides, the buccal one may be slightly undulate, particularly in M₁. The entoconid is high and placed far backward; the entoconid crest is present but not very high. The buccal re-entrant valley opens directly above the cingulum. Some specimens from Csarnóta 2 develop a little entostylid at the lingual end of the hypolophid. When seen from the lingual side, the lower margins of the molars are slightly convex (navicular).

M₃ — The lingual cingulum in M₃ is usually only weakly developed; the talonid is not reduced but always basined and possessing both entoconid and hypoconid.

Mandible — The anterior margin of the coronoid process is usually slightly concave. The posterior margin is also concave. A coronoid spicule is present and moderately to well developed; it is placed about half-way between the upper sigmoid notch and the tip of the coronoid. The external temporal fossa is very shallow; it reaches to half-way down the condyle. The internal temporal fossa is relatively small and narrow;

morphotype sample	A	B
" <i>Soriculus kubinyii</i> " (type, Villány Kalkberg)	•	
Villány 3 (n=1)		•
Csarnóta 2	•	
Osztramos 7	•	•
<i>E. "borsodensis"</i> (type, Osztramos 1C)	•	
Osztramos 1		•
<i>E. "tornensis"</i> (type, Osztramos 13)		•
Osztramos 9	•	

Fig. 15. Scheme showing the distribution of the morphotypes A and B over the studied samples of *Episoriculus gibberodon* and of the included holotypes.

it continues upwards as a shallow groove to just below the tip of the coronoid. Below the internal temporal fossa is a horizontal bar separating the fossa from the depressed ventral part of the ascending ramus. The upper condylar facet is narrow, long and cylinder-shaped. The lower facet is strongly elongated linguallly, pointing downwards and provided with a concave upper rim. The lower facet and the lower sigmoid notch are separated by a narrow groove. The interarticular area is notched linguallly and hence quite narrow and elongate. Both condylar facets are nearly parallel to each other. When seen from the buccal side, the lower facet is partly hidden behind the lower sigmoid notch. The superior pterygoid fossa is excavated; a pterygoid spicule or boss is occasionally present. The mandibular foramen is of variable size; the mental foramen is placed below the re-entrant valley or below the hypocond of M_1 .

Remarks — The variability of the material from the different samples is striking. The two morphotypes (A and B) are both present in Osz7 and easily separable, not only on the basis of the configuration of the talon, but also in the degree of the posterior emargination (see Table 54 and Fig. 18). The holotype of *Soriculus kubinyii* is of morphotype A, whereas the single other tooth available from Vi3 is of morphotype B. A similar discrepancy is found in Osz1 between the type of *E. borsodensis* (morphotype A) and the rest of the sample we studied (see Fig. 15).

Combining the morphotypes and the sizes (we have samples with typically small specimens: Osz9, Osz1 and Vi3 and with large specimens: Cs2 and Osz7, see Fig. 12) gives four combinations:

- 1) The combination morphotype A-large applies to Osz7 (half) and to Cs2;
- 2) The combination B-large applies only to the other half of the Osz7 sample;
- 3) The combination A-small applies to the *Soriculus kubinyii* type and to the *E. borsodensis* type, as well as to the Osz9 sample. Within this group it is worth noting that the two holotypes do not differ in other characters either, such as the size of A^4 .
- 4) The combination B-small applies to the *E. tornensis* type and furthermore to the Osz1 and Vi3 material, excluding the earlier mentioned types of *S. kubinyii* and *E. borsodensis*.

It would perhaps be preferable to have four species names, one for each of the combinations. Combination 3 applies to both the *S. kubinyii* type and the *E. borsodensis* type. Of these, the first is older and has priority. Combination 4 can be assigned to the species *E. tornensis*. There is no name available for combinations 1 and 2.

The four combinations do not show any trend. For instance, as to size, the Csarnótian teeth (Osz7 and Cs2) are larger than the older ones (Osz9 and Osz1) and the younger ones (Vi3).

Apparently, the four combinations have no time order. In several localities (Osz7, Osz1, Vi3) two of them were found together. If we take other morphological characters into consideration, such as the size and the position of the A⁴, it becomes less easy to separate four independent groups. In addition, the gaps between the supposed four species seem to become filled as more material is considered.

Jánossy (1973b) lists several characters that should differentiate the three species he distinguished (*tornensis*, *borsodensis* and *gibberodon*). As is found here, most of these characters are variable with considerable overlaps. The gap in Jánossy's scatter diagram between *tornensis/borsodensis* on the one hand and *gibberodon* on the other is filled in by Rzebik-Kowalska (1981) with *E. borsodensis* from Podlesice.

The only solution for these problems appears to be the application of one name to all the samples: *E. gibberodon*. Rzebik-Kowalska (1981) already suggested that we have to accept that all European *Episoriculus* belonged to this species. In this concept *E. tornensis* Jánossy, 1973 and *E. borsodensis* Jánossy, 1973 are synonyms of *E. gibberodon*.

Since the scanty material of *E. castellarini* Pasa, 1947 from Soave, Italy has not been studied, it cannot be decided whether this is yet another synonym.

Soriculini gen. et sp. indet.

Pl. 31, figs. 3, 4.

Locality — Osztramos 9.

Age — Early Ruscinian (MN14).

Available material — 1 I sup., 1 I inf.

Measurements — I sup.: LT = 6.1, L = 14.6, H = 12.0;

I inf.: L = 33.5 (0.1 mm units).

Description — Both elements are stained a very dark red.

I sup. — Fissident, the buccal posterior margin is slightly convex, provided with a cingulum along its entire length; this cingulum is uniform in width.

I inf. — Bicuspluate, the apex is upturned and high, the first cusplule rather low. Cingula are present both buccally and symphysially, but they are very weak.

Remarks — The two incisors described above are the only soriculine material that could not be attributed to *Episoriculus*. The present material differs from that genus chiefly in the intense pigmentation, in the convex buccal posterior margin of I sup. and the weak cingula of I inf.

Tribe Beremendiini new tribe

Genus *Beremendia* Kormos, 1934

Type species — *Crossopus fissidens* Petényi, 1864.

Remarks — Within the Soricinae, the Beremendiini are the only tribe that contains only one genus: *Beremendia*. The genus was erected by Kormos in 1934. He did not give a formal diagnosis but a description, from which the following items may be used as diagnostic features: I sup. fissident; upper antemolars diminishing in size from front to rear, A⁴ hidden; M³ relatively small. Ramus robust; coronoid process flexed antero-laterad; angular process short and blunt; I inf. curved and acusulate; M₃ reduced. Teeth intensively stained a dark red.

Four species have been described: *B. fissidens* (Petényi, 1864), *B. sinensis* (Zdankski, 1928), *B. ucrainica* (Pidoplichko, 1956), and *B. minor* Rzebik-Kowalska, 1976.

Beremendia minor Rzebik-Kowalska, 1976
Pl. 32, figs. 14, 15; Pl. 33, figs. 7-9; Pl. 35, figs. 3-6.

Original description — Rzebik-Kowalska, 1976, p. 369.

Type locality — Rębielice Królewskie 1, Poland.

Studied localities — Osztramos 1 and 7.

Stratigraphic range — Ruscinian and early Villányian (MN 14-16).

Available material

Osztramos 1B: 1M₁.

Osztramos 1C: 4 M₁, 4 M₂, 1 M₃.

Osztramos 1E: 1 M₁, 1 M₃, 1 fragmentary P⁴.

Osztramos 7: 2 I sup., 4 AA sup., 1 P⁴, 1 M¹, 1 M², 2 I inf., 2 A₁, 2 P₄, 3 M₁, 2 M₂, 1 M₃, 1 condyle.

Measurements — See Tables 43, 44 and Fig. 16.

Description — Morphologically, *Beremendia minor* is identical to *B. fissidens* (see below). The two species differ only in size: *B. minor* is considerably smaller than *B. fissidens* (Rzebik-Kowalska, 1976; see also Fig. 16).

Beremendia fissidens (Petényi, 1864)
Pl. 32, figs. 1-13; Pl. 33, figs. 1-6; Pl. 34; Pl. 35, figs. 1, 2.

Type locality — Beremend 1.

Studied localities — Osztramos 1, 7, 3/3; Csarnóta 2; Villány 3; Tegelen.

Selected other localities — Węże 1 (Poland, Sulimski, 1959, 1962; Rzebik-Kowalska, 1976); Rębielice Królewskie I and II (Poland, Kowalski, 1960; Rzebik-Kowalska, 1976); Zamkowa Dolna, Kadzielnia, Kielniki, Kamyk, Zalesiaki, and Kozi Grzbiet (all Poland, Rzebik-Kowalska, 1976); Hajnáčka (Czechoslovakia, Fejfar, 1964), Ivanovce, Plešivec, Chlum 6 (all Czechoslovakia, Fejfar, 1961); Sackdillinger Höhle (Germany, Heller, 1930); Deinsdorf (Germany, Heller, 1963); Weissenburg 7 (Germany, von Koenigswald, 1971); Brielle (The Netherlands, van der Meulen & Zagwijn, 1974); Sugworth (England, Stuart, 1980); Monte Peglia (Italy, van der Meulen, 1973); Soave (Italy, Pasa,

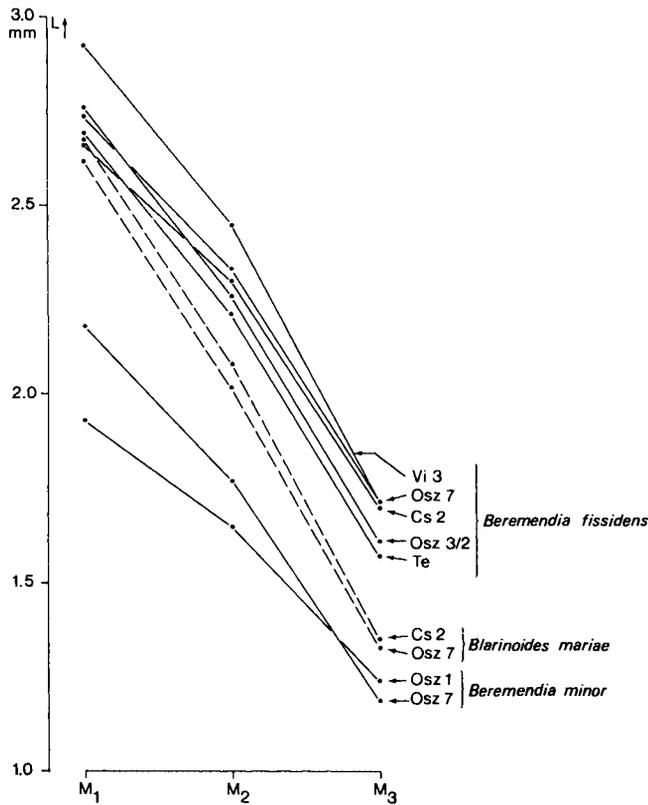


Fig. 16. Diagram showing the mean lengths of M_1 , M_2 , M_3 of the studied samples of *Beremendia fissidens*, *B. minor* and *Blarinoidea mariae*.

Plate 32

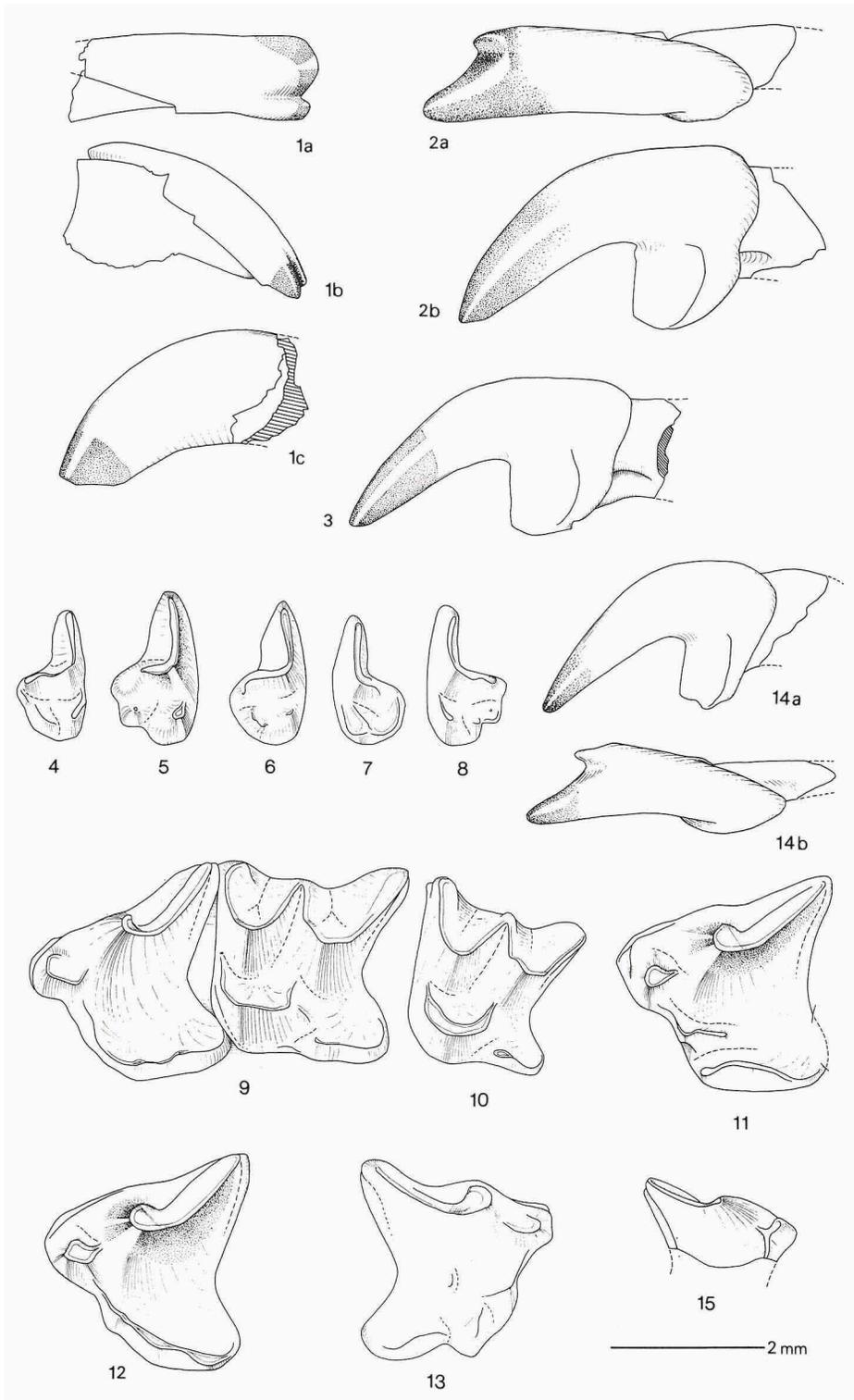
Beremendia fissidens (Petényi, 1864)

1. Fragmentary left I sup., Osz1E; a: dorsal view; b: medial view; c: buccal view.
2. Left I sup., Osz7; a: dorsal view; b: buccal view.
3. Left I sup., Osz3/2.
4. Right M^3 , Te, RGM 257 031.
5. Right M^3 , Vi3 felső.
6. Right M^3 , Vi3 felső.
7. Left M^3 , Te, RGM 257 136.
8. Left M^3 , Te, RGM 257 362.
9. Left P^4 - M^1 , Cs2/19.
10. Left M^2 , Cs2/20.
11. Left P^4 , Vi3 felső.
12. Left P^4 , Vi3 felső.
13. Right P^4 , Cs2/7 (note extra cusplet).

Beremendia minor Rzebik-Kowalska, 1976

14. Left I sup., Osz7; a: buccal view; b: dorsal view.
15. Fragmentary right P^4 , Osz1E.

Plate 32



1947); Deutsch-Altenburg 9 (Austria, Mais & Rabeder, 1977a); Bettfia 13 (Rumania, Terzea, 1973); Osztramos 2, 4, 8, and 14 (Hungary, Jánossy & Kordos, 1977, Jánossy, 1979); Beremend 5 and 11, Villány 5, 6, 7, and 8, Dunaalmás 4, Nagyharsányhegy 2, 4 and 5, Somssichhegy 1, and Tarkó (all Hungary, Jánossy, 1979).

Original description — *Crossopus fissidens*, in: Petényi, 1864, p. 60.

Synonymy (only concerning the studied localities)

Beremendia n. gen., in: Kormos, 1934, p. 299 (Vi3).

Beremendia fissidens (Pet.), in: Kormos, 1937, p. 1089 (Cs2), 1090 (Vi3).

Beremendia fissidens (Petényi), in: Kretzoi, 1956, pp. 47, 170 (Cs2), pp. 61, 184 (Vi3).

Beremendia fissidens (Petényi), in: Kretzoi, 1959a, pp. 238, 245 (Cs2).

Beremendia fissidens (Petényi), in: Kretzoi, 1962, pp. 301, 349 (Cs2).

Beremendia fissidens (Petényi), 1864, in: Repenning, 1967.

Beremendia fissidens (Petényi), in: Jánossy, 1973a (Osz7).

Beremendia fissidens (Petényi, 1864), in: Freudenthal et al., 1976 (Te).

Beremendia fissidens (Petényi), in: Jánossy & Kordos, 1977, p. 44 (Osz3), p. 47 (Osz7).

Beremendia fissidens Petényi, in: Jánossy, 1978, p. 69 (Osz7).

Beremendia fissidens (Petényi), in: Jáanosy, 1979, p. 23 (Cs2), p. 27 (Osz7), p. 34 (Vi3), p. 36 (Osz3).

Available material

Osztramos 1E: 2 fragmentary I sup.

Osztramos 7: 27 I sup., 53 AA sup., 33 P⁴, 33 M¹, 31 M², 16 M³, 25 I inf., 15 A₁, 28 P₄, 60 M₁, 56 M₂, 46 M₃, 16 condyles.

Csarnóta 2: 60 I sup., 12 AA sup., 32 P⁴, 25 M¹, 22 M², 62 I inf., 8 A₁, 13 P₄, 49 M₁, 55 M₂, 18 M₃, 47 condyles.

Villány 3: 2 I sup., 1 A sup., 1 P⁴, 5 M¹, 4 M², 1 M³, 7 I inf., 3 A₁, 4 P₄, 3 M₁, 6 M₂, 5 M₃, 4 condyles.

Villány 3 also: 6 I sup., 2 AA sup., 2 P⁴, 3 M², 6 I inf., 1 A₁, 3 P₄, 5 M₁, 6 M₂, 3 M₃, 4 condyles.

Villány 3 felső: 13 I sup., 17 AA sup., 6 P⁴, 9 M¹, 9 M², 4 M³, 19 I inf., 13 A₁, 14 P₄, 17 M₁, 21 M₂, 14 M₃, 12 condyles.

Tegelen: 6 I sup.: RGM 179 054, 257 041, 055, 097, 125.

8 P⁴: RGM 179 054, 257 071, 093, 094, 126, 174, 263, 326.

10 M¹: RGM 179 054, 257 054, 092, 126, 146, 147, 154, 173, 228, 262.

4 M²: RGM 179 054, 257 144, 146, 226.

3 M³: RGM 257 031, 136, 362.

5 I inf.: RGM 257 014, 098, 175, 264, 265.

2 P₄: RGM 257 332, 415.

8 M₁: RGM 179 053, 257 078, 095, 096, 145, 148, 406, 418.

5 M₂: RGM 179 053, 257 040, 047, 078, 079.

3 M₃: RGM 179 053, 257 079, 335.

4 condyles: RGM 179 053, 257 079, 121, 150.

Osztramos 3/2: 3 I sup., 5 AA sup., 1 P⁴, 1 M¹, 6 I inf., 6 A₁, 7 P₄, 13 M₁, 11 M₂, 11 M₃, 5 condyles.

Plate 33

Beremendia fissidens (Petényi, 1864)

1. Left I sup.-M², Osz7; a: occlusal view; b: buccal view of anterior dentition.

2. Left I sup. and P⁴-M², Te, RGM 179 054.

3. Right I sup.-M³, Vi3 felső.

4. Left ramus with complete dentition, Vi3 felső; a: buccal view; b: lingual view; c: caudal view of condyle.

5. Left I inf., Te, RGM 257 175.

6. Right I inf., Osz7; a: buccal view; b: symphysial view.

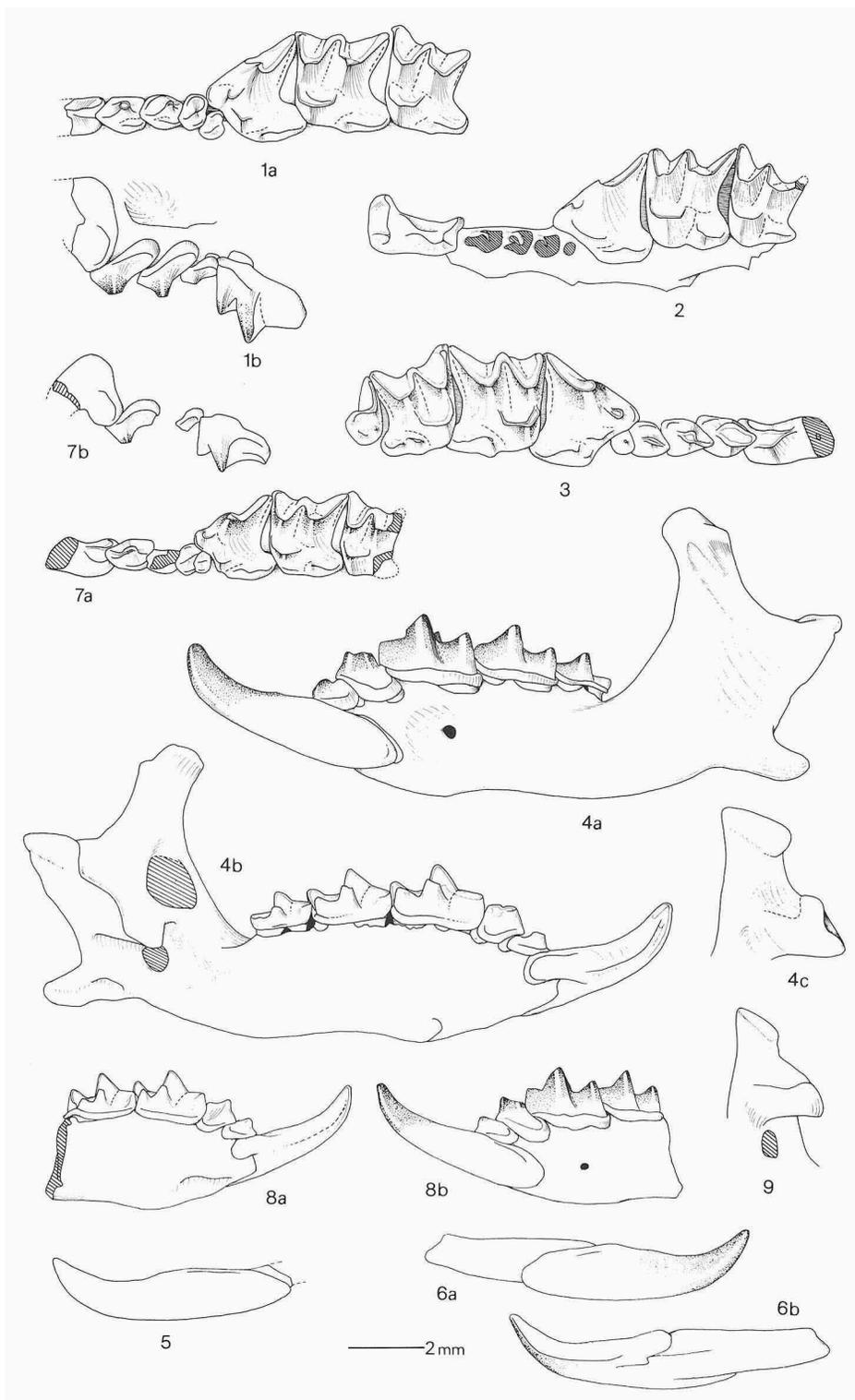
Beremendia minor Rzebik-Kowalski, 1976

7. Left I sup.-M², Osz7, same views as fig. 1.

8. Left I inf.-M₂, Osz7; a: lingual view; b: buccal view.

9. Caudal view of left condyle, Osz7.

Plate 33



Measurements — Osztramos 1E: I sup.: LT = 14.3; H = 21.2 (n = 1). For other localities see Tables 45-49 and Fig. 16.

Description — All dental elements are stained a dark red.

I sup. — Strongly fissident, the two cusps are slightly divergent and separated by a wide, deep groove on the dorsal side of the tooth. The posterior buccal edge is somewhat undulate and placed at a sharp angle to the dorsal edge. The cingulum along the posterior buccal edge is only present behind the talon.

AA sup. — Four upper antemolars are present. A¹ and A² are of about equal size, A³ is smaller and A⁴ is smaller again, and not visible in buccal view (Pl. 33, fig. 1a). All four antemolars are unicuspid, the central crest of A¹ and A² is somewhat S-shaped.

P⁴ — The shape of the lingual part of P⁴ is variable. As a rule, the protocone is low and situated close to the parastyle, and the hypocone is placed far anteriorly. A valley separates protocone and hypocone (e.g. Pl. 33, fig. 1a). In some specimens, however, there is no such valley (e.g. Pl. 32, figs. 9, 12). Some other specimens are somewhat aberrant in the shape and the position of the hypocone (Pl. 32, figs. 11, 13), showing the large variation in P⁴. Therefore, the occlusal outline may vary from nearly quadrate (Pl. 32, fig. 11) to nearly triangular (Pl. 32, fig. 12). The buccal part is always the same, with a rather large parastyle and a high parastylar crest.

M¹ and M² — The protocone is situated on a U-shape crest, which connects it to both the paracone and the metacone. The hypocone is low and more or less reduced; it is separated from the protocone by a deep valley. A tendency towards the formation of a parastyle can be observed. There is often a small cingulum underneath the protocone.

M³ — M³ is also quite variable in the development of its lingual part. The lingual basin is sometimes surrounded by a near-circular ridge, but in other cases this ridge is split up into several individual cusps. The lingual margin may either be circular or undulate (see Pl. 32, figs. 4-8).

I inf. — Acuspluate, the dorsal margin may be provided with little serrations, but not with cuspules. The apex is strongly upturned and pointed. The symphyisial side of the tooth is provided with a deep longitudinal furrow. The postero-buccal cingulum is usually present; however, it is very short, narrow and hardly pronounced; it may even be absent. I inf. reaches as far backwards as does P₄.

A₁ — This element is small and flat; for about half its length it lies between I inf. and P₄. A postero-lingual basin may be faintly present. A cingulum is moderately well developed on both sides.

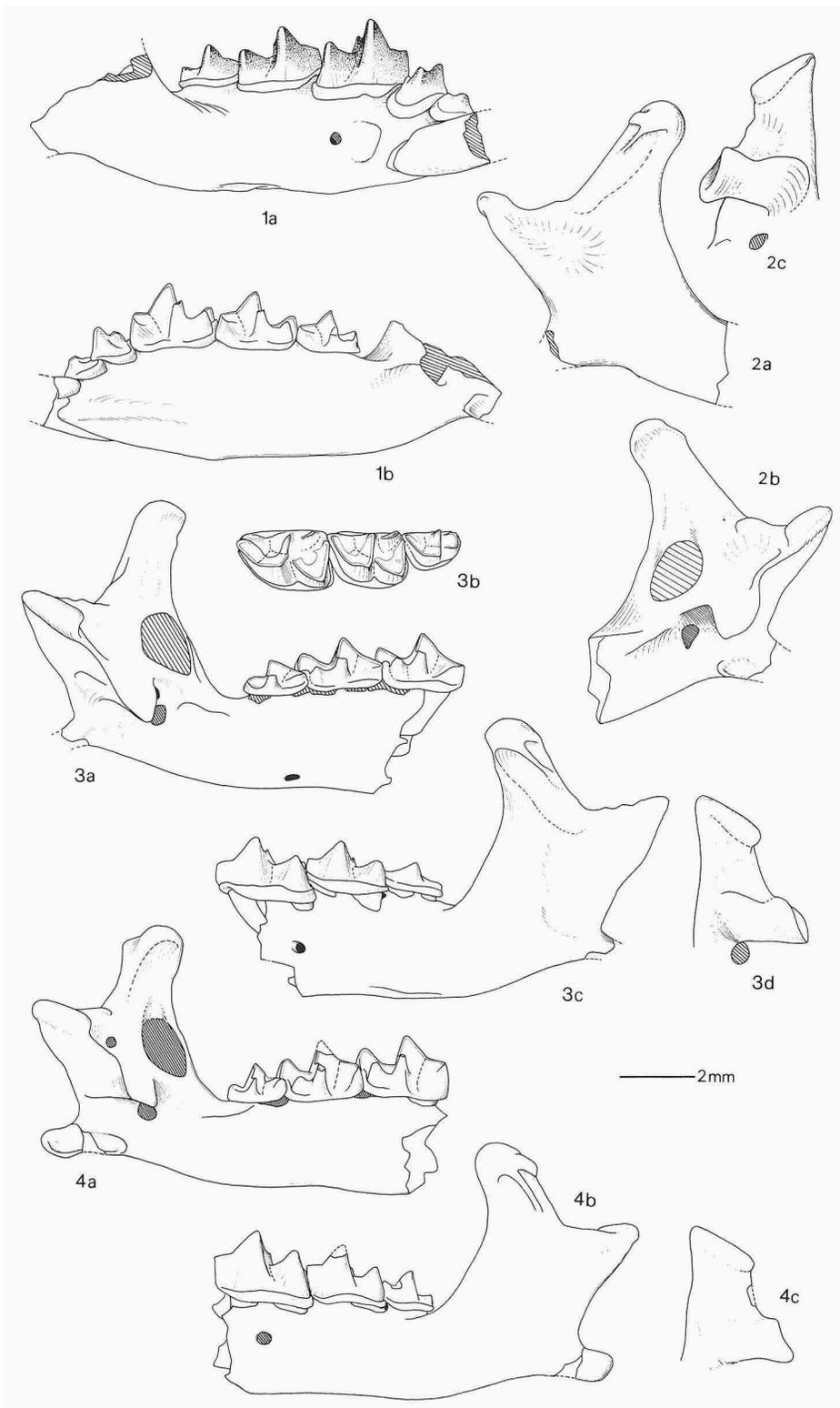
P₄ — Generally speaking, the postero-lingual basin is neither very deep nor clearly bordered. The buccal overhang over the root is not as extreme as in *Blarinoides*, neither is the width of the buccal cingulum. The lingual cingulum is quite well developed. A little cusplet may be present on the cingulum along the posterior edge, closing off the postero-lingual basin on the posterior side.

Plate 34

Beremendia fissidens (Petényi, 1864)

1. Right I inf. (broken)-M₃, Osz7; a: buccal view; b: lingual view.
2. Right ascending ramus, Osz7; a: external view; b: internal view; c: caudal view of condyle.
3. Left ramus with M₁-M₃, Cs2/19; a: lingual view; b: occlusal view; c: buccal view; d: caudal view of condyle.
4. Left ramus with M₁-M₃, Te, RGM 179 053; a: lingual view; b: buccal view; c: caudal view of condyle.

Plate 34



M_1 and M_2 — The lower molars show a deep and wide trigonid basin due to a slight posterior-ward shift of the metaconid. This is a characteristic feature of *Beremendia*. The entoconid crest is short and only moderately high. The lingual cingulum is only slightly developed and is often missing below the metaconid. The buccal cingulum is well developed and sometimes slightly undulate. In M_1 the talonid is wider developed than the trigonid, in M_2 the trigonid is wider.

M_3 — The last lower molar, like P^4 and M^3 , is variable in its development. The talonid is usually basined; entoconid and hypoconid may be present as separate cuspids (Pl. 35, fig. 2), but the cuspids have sometimes disappeared into a horseshoe-shaped ridge (Pl. 35, fig. 1). Also the size of the talonid may vary. Specimens as reduced as the one depicted by Rzebik-Kowalska (1976, p. 366, fig. 11) have not been observed, however. Normally there is no lingual cingulum.

Mandible — The coronoid process is short and pointed. It has a concave anterior border; the tip is rounded with often a conspicuous emargination; it bends strongly forwards. As a rule, the posterior margin is also concave. The whole of the coronoid leans laterally. A coronoid spicule is present, but it is low and usually nearly 'vertically' directed. The external temporal fossa is not clearly delineated. The internal temporal fossa is small and deep, it does not continue far upwards. The superior pterygoid fossa is deeply pocketed; in one specimen from Tegelen it has a central foramen (Pl. 34, fig. 4a); a small pterygoid spicule is present. The angular process is very short. The condyle is characteristic in its Blarinini-like morphology. The lower facet is broad and placed far anteriorly of the lower sigmoid notch; the upper facet is long and slightly triangular to cylindrical. The interarticular area is broad and somewhat excavated. On the buccal side of the ascending ramus, below the external temporal fossa, a shallow depression can be seen. The mandibular foramen is large; the mental foramen is placed below the re-entrant valley or below the talonid of M_1 , sometimes in a depression of the ramus.

Remarks — Not much can be added here to the excellent monograph by Rzebik-Kowalska (1976). The two described species are, as stated, morphologically similar but different in size.

Two more species are known from the literature: *B. ucrainica* (Pidoplichko, 1956) and *B. sinensis* (Zdansky, 1928). *B. ucrainica* has not been studied by the present author; Rzebik-Kowalska (1976) suggests that it is identical to *B. fissidens*.

Plate 35

Beremendia fissidens (Petényi, 1864)

1. Right M_3 , Osz7.
2. Left M_3 , Osz7.

Beremendia minor Rzebik-Kowalska, 1976

3. Right M_3 , Osz7; a: buccal view; b: occlusal view; c: lingual view.
4. Left M_3 , Osz7, same views as fig. 3.
5. Right M_1 - M_2 , Osz1C; a: buccal view; b: lingual view.
6. Left M_2 - M_3 , Osz1C, same views as fig. 5.

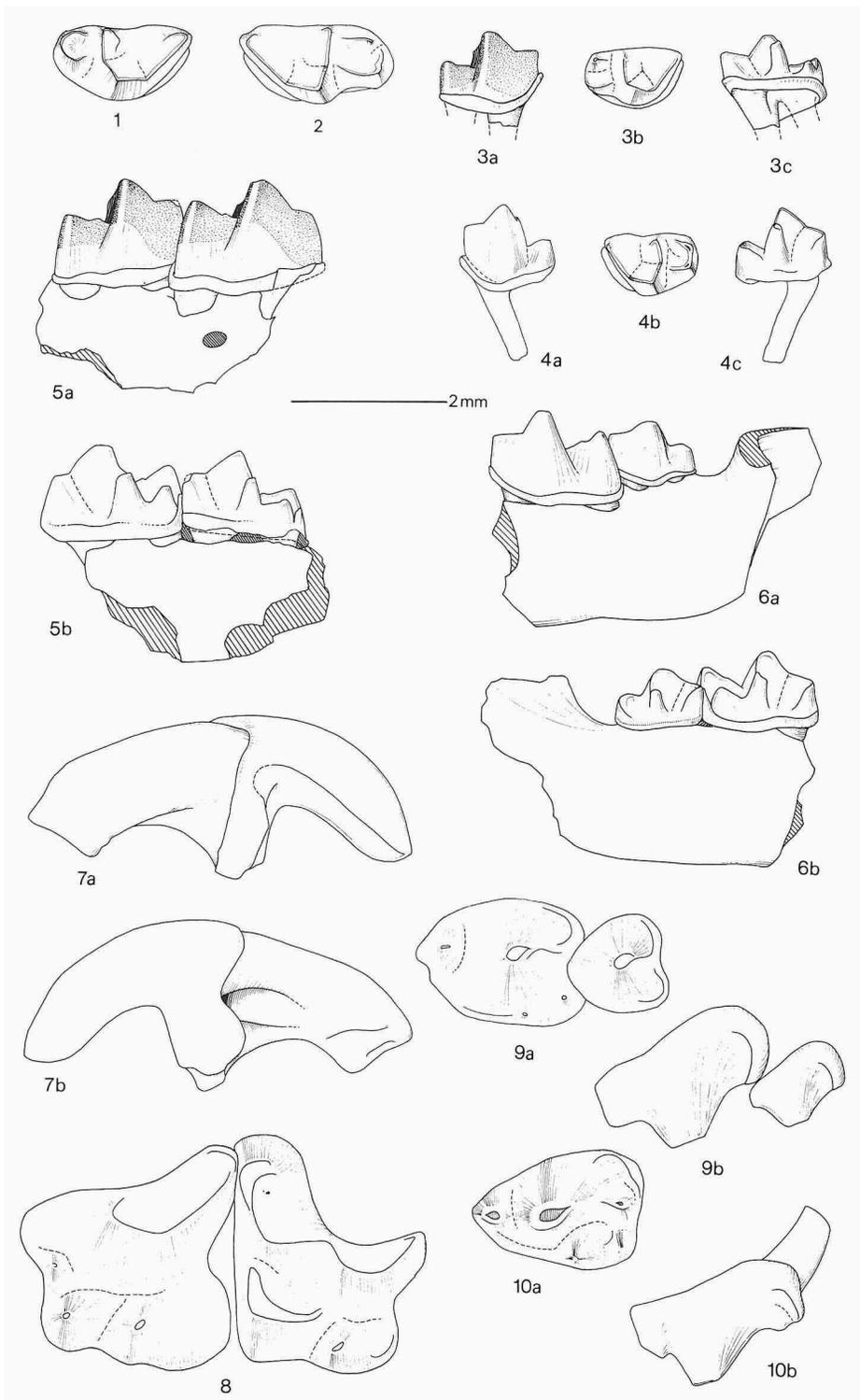
Amblycoptus topali Jánossy, 1972, all Osz1C, coll. TTM no. V.73.18

7. Left I sup., Osz1C; a: medial view; b: buccal view.
8. Left P^4 - M^1 , Osz1C.
9. Left A^1 - A^2 , Osz1B; a: occlusal view; b: buccal view.

Amblycoptus sp., Osz7

10. Left A^1 , same views as fig. 9.

Plate 35



B. sinensis (described as *Neomys sinensis* by Zdansky, 1928, but referred to *Beremendia* by Kretzoi, 1956) seems to differ from our two species mainly by having a more posteriorly placed condyle (see Zdansky, 1928, pl. I, fig. 29). It is slightly smaller than *B. fissidens*, but not nearly as small as *B. minor*.

The presence of *B. minor* in Osztramos 1 and 7 greatly expands the known stratigraphic range of this species, previously known only from the early Villányian of Rębielice Królewskie. So far, *B. minor* has been found only in localities where *B. fissidens* is also present.

Tribe Amblycoptini Kormos, 1926

Genus *Amblycoptus* Kormos, 1926

Type species — *A. oligodon* Kormos, 1926.

Remarks — The genus *Amblycoptus* was established in 1926 by Kormos, for an aberrant shrew with unstained, bulbous teeth and without M3.

Dimyloid shrews (i.e. missing M3) are very rare; apart from *Amblycoptus*, the only European genus known to lack the M3 is *Dimylosorex* Rabeder, 1972.

Amblycoptus topali Jánossy, 1972
Pl. 35, figs. 7-9; Pl. 36, figs. 1-3.

Holotype — Fragmentary ramus with I inf. - M₁, coll. TTM no. V.71.149 (Pl. 36, fig. 1).

Original diagnosis — An evolved form of the genus *Amblycoptus*, with an M₁ allometrically different from that of the only other known species (*A. oligodon*) and with more reduced A₁ and M₂.

Type locality — Osztramos 1.

Studied locality — Osztramos 1.

Plate 36

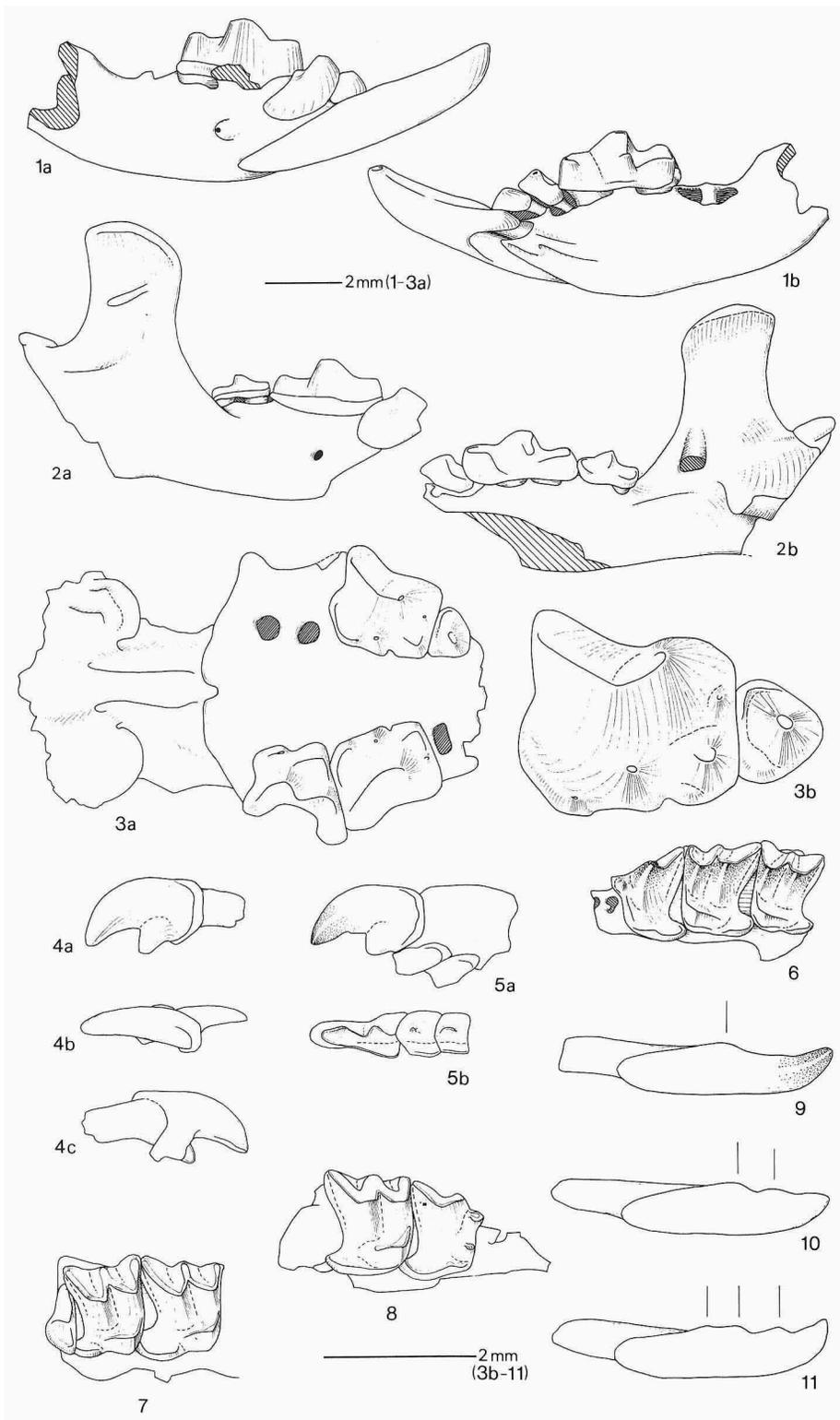
Amblycoptus topali Jánossy, 1972, Osz1

1. Holotype, fragmentary ramus with I inf.-M₁, coll. TTM no. V.71.149; a: buccal view; b: lingual view.
2. Ramus with P₄-M₂, Osz1C, coll. TTM no. V.73.18, same views as fig. 1.
3. Fragmentary cranium with left P⁴-M¹ and right A³-P⁴, Osz1C, coll. TTM no. V.73.18; a: occlusal view of whole specimen; b: enlarged detail, right A³-P⁴.

Paenelimnoecus pannonicus (Kormos, 1934)

4. Left I sup., Cs2/3; a: buccal view; b: dorsal view; c: medial view.
5. Left I sup.-A², Cs2/1; a: buccal view; occlusal view.
6. Left P⁴-M², Osz7.
7. Right M¹-M³, Cs2/2.
8. Right P⁴-M¹, Cs2/23.
9. Right I inf. Cs2/0, monocuspulate.
10. Right i inf., Cs2/18, bicuspulate.
11. Right I inf., Cs2/19, tricuspulate.

Plate 36



Other localities — Zamkowa Dolna, layer C (cf., Poland, Rzebik-Kowalska, 1975) and Mała Cave (Poland, Sulimski et al., 1979).

Stratigraphic range — Early Ruscian (MN 14 and 15). See also the remarks below.

Synonymy (complete)

Amblycoptus topali sp. n., in: Jánossy, 1972, p. 38.

Amblycoptus cf. *topali* Jánossy, 1972, in: Rzebik-Kowalska, 1975.

Amblycoptus topali Jánossy, in: Jánossy & Kordos, 1977, p. 41.

Amblycoptus topali Jánossy, 1972, in: Sulimski et al., 1979, p. 387.

Available material

Osztramos 1: 3 I inf., 1 A₁, 1 P₄, 3 M₁, 1 M₂, 2 condyles, all coll. TTM, no. V.73.18.

Osztramos 1B: 2 AA sup. (1 A¹, 1 A²), 1 P⁴, 1 I inf., coll. TTM no. V.73.18.

Osztramos 1C: the holotype, a fragmentary mandible with I inf.-M₁, coll. TTM no. V.71.149. Furthermore a cranium with 1 A³, 2 P⁴ and 1 M¹; 7 I sup., 1 P⁴, 5 M¹, 7 I inf., 1 A₁, 4 P₄, 6 M₁, 3 M₂, 4 condyles, coll. TTM no. V.73.18.

Osztramos 1E: 2 fragmentary I sup., 4 fragmentary I inf., 1 edentulous ramus, all coll. TTM no. V.75.12.

Measurements — See Table 50.

Description — The teeth are not pigmented.

I sup. — Non-fissident; the posterior buccal margin is strongly emarginated. A buccal cingulum is usually absent, although in some cases a faint trace can be observed behind the talon. The apex protrudes and is not much down-turned.

AA sup. — Of the three upper antemolars, A¹ is by far the largest. It has a large central cusp, an anterior cusp and two little cusps on the lingual cingulum: one centrally and one in the postero-lingual corner. A² is considerably smaller and unicuspid; it is slightly heart-shaped in occlusal view. A³ is somewhat smaller than A², triangular and also unicuspid. A³ is visible in buccal view.

P⁴ — In occlusal view, P⁴ has a trapezoidal shape. Its largest cusp is the paracone. The parastyle is small and shifted lingually. It thus does not lie in the antero-buccal corner as it usually does in shrews. There is no parastylar crest. Protocone and hypocone are about the same size and are separated by a valley. The protocone forms the antero-lingual corner of the tooth. The lingual margin is serrate.

M¹ — M¹ is characterized by the large, protruding parastyle. Also the metastyle is pointed; hence the buccal margin of the tooth is U-shaped. The metacone is the highest cusp; protocone and paracone are lower and about equal in height. The talon is small and narrow; there is hardly any hypoconal flange; the hypocone is well developed.

No M² is preserved in our material.

I inf. — The lower incisor is acuspulate or feebly monocuspulate. The apex is only slightly upturned. There is no cingulum on the buccal side; on the symphyseal side the tooth is flat, without grooves. On the buccal side of the mandible, I inf. reaches back to beyond P₄, roughly underneath the protoconid of M₁.

A₁ — A₁ has the shape of a tetrahedron; it is relatively small and compressed between the incisor and P₄. The element is unicuspid.

P₄ — P₄ is also unicuspid and essentially of a tetrahedral shape. A trace of the postero-lingual basin can be observed, however. The buccal overhang over the root is considerable. There are usually no cingula on P₄, nor are there on A₁.

M₁ — The trigonid of M₁ is long, due to a forward shift of the paraconid. The entoconid has a tendency to disappear into and be replaced functionally by the entostylid. the entoconid crest is present. Along the buccal and posterior rims there is a wide but hardly pronounced cingulum. Lingually there is no cingulum.

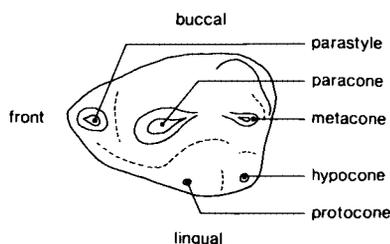


Fig. 17. Interpretation of the cusps on the A^1 of *Amblycoptus* sp. from Osztramos 7.

M_2 — The M_2 looks like a 'normal' soricid M_3 . The talonid is basined and bears an entoconid crest. Buccally there is a narrow cingulum, lingually there is none.

Mandible — The horizontal ramus is short and has the mental foramen below the protoconid or the re-entrant valley of M_1 . The coronoid process is very broad and spatulate, with concave anterior and posterior margins. The coronoid spicule is well pronounced and elongate. It divides the external temporal fossa into two parts of equal size and it points towards the upper condylar facet. The external temporal fossa is shallow; it continues ventrally to halfway down the condyle. The mandible is somewhat depressed below the external temporal fossa. The internal temporal fossa is extremely small; it is merely a near-circular foramen. On the other hand, the superior pterygoid fossa is large and strongly excavated. There is no pterygoid boss or spicule. The mandibular foramen is large. The condylar facets are strongly separated; the upper facet is somewhat triangular and makes an angle of c. 45° with the lower facet. This lower facet is narrow and elongate, and gets narrower towards the lingual side. There is a slight lingual offset of the lower facet from the lower sigmoid notch. Due to the extreme excavation of the superior pterygoid fossa there is no interarticular area left. Both condylar facets are connected by a sharp ridge only.

Remarks — See the Remarks of the next species.

Amblycoptus sp.

Pl. 35, fig. 10; Fig. 17.

Studied locality — Osztramos 7.

Available material — 1 A^1 .

Description — The only available *Amblycoptus* tooth from Osz7, an A_1 , is quite different from that of *A. topali* from Osz1 and from *A. oligodon* from Polgárdi. It is narrower anteriorly; the main cusp is situated more towards the front. Behind this main cusp there is an extra cusp, located ventrally and connected to the main cusp by a low and short ridge. The anterior of the two lingual cusps is relatively larger.

Remarks — The apparent reduction of the entoconid, combined with the functional replacement of the entoconid by the entostylid, and the lengthening of the trigonid in M_1 are features that *Amblycoptus* shares with the tribe Allosoricini.

Furthermore, the development of the A_1 is very interesting.

Figure 17 shows the interpretation of the different cusps that are found on the most complicated specimen, the A¹ from Osz7. It will be apparent that this tooth is in a highly developed state of molarization.

Normally, molarization is a process affecting the promolars, decreasing in degree at greater distance from the molars. In this case, however, P⁴ is molarized, A³ and A² are not and A¹ is again molarized. Also, it is very doubtful whether the A¹ is a premolar; usually this element is interpreted as the second incisor (I²).

The A¹ of *Amblycoptus* is therefore quite unique among mammalian teeth, representing not only a second, independent 'field' of molarization, but also by probably being a molarized incisor.

Within the tribe Amblycoptini, *Amblycoptus* is the only dimyloid genus. It is possibly a descendant from the early Turolian *Anourosorex*, known from e.g. Kohfidisch and Eichkogel (Bachmayer & Wilson, 1970; Rabeder, 1970). These fossil *Anourosorex* species still have an M₃; like *Amblycoptus* they have three upper antemolars. Recent Asian *Anourosorex* species have only two upper antemolars and thus appear to constitute a different branch within the tribe.

Amblycoptus is known from the late Turolian of Polgárdi (*A. oligodon* Kormos, 1926, see e.g. Jánossy, 1972) and from the Ruscinian (*A. topali* Jánossy, 1972). A presumably intermediate form has been described from the late Turolian of Kavurca in Turkey by Engesser, 1980 (as *Amblycoptus* nov. sp.).

It is difficult to establish the date of extinction of *Amblycoptus*. The material from Zamkowa Dolna, layer C is of unknown age. The main faunule of Zamkowa Dolna is of Villányian age (Rzebik-Kowalska, 1975, 'Middle Villafranchian'), but layer C is probably older and may well be of Ruscinian age (see Sulimski et al., 1979). The age of the single tooth from Osztramos 7 may range from middle Ruscinian to early Villányian.

Tribe Allosoricini Fejfar, 1966

Genus *Paenelimnoecus* Baudelot, 1972

Type species — *P. crouzeli* Baudelot, 1972.

Remarks — There is considerable confusion concerning the taxonomy of this genus.

In 1864, Petényi described a small shrew from Beremend as *Sorex gracilis*. The type material has since been lost. Judging from Petényi's illustration, *S. gracilis* is indeed a true *Sorex*: the horizontal ramus is long and provided with a clearly concave lower margin. *Sorex gracilis* is here considered to be a synonym of *Sorex minutus*.

In 1934, Kormos described a little shrew from Beremend as *Pachyura pannonica* n. sp. The generic attribution to *Pachyura* (a synonym of *Suncus* Ehrenberg, 1832 which belongs to the Crocidurinae) is based on the reported lack of pigmentation in Kormos' type specimens, and on the reduced, single-topped talonid in M₃. In case a new genus-name should be required, Kormos suggested the name *Allopachyura*. However, he did not formally coin the name nor did he give an adequate diagnosis of the genus. Therefore, *Allopachyura* Kormos, 1934 is considered to be a nomen nudum.

In 1956, Kretzoi created a new genus, *Petenyiella*, with the following diagnosis: '*Sorex minutus* an Grösse gleichkommende rotzähnige Spitzmausform, mit höheren, spitzeren Zähnen' (Red-toothed shrew, similar in size to *S. minutus*, with higher, more pointed teeth). *Petenyiella* is based on the type species *Sorex gracilis* Petényi. Therefore,

as *S. gracilis* is a synonym of *S. minutus*, *Petenyiella* must be considered to be a synonym of *Sorex* L., 1758.

In 1959, Kretzoi (1959a, 1962) erroneously united the two different species, *Sorex gracilis* and *Pachyura pannonica*, in his *Petenyiella gracilis*. Kretzoi rightly noted that *Pachyura pannonica* was not a representative of the Crocidurinae and that it could therefore not be called *Suncus* (= *Pachyura*). He also noted that the upper incisor was not fissident, that the dentition was pigmented a light yellow, and that there were four upper antemolars.

Repenning (1967, pp. 46-47), who accepted Kretzoi's erroneous unification, furthermore assumed the presence of entoconid crests, on the basis of an interpretation of a passage by Sulimski (1959) that the M_1 resembled *Suncus*.

In 1972, Baudelot, apparently unaware of these literature data, described a new genus of shrew as *Paenelimnoecus*, with the following (translated) diagnosis: 'Limnoecinae, characterized by the loss of the entoconid in the molars and by its small size; in M_1 the buccal re-entrant valley opens well above the cingulum and the metaconid is very close to the protoconid; the talonid of M_3 is reduced to a sharp crest and retains a feeble remnant of a lingually open basin; the teeth are pigmented'.

This new genus does not belong to the subfamily Limnoecinae, which, as is shown by Engesser, 1979, is restricted to North America. But apart from this, the diagnosis of *Paenelimnoecus* applies extremely well to the material so far called *Petenyiella gracilis* or *Suncus pannonicus*.

A comparison of the illustrations in Baudelot (1972, fig. 36), Engesser (1979, fig. 6) and also in Engesser (1980, fig. 74) with our material (Pl. 36, 37) reveals the many similarities.

Concluding, since *Petenyiella* is a synonym of *Sorex*, since *Suncus* is something different (a Crocidurinae), since *Pachyura* is a synonym of *Suncus*, and since *Allopachyura* is a nomen nudum, our material is now referred to the genus *Paenelimnoecus* Baudelot, 1972.

Paenelimnoecus is here placed in the newly formed tribe Allosoricini Fejfar, 1966.

Paenelimnoecus pannonicus (Kormos, 1934)

Pl. 36, figs. 4-11; Pl. 37.

Type locality — Beremend (1?, 4?).

Studied localities — Osztramos 9, 7, Csarnóta 2.

Other localities — Węże 1 (Poland, Sulimski, 1959, 1962; Sulimski et al., 1979); Podlesice (Poland, Kowalski, 1956); Mała Cave (Poland, Sulimski et al., 1979); Betfia 13 (Rumania, Terzea, 1973; Terzea & Jurcsák, 1976).

Stratigraphic range — Early Ruscianian - early Villányian (MN 14-16).

Original reference — *Pachyura pannonica*, in: Kormos, 1934, p. 306, not: *Sorex gracilis*, in: Petényi, 1864, p. 70-72.

Synonymy:

Pachyura pannonica n. sp., in: Kormos, 1934, p. 306.

(? *Allopachyura* n. gen.), in: Kormos, 1934, p. 306.

Pachyura hungarica Korm., in: Kormos, 1937a, p. 320.

Pachyura hungarica Korm., in: Kormos, 1937b, p. 1088.

Pachyura pannonica Kormos, in: Friant, 1947, p. 259.

Pachyura pannonica Korm., in: Kretzoi, 1956, pp. 39, 162.

Suncus cf. pannonicus (Kormos, 1934), in: Kowalski, 1956, p. 354.

Petényiella gracilis (Petényi), in: Kretzoi, 1959a, pp. 239, 245.

Suncus pannonicus (Kormos, 1934), in: Sulimski, 1959, p. 157. ¹⁾

Suncus zelceus n. sp., in: Sulimski, 1959, p. 158. ¹⁾

Petényiella gracilis (Petényi), in: Kretzoi, 1962, pp. 306, 353.

Petényiella gracilis (Petényi, 1864), in: Sulimski, 1962, p. 479. ¹⁾

Petenyiella zelcea (Sulimski, 1959), in: Sulimski, 1962, p. 480.

Petenyiella gracilis, in: Repenning, 1967, p. 46.

Petenyiella zelcea, in: Repenning, 1967, p. 46. ¹⁾

Petenyiella gracilis (Petényi), in: Gureev, 1971, p. 193.

Petényiella gracilis (Petényi), in: Jánossy, 1973a, p. 102.

Petenyiella gracilis (Petényi), in: Terzea, 1973, p. 2.

Petenyiella gracilis (Petényi), in: Terzea & Jurcsák, 1976, p. 175.

Petényiella cf. gracilis (Petényi), in: Jánossy & Kordos, 1977, p. 47.

Petenyiella cf. gracilis (Petényi), in: Jánossy, 1978, p. 69.

Petenyiella gracilis (Petényi, 1864), in: Sulimski et al., 1979, p. 385.

non: *Sorex gracilis*, in: Petényi, 1864, p. 70-72.

nec: *Sorex gracilis* Petényi, in: Kretzoi, 1956, pp. 37, 160.

nec: *Petényiella* n.g., in: Kretzoi, 1956, pp. 37, 160.

¹⁾ Tentatively included (see below).

Available material

Osztramos 9: 3 I sup., 3 I inf., 2 P₄, 4 M₁, 3 M₂, 2 M₃, 2 condyles.

Osztramos 7: 1 P⁴, 3 M¹, 3M², 1 I inf., 3 M₁, 4 M₂, 4 M₃, 2 condyles.

Csarnóta 2: 16 I sup., 2 AA sup., 9 P⁴, 25 M¹, 17 M², 1 M³, 18 I inf., 1 A₁, 1 P₄, 35 M₁, 61 M₂, 28 M₃, 169 condyles.

Measurements — see Tables 51-53.

Description — The dental elements are weakly stained a light orange.

I sup. — Not fissident, small. A narrow but well-developed cingulum is present along the buccal posterior border; this border is convex without undulations. The talon has a central groove on its occlusal surface.

AA sup. — Presumably four are present (see Kretzoi, 1962); in our material only A¹ and A² are preserved (Pl. 36, fig. 5). The central cusp is bordered lingually by a deep and wide groove; the lingual cingulum has developed into a high ridge. The buccal cingulum is weakly developed.

P⁴ — Broad, with a trapezoidal rather than a triangular outline when seen from the occlusal side. The protocone is placed far lingually at quite a distance from the parastyle. All cusps except the paracone are weak; there is no hypocone on the ridge bordering the hypoconal flange. This flange is low and flat.

M¹ and M² — The upper molars are quite broad and short. The paracone is lower than the metacone, particularly in M¹. The trigon basin is not closed off by a metaloph but is open posteriorly. The hypocone is not developed as a cusp; the hypoconal flange is

Plate 37

Paenelimnoecus pannonicus (Kormos, 1934)

1. Left ramus with I inf. and M₁-M₃, Osz9; a: lingual view; b: buccal view; c: caudal view of condyle.

2. Detail of fig. 1, the M₁, showing absence of entoconid; a: lingual view; b: occlusal view.

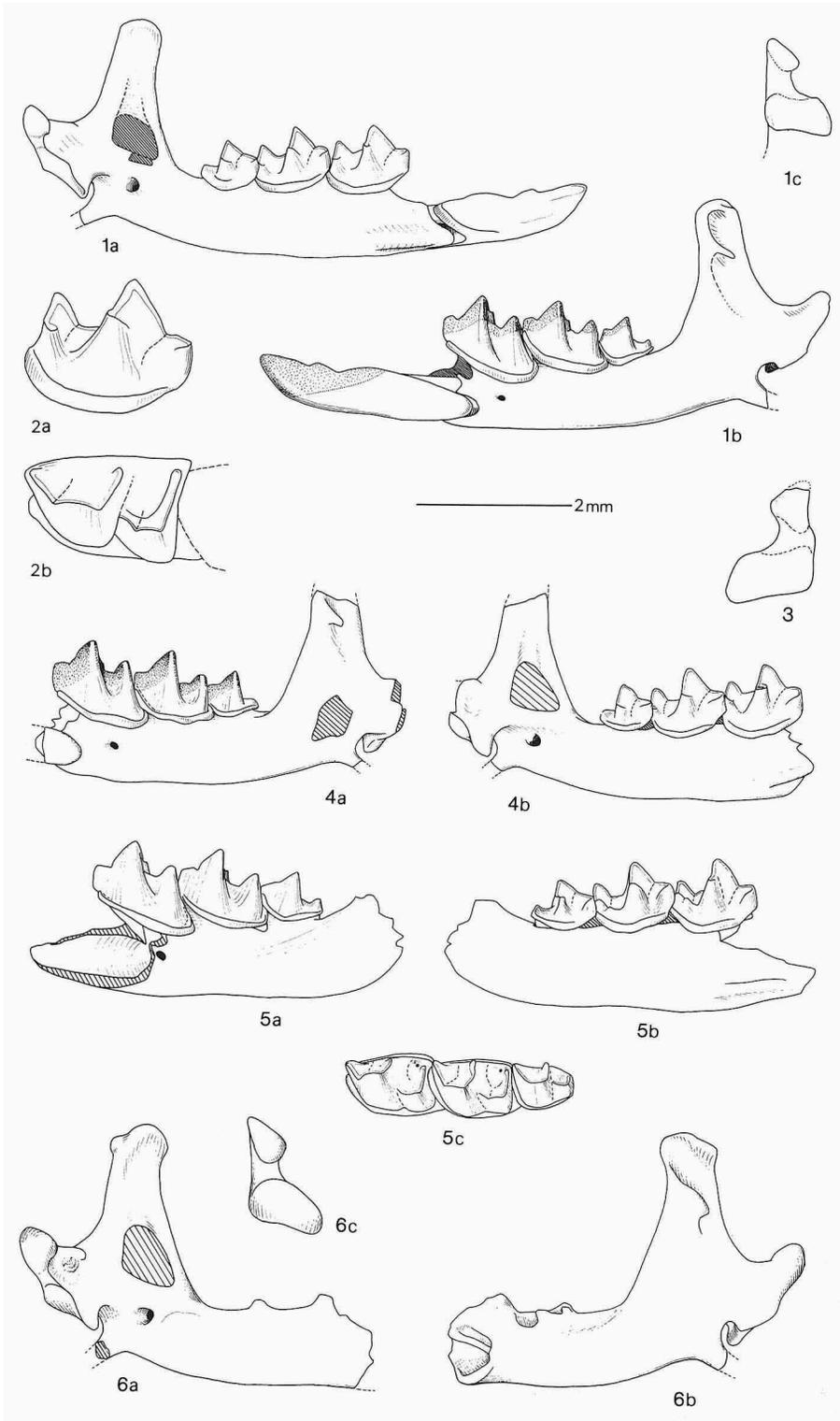
3. Right condyle, Osz7, caudal view.

4. Left ramus with M₁-M₃, Osz7; a: buccal view; b: lingual view.

5. Left ramus with M₁-M₃, Cs2/9, note the rudimentary entoconids; a: buccal view; b: lingual view; c: occlusal view.

6. Left ramus, Cs2/2; a: internal view; b: external view; c: caudal view of condyle.

Plate 37



flat and low and protrudes far backwards, giving rise to a strong posterior emargination (see Table 54 and Fig. 18). Underneath the protocone there may be a narrow cingulum.

M^3 — There is only one M^3 preserved in the studied collections (Pl. 36, fig. 7); it is small and has a well-developed paracone, but hardly any protocone.

I inf. — The lower incisor is weakly bicuspluate, but monocuspluate and tricuspluate specimens also occur (see Pl. 36, figs. 9-11). As a rule, there is no buccal cingulum. I inf. extends backwards on the buccal side of the mandible to underneath the protocone of M_1 .

A_1 — The A_1 is extremely small and for half its length wedged in between I inf. and P_4 .

P_4 — The postero-lingual basin is weak; cingula are present on both the buccal and the lingual side, but they are weak too.

M_1 and M_2 — These two elements are very characteristic in the near or complete absence of both the entoconid and the entoconid crest. The entoconid can still be seen as a vestigial rudiment in some specimens (Pl. 37, fig. 5) but as a rule it is lacking. Instead, the entostylid takes the shape of a cusp. The lingual border of the molars shows a strong convexity ('boat-shape'). The buccal re-entrant valley opens at some distance above the cingulum. When seen from the buccal side, the posterior end of M_1 extends backwards underneath the M_2 ; hence the back of the hypoconid of M_2 is somewhat concave. The metaconid and the protoconid are close together, particularly in M_1 , causing the parolophid to be almost parallel to the longitudinal axis of the jaw, resembling to some degree the carnassial blade in carnivores.

M_3 — The talonid of M_3 is reduced to a single, comma-shaped cusp. All lower molars have well-developed buccal cingula and weak lingual ones.

Mandible — The ascending ramus is relatively small. The coronoid process is high and narrow; the lower half of the anterior margin, which rises from the horizontal ramus far behind M_3 , leans slightly backwards. The upper half is at right angles to the horizontal ramus. The coronoid spicule is large, oblique and placed rather far ventrally, i.e. half-way between the tip of the coronoid and the upper sigmoid notch. The external temporal fossa goes down ventrally to a level half-way down the condyle. At the medial side, the internal temporal fossa goes up to the level of the upper sigmoid notch; above this level a shallow groove may run to the apex of the coronoid process. The pterygoid fossa is deeply excavated. The upper facet of the condyle is of triangular shape, its upper edge being placed at an angle of about 30° to the lower facet. The lower, which is entirely visible when seen from the buccal side, is provided with either a convex or a concave upper edge. Its lingual corner protrudes to a considerable extent. A lingual offset of the lower facet (as in Soriculini) is not present. The interarticular area is slightly narrower than the length of the upper facet; it runs to the dorso-medial corner of the lower facet. The foramen mentale is situated between the buccal re-entrant valley or the hypoconid of M_1 .

Remarks — Three species are known: *Paenelimnoecus pannonicus* (Kormos, 1934) from the early Ruscinian to the early Villányian (MN 14-16), *P. repenningi* (Bachmacher & Wilson, 1970) from the early Turolian of Kohfidisch (MN 11) and *P. crouzeli* Baudelot, 1972 from the Aragonian of Sansan (MN 6) and Eskihisar in Turkey (MN 8, see Engesser, 1980: *Paenelimnoecus* sp.). So far, no representatives are known from the Vallesian (MN 9-10).

The three species are very similar in size and molar morphology. The lengths of the molars as given by Baudelot, 1972 ($LM_1=0.85$ mm, $LM_2=0.83$ mm, $LM_3=0.75$ mm) are

not understood. Engesser (1980) also measured *P. crouzeli* material from Sansan, and found $LM_1=1.04-1.06$ mm, $LM_2=1.00-1.12$ mm and $LM_3=0.80$ mm. The only *P. crouzeli* specimen in the Utrecht collection measures $LM_1=1.12$ mm, $LM_2=1.13$ mm and $LM_3=0.86$ mm. Therefore, it is assumed that Baudelot's measurements are based on different parameters (length at the buccal side?) and can not be used for comparison. The measurements of *P. crouzeli* are not significantly different from those of *P. pannonicus*.

Differences can be found in the development of the lower incisor (in *P. crouzeli* it does not reach M_1 , in *P. pannonicus* it ends below the protoconid of M_1) and in the position of the mental foramen (in *P. crouzeli* below the protoconid of M_1 , in *P. pannonicus* below the re-entrant valley or the hypoconid).

Petenyiella repenningi from Kohfidisch, Austria (Bachmayer & Wilson, 1970) also belongs to *Paenelimnoecus*. It is also recorded from Mala Cave as *Petenyiella* aff. *repenningi* (Sulimski et al., 1979). It is doubtful whether the Mala material belongs to *Paenelimnoecus*, since Sulimski et al. (1979, fig. 4.2) indicate an entoconid crest in M_2 and a slender, *Sorex*-like condyle. Therefore, it cannot be ruled out that *Petenyiella* aff. *repenningi* from Mala is in reality *Sorex minutus*, known from the contemporaneous fauna of Osztramos 1 also.

Paenelimnoecus repenningi seems to be closer to *P. crouzeli* in morphology than to *P. pannonicus*, but as both *repenningi* and *crouzeli* have not been studied by the present author, no definite statement can be made about their status.

Sulimski et al. (1979) included *Petenyiella gracilis* and *Petenyiella zelcea* from Weże 1 (Sulimski, 1962), originally described as *Suncus pannonicus* and *S. zelceus* nov. sp., respectively, by Sulimski (1959) within *Petenyiella gracilis*. The condyle of Sulimski's *Suncus pannonicus* (Sulimski, 1959, pl. 4, fig. 2b) possibly shows the characteristic triangular upper facet of *Paenelimnoecus pannonicus*, but his *Suncus zelceus* does not show this feature according to the illustrations. Based on the strange tilted position of the condyle in Sulimski's pictures (1959, pl. 3, fig. 1a; pl. 4, fig. 2a) of *S. pannonicus*, Repenning (1967) suggested that Sulimski had two different genera, and that Sulimski referred the wrong one to *pannonicus* (= *Petenyiella gracilis*). It is difficult for us to decide whether the Weże specimens represent two genera, two species or only one species, because Sulimski's illustrations are rather small and indistinct. *Petenyiella gracilis* and *P. zelcea* from Weże 1 are here tentatively included in the synonymy of *Paenelimnoecus pannonicus* (see list above).

From the Austrian Eichkogel fauna two species are mentioned: *Petenyiella* cf. *pannonica* (Kormos) and *Petenyiella* sp. (Rabeder, 1970). Since the Eichkogel material is neither illustrated nor adequately described, nothing can be said about the generic or specific attribution.

As suggested above, the *Paenelimnoecus* material from Eskihisar in Turkey (Engesser, 1980) is so similar to *P. crouzeli* from Sansan that it may well belong to this species.

Soricinae gen. et sp. indet. 1
Pl. 8, fig. 8.

Locality — Osztramos 7.

Available material — 1 M_2 in a mandibular fragment.

Measurements — M_2 : TRW=9.3, TAW=9.2, L=16.0.

Description — The entoconid crest is low, the valley between the entoconid and the hypolophid is however closed off by a high wall. The buccal cingulum is well developed; there is no lingual cingulum.

Soricinae gen. et sp. indet. 2
Pl. 24, fig. 7.

Locality — Csarnóta 2 (Cs2/20).

Available material — 1 M¹.

Measurements — M¹: PE=9.7, LL=12.6, BL=12.2, AW=13.0, PW=14.2; PE-index: 0.28.

Description — The hypocone is more lingually placed than the protocone. There is no metaloph. A small cingulum is present below the protocone.

Remark — Morphologically, this tooth closely resembles some specimens of *Episoriculus gibberodon*, particularly the morphotype B material from Osztramos 7. However, it is much smaller.

Soricinae gen. et sp. indet. 3
Pl. 24, fig. 8.

Locality — Osztramos 7.

Available material — 1 M².

Measurements — M²: PE=8.9, BL=11.8, AW=14.2, PW=12.8.

Description — The hypoconal flange is partly missing, but it must have been small and low. The hypocone is weakly developed; a metaloph is present.

Soricidae gen. et sp. indet.
Pl. 24, fig. 9.

An interesting anomaly is worth noting: from Csarnóta 2/22 we have a maxillary fragment with an antemolar that seems divided into a still single, but two-cusped and two-rooted element. A similar phenomenon has been observed by Vesmanis & Vesmanis (1980) in a skull of a recent *Crocidura russula*. In their case, A² is split into a double-crowned, but single-rooted element in the right maxilla; A² is divided into two separate elements in the left maxilla. The right double-crowned A² shows remarkable resemblance to our specimen.

THE PE-INDEX

The degree of emargination of the posterior edge of the P⁴ and M¹ and M² is an important

character in the description of Soricidae. Some taxa are characterized by no emargination, some by a very slight emargination and others by a strong emargination. For example, no, or a very slight emargination can be seen in the subfamily Heterosoricinae (see Engesser, 1975), or in the genus *Petenya*.

It has always been a problem for authors to describe the degree of emargination adequately. This can be illustrated by the following random selection of terms: moderate, extreme, slight, no, very slight, strong, somewhat greater (all from Repenning, 1967); less excavated (Reumer, 1980); less pronounced (Reumer, 1979); more pronounced (van der Meulen, 1973); schwach, normal, stark (all from Rabeder, 1972b); sehr stark konkav, geringfügig konkav (both from Engesser, 1980). It is therefore necessary to adequately quantify the degree of posterior emargination by establishing the relative 'depth' of the emargination. This is done for M^1 and M^2 by means of the formula:

$\frac{LL + BL}{2 \cdot PE} - 1$, in which formula LL is the lingual length, BL the buccal length and PE

the shortest distance from the orientation line to the posterior emargination (see Fig. 4c and the Introductory part). If no emargination is present, the value of the index will be 0; if the teeth are emarginated to half-way along the crown, the index will be 1.

The results of the calculations are given in Table 54 and in Fig. 18. In both the table and the text-figure the index is given for each individual species from each locality; altogether there are 43 samples of M^1 and 35 of M^2 . In Fig. 18 the genera are indicated by brackets.

In general, it can be concluded that the mean values are rather constant for each genus, with ranges that hardly ever exceed 0.10 of the scale. It appears that the degree of emargination is a fairly constant factor within genera. An exception is *Episorculus gibberodon*, in which a large array of mean values occurs, coinciding with the observed large morphological variation in this species. The values for the two morphotypes (A and B) in Osztramos 7 are far apart; the ranges of the values do not overlap (nos. 20 and 21 in Table 54 and Fig. 18). On the other hand, the values for *Petenya* (nos. 1-7) show a very restricted variation.

Establishing of the value of the PE-index can contribute to the determination of fossil Soricidae, particularly when it is used in combination with other morphological characters. For example, isolated upper molars of *Sorex minutus* and *Paenelimnoecus pannonicus* are sometimes difficult to separate. The PE-index may then be used to identify the species; in *P. pannonicus* it is higher than in *S. minutus*, with some overlap of values in the M^1 , but hardly any in the M^2 .

In order to qualify the values verbally, the following terms are suggested: slight (0-0.15 in M^1), moderate (0.16-0.30 in M^1) and strong (values above 0.30 in M^1). In M^2 the corresponding values are roughly 0-0.13, 0.14-0.25 and above 0.25, respectively.

TAXONOMICAL CONCLUSIONS

The following taxa have been described in the present study:

Subfamily Crocidurinae Milne-Edwards, 1874

Crocidura kornfeldi Kormos, 1934, from Vi3 and Osz3

Subfamily Soricinae Fischer von Waldheim, 1817

Tribe Soricini Fischer von Waldheim, 1817

Sorex minutus L., 1766, from Osz7, Cs2, Vi3, Te, and Osz3

Sorex bor sp. nov., from Osz1, Osz9 and Osz7

Sorex sp., from Osz7 and Cs2

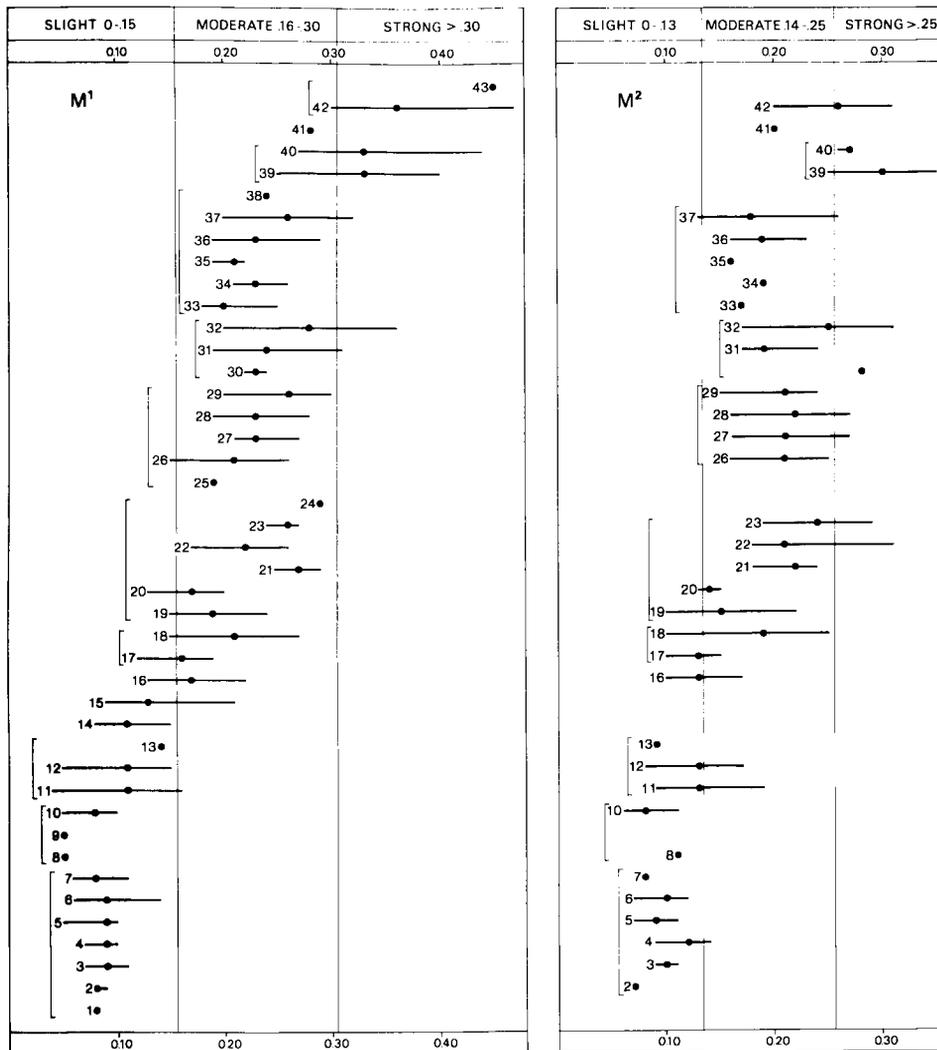


Fig. 18. Visualization of the results of the PE-index, as given in Table 54.

Drepanosorex praeearaneus (Kormos, 1934) ¹⁾, from Te, Vi3 and Osz3

Deinsdorfia janossyi sp. nov., from Osz9

Deinsdorfia hibbardi (Sulimski, 1962) ¹⁾, from Osz7

Deinsdorfia kordosi sp. nov., from Cs2

Petenya hungarica Kormos, 1934, from Osz1, Osz7, Cs2, Vi3, Te, and Osz3

Petenya aff. *hungarica* Kormos, 1934, from Osz9

Blarinella dubia (Bachmayer & Wilson) ¹⁾, from Osz9

Blarinella europaea sp. nov., from Osz1, Osz7 and Cs2

Zelceina soriculoides (Sulimski, 1959), from Cs2

Soricini indet., from Osz1

Tribe Blarinini Kretzoi, 1965

Mafia csarnotensis gen. et sp. nov., from Cs2

Blarinoides mariae Sulimski, 1959, from Osz9, Osz7 and Cs2

Sulimskia kretzoi (Sulimski, 1962) ¹⁾ from Osz7

Tribe Soriculini Kretzoi, 1965

Episorculus gibberodon (Petényi, 1864), from Osz9, Osz13, Osz1, Osz7, Cs2, and Vi3

Soriculini gen. et sp. indet., from Osz9

Tribe Beremendiini Gureev, 1971

Beremendia minor Rzebik-Kowalska, 1976, from Osz1 and Osz7

Beremendina fissidens (Petényi, 1864), from Osz1, Osz7, Cs2, Te, Vi3, and Osz3

Tribe Amblycoptini Kormos, 1926

Amblycoptus topali Jánosy, 1972, from Osz1

Amblycoptus sp., from Osz7

Tribe Allosoricini Fejfar, 1966

Paenelimnoecus pannonicus (Kormos, 1934)¹⁾, from Osz9, Osz7 and Cs2

¹⁾ New combinations.

A few names are not used any more:

Sorex praeearaneus Kormos, 1934 (now *Drepanosorex praeearaneus*)

Sorex hibbardi Sulimski, 1962 (now *Deinsdorfia hibbardi*)

Deinsdorfia franconica Heller, 1963 (syn. of *D. hibbardi*)

Petenya neglecta Kretzoi, 1943 (syn. of *P. hungarica*)

Petenya stehlini Kretzoi, 1943 (referred to *Sorex*)

Petenya suavensis Pasa, 1948 (syn. of *Sorex minutus*)

Petenya dubia Bachmayer & Wilson, 1970 (now *Blarinella dubia*)

Sorex kretzoi Sulimski, 1962 (now *Sulimskia kretzoi*)

Sorex dehneli Kowalski, 1956 (now *Mafia dehneli*)

Episoriculus borsodensis Jánosy, 1973 (syn. of *E. gibberodon*)

Episoriculus tornensis Jánosy, 1973 (syn. of *E. gibberodon*)

Petenyiella repenningi Bachmayer & Wilson, 1970 (now *Paenelimnoecus repenningi*)

Sorex gracilis Petényi, 1864 (syn. of *Sorex minutus*)

Petenyiella gracilis (Petényi, 1864) (now *Paenelimnoecus pannonicus*)

Petenyiella zelcea (Sulimski, 1959) (syn. of *Paenelimnoecus pannonicus*)

Concluding part

PALAEOECOLOGY

For the reconstruction of the palaeoenvironment of a taxon (or a fauna) several different approaches can be used.

The actualistic approach — Often taxa found in fossil faunas are either still living or have closely related extant forms. The present ecological requirements are extrapolated to the fossil relatives. Of course this can only be done if the fossil and the extant taxa are both morphologically very similar and systematically closely related.

This procedure can be used on all systematic levels: species (e.g. *Sorex minutus*), genus (e.g. *Crocidura*) or higher groups (e.g. Soriculini), see below. The result is a palaeoecological indication, i.e. a taxon that can be considered indicative for a certain type of environment.

The morphological approach — In some cases a specific way of living is expressed in very typical morphological traits. A good example is the so-called exoedaenodonty of the dentition, which is an adaptation for a malacophagous diet. It can be observed in such different animals as some fish, certain lizards and mammals.

Amongst the Soricidae, a more or less exoedaenodont dentition is found in the genera *Drepanosorex*, *Macroneomys*, *Amblycoptus*, *Anourosorex*, *Dimylosorex*, and *Deinsdorfia* (Kormos, 1926, 1935; Rabeder, 1972; Fejfar, 1966b).

Since terrestrial molluscs are only active under humid circumstances (e.g. after a shower or in the little layer) and as shrews need to feed constantly, it can be deduced that

exoedaenodont shrews indicate a moist environment such as deciduous forest, a marshy area or even open water. This approach also leads to indications.

The faunistic approach — Most of the fossil samples contain many taxa; these include not only shrews, but also rodents, carnivores, herbivores, etc., in addition to non-mammalian vertebrates and invertebrates. All together they can provide a detailed picture of the palaeoenvironment at the time of deposition. For example, the presence of Castoridae and Desmaninae in Tegelen indicates an environment with open water. This is confirmed by the many remains of fish and fresh-water molluscs and of aquatic plants (Schreuder, 1939, 1940, 1945; Gaudant, 1979; van der Hammen, 1951; Zagwijn, 1963; Freudental et al., 1976; Rümke, in prep.).

By the means it is possible to check the value of indications established by means of the two former approaches.

The facies approach — Differences in the facies of the sediments may represent differences in environment. The difference between the contemporaneous localities of Tegelen (a fluvialite lignitic clay) and Villány 3 (a karstic terra rossa) is a reflection of the different environments: moist and forested, with a rather oceanic climate in Tegelen, versus dry and open, with a more continental climate in Villány 3. This approach can also serve as a check on the indications arrived at along other lines of reasoning.

Turning to the Soricidae and our localities, the following picture can be reconstructed.

Of the many taxa studied, only a few are still living or have closely related living species.

Sorex minutus is the only species that is still living; it has a preference for wooded and bushy areas, where it spends part of the time burrowing and part on the surface. Other species of the genus *Sorex* may even spend relatively more time burrowing (Croin Michielsen, 1966). This implies that the humidity cannot be extremely low or high: for shrews tunnelling activities are difficult or impossible in extremely dry or very wet soils (Croin Michielsen, 1966). We therefore assume that fossil *Sorex* is indicative for a moist environment with well-developed (woody) vegetation and a rather loose soil.

Crocidura is at present widespread with a long range of habitats, mainly in Africa. However, if we only take the European forms into consideration, the following picture emerges. *Crocidura* is restricted to latitudes below c. 53° (van den Brink, 1978) and hence apparently avoids low temperatures. *Crocidura* prefers dry terrains, more or less open, such as gardens, dry meadows, forest edges, rocky land, and maquis.

Blarinella is still living in a restricted area of mountains and highlands in Asia (Walker, 1964), which is a relict situation. Not much is known of its habits, but the animals have been recorded tunnelling through the uppermost layer in woods, much like *Sorex*.

Amblycoptus has a living relative, viz. *Anourosorex squamipes* from Southeast Asia. It lives in forests, where it leads a burrowing life, to which it is highly adapted (reduced eyes, concealed ears; Walker, 1964). As the morphological resemblance between *Anourosorex* and *Amblycoptus* is quite striking (e.g. the presence of a sagittal crest on the skull and the exoedaenodont dentition), it can be assumed that *Amblycoptus* also led a fossorial life in forested areas. The tunnelling activities indicate a not too dry environment with loose soil, as already stated for *Sorex*.

A living, but far relative of *Blarinoides mariae* is the North American shorttail shrew, *Blarina brevicauda*. *Blarina* is a typical opportunist: it lives in forests, grasslands, marshes and brushy areas and it is not restricted to any habitat (Burt & Grossenheimer,

1964). Sulimski (1962) suggested a 'supra-aquatic' life for *Blarinoides mariae*, like that of *Neomys*, based on the apparently mistaken assumption that *Blarina brevicauda* 'leads a similar mode of life'. As will be shown below, *Blarinoides* seems to avoid wet situations, but otherwise it is an opportunist.

Episoriculus, and the tribe Soriculini in general, lead a largely aquatic life or they prefer damp forest (Walker, 1964). Hence, although extinct, the species *E. gibberodon* is here assumed to be indicative for a rather moist or even wet environment, with a good covering of woody vegetation.

So far, these considerations have been based on the actualistic approach. From a morphological point of view something can be said about *Drepanosorex* and – to a lesser degree – *Deinsdorfia*. *Drepanosorex*, with its exoedaenodont anterior dentition is supposed to have lived on a diet consisting of molluscs (Kormos, 1935; Rabeder, 1972a). As has been explained above, *Drepanosorex* is thought to indicate a rather moist environment, perhaps even with open water.

The same line of reasoning could apply to *Deinsdorfia*, with more caution however, as the exoedaenodonty in this genus is less well developed.

Several taxa in the studied samples have no living close relatives, but still something can be said about their ecology from the comparison of fossils associations. They form a group of ecological opportunists, species which apparently do not have narrow preferences. They are found in almost every sample in reasonably high numbers, no matter whether the fauna can be characterized as 'dry' or 'wet': e.g. *Petenya hungarica* and *Beremendia fissidens*.

Summarizing, we arrive at four different groups:

- 1) a 'wet' group, indicating the presence of open water, with *Episoriculus* as an indicator, and perhaps also *Drepanosorex*;
- 2) a 'forest' group, indicating a humid environment with a good covering of vegetation; indicators are *Sorex* and *Amblycoptus* and perhaps *Blarinella*;
- 3) a 'steppe' group, indicating a rather dry and open terrain, *Crocidura* is an indicator;
- 4) an 'opportunist' group, consisting of genera that are ubiquitous: *Beremendia*, *Blarinoides* and *Petenya*.

INTERPRETATION OF OUR SORICID ASSOCIATIONS

We can now look at the composition of the soricid associations and try to draw some ecological conclusions. The number of dental elements (with two adjustments for the varying number of elements in the different taxa) is used to calculate the percentual composition of the faunas.

The number of elements in the lower jaw is invariable 6 (I inf., A₁, P₄, M₁, M₂, M₃); in the upper jaw the number may vary with the number of antemolars. Only the 5 constantly present elements (I sup., P⁴, M¹, M², M³) are used in the counts. The upper antemolars are not included; the number of elements used in the calculations therefore is: n-AA sup.

One of the studied genera (*Amblycoptus*) is dimylid, i.e. the M₃ and M³ are missing. The number of elements in the lower jaw is 5, in the upper jaw there are 4 elements (upper antemolars excluded). Therefore, the number of elements of *Amblycop-*

tus is multiplied by $\frac{6+5}{5+4} = \frac{11}{9}$, so that the counts can be compared with those for the other, non-dimylid, taxa.

In addition, the condylar processes have been counted (n_{cond}) and expressed in percentages.

The samples give the following picture .

Osztramos 9	n-AA sup.	%	n_{cond}	%
<i>Episoriculus gibberodon</i>	122	47.7	5	35.7
<i>Deinsdorfia janossyi</i>	48	18.8	2	14.3
<i>Petenya aff. hungarica</i>	23	9.0	—	—
<i>Sorex bor</i>	20	7.8	2	14.3
<i>Paenelimoecus pannonicus</i>	17	6.6	2	14.3
<i>Blarinella dubia</i>	17	6.6	1	7.1
<i>Blarinoides mariae</i>	7	2.7	2	14.3
Soriculini gen. et sp. indet	2	0.8	—	—

The fauna is strongly dominated by *Episoriculus gibberodon*, a 'wet' element. *Deinsdorfia janossyi* is not exoedaenodont, and might have had preferences like those of *Sorex*. *Sorex bor* and *Blarinella* are suggestive of a forested environment. The 'wet' and 'forest' groups constitute some 80% of the fauna, 12% are opportunists.

The accompanying faunal elements suggest a wooded environment. Amongst these are a flying squirrel (*Pteromys* sp.), several Gliridae (*Glirulus*, *Glis* and two *Muscardinus* species), a member of the Eomyidae, and an *Apodemus* (Jánossy, 1974). There are no Cricetidae, but two other rodents, *Prospalax* and *Meriones*, indicate open country. The presence of indeterminate fish, amphibians and a few Desmaninae suggests the presence of some open water.

Osztramos 1	n-AA sup.	%	n_{cond}	%
<i>Amblycoptus topali</i>	58 ¹⁾	30.7	7	53.9
Soricini gen. et sp. indet	45	19.5	1	7.7
<i>Episoriculus gibberodon</i>	40	17.3	2	15.4
<i>Sorex bor</i>	29	12.6	1	7.7
<i>Petenya hungarica</i>	25	10.8	—	—
<i>Beremendia minor</i>	13	5.6	—	—
<i>Blarinella europaea</i>	6	2.6	2	15.4
<i>Beremendia fissidens</i>	2	0.9	—	—

1) $\times 11/9 = 71$ used in calculation.

Osztramos 1 is dominated by supposedly forest-dwelling species: *Amblycoptus topali*, *Sorex bor* and a Soricini indet., which appears not too far removed from the *Sorex* stock. Over 60% of the teeth and the condyles belong to these taxa. The 'wet' *Episoriculus* is also present, while the rest of the fauna consists mainly of opportunists.

Most of the accompanying fauna is suggestive of a wooded biotope: flying squirrels, four genera of Gliridae, *Apodemus*, several Mustelidae, and a member of the Cercopithecidae (Jánossy & Kordos, 1977). Nevertheless, some forms are present that may indicate a somewhat more open environment; the most notable of these are ochotonids, *Sminthozapus*, *Prospalax* and *Kowalskia* (Cricetidae). Jánossy (1972) comes to the conclusion that the environment of Osztramos 1 'seems to have been of a mixed nature, with forests prevailing over the steppic vegetation' (Jánossy, 1972, p. 45).

For the contemporaneous fauna of Podlesice (Poland), Kowalski reconstructed the ecology as 'sylvian, while the climate was moderate, somewhat warmer than that of recent times' (Kowalski, 1956, p. 341). Though not very rich, the fauna from Mala in Poland shows a similar picture: forest, with some open area (see Sulimski et al., 1979).

Csarnóta 2 (total)	n-AA sup.	%	n _{cond}	%
<i>Episoriculus gibberodon</i>	928	38.4	274	39.6
<i>Blarinoides mariae</i>	443	18.4	55	8.0
<i>Beremendia fissidens</i>	344	14.3	47	6.8
<i>Paenelimnoecus pannonicus</i>	212	8.8	169	24.4
<i>Deinsdorfia kordosi</i>	171	7.1	42	6.1
<i>Zelceina soriculoides</i>	125	5.2	48	6.9
<i>Blarinella europaea</i>	72	3.0	17	2.5
<i>Sorex minutus</i>	43	1.8	12	1.7
<i>Mafia csarnotensis</i>	41	1.7	6	0.9
<i>Petenya hungarica</i>	29	1.2	21	3.0
<i>Sorex</i> sp.	5	0.2	1	0.1
Soricinae indet. 2	1	—	—	—

The most dominating element is *Episoriculus gibberodon*, followed by two opportunists, *Beremendia* and *Blarinoides*. Species of the 'forest' group are relatively scarce. Several other species, viz. *Paenelimnoecus pannonicus*, *Zelceina soriculoides* and *Mafia csarnotensis* cannot at first sight be referred to an ecological group.

As Csarnóta 2 has been sampled in separate layers, a more detailed picture of its palaeoenvironment can be reconstructed. Figs. 19 and 20 show the relative abundance of the species throughout the layers 0-25, for teeth and condyles, respectively.

The teeth diagram shows a clear negative correlation between *Episoriculus* and *Blarinoides*. Whereas *Episoriculus* shows an upward decreasing trend, *Blarinoides* shows a similar, though less distinct, upward increase. In the lower levels *Sorex* can be found (*S. minutus* and *S. sp.*); teeth of this genus are not found in the upper levels. *Mafia* is only present in the upper half of the section.

The condyle diagram is somewhat different, because here the negative correlation between *Episoriculus* and *Blarinoides* is not quite as clear. Instead, *Episoriculus* and *Paenelimnoecus* are negatively correlated. Here too, *Sorex* is more frequent in the lower levels than in the upper ones.

The difference between the two diagrams may be caused by the small size of the teeth of *Paenelimnoecus*, resulting in a lower frequency in the teeth diagram than in the condyle diagram, due to loss during the preparation and sieving of the material.

As in both diagrams *Episoriculus* decreases upwards, it can be concluded that the environmental conditions became drier. This is in agreement with the virtual absence of *Sorex* in the upper layers. As *Episoriculus* is a warmth-loving genus, these data are suggestive of both a drying and a cooling of the climate during the Csarnótian (MN 16A). It can furthermore be concluded that *Mafia* prefers a more open environment.

The rodent spectrum of part of Csarnóta 2, published by Kretzoi (1962) shows a change from a more wooded biotope to a more open steppe-like environment. This conclusion is based on the decrease of sylvan elements such as Gliridae, Petauristinae and low-crowned Muridae, the appearance of Cricetidae and of *Rhagapodemus* and an increase in Arvicolidae (Kretzoi, 1962, fig. 10, pp. 320, 363).

The transition from a wooded to an open biotope takes place in the central part of the section, viz. in layers 8-12. The fauna seems to represent the beginning of the cooler climate and more open terrain represented by localities such as Beremend 5 (Jánossy, 1979; Kretzoi, 1956) and Rębielice Królewskie (Kowalski, 1960) with faunas dominated by Arvicolidae and Lagomorpha.

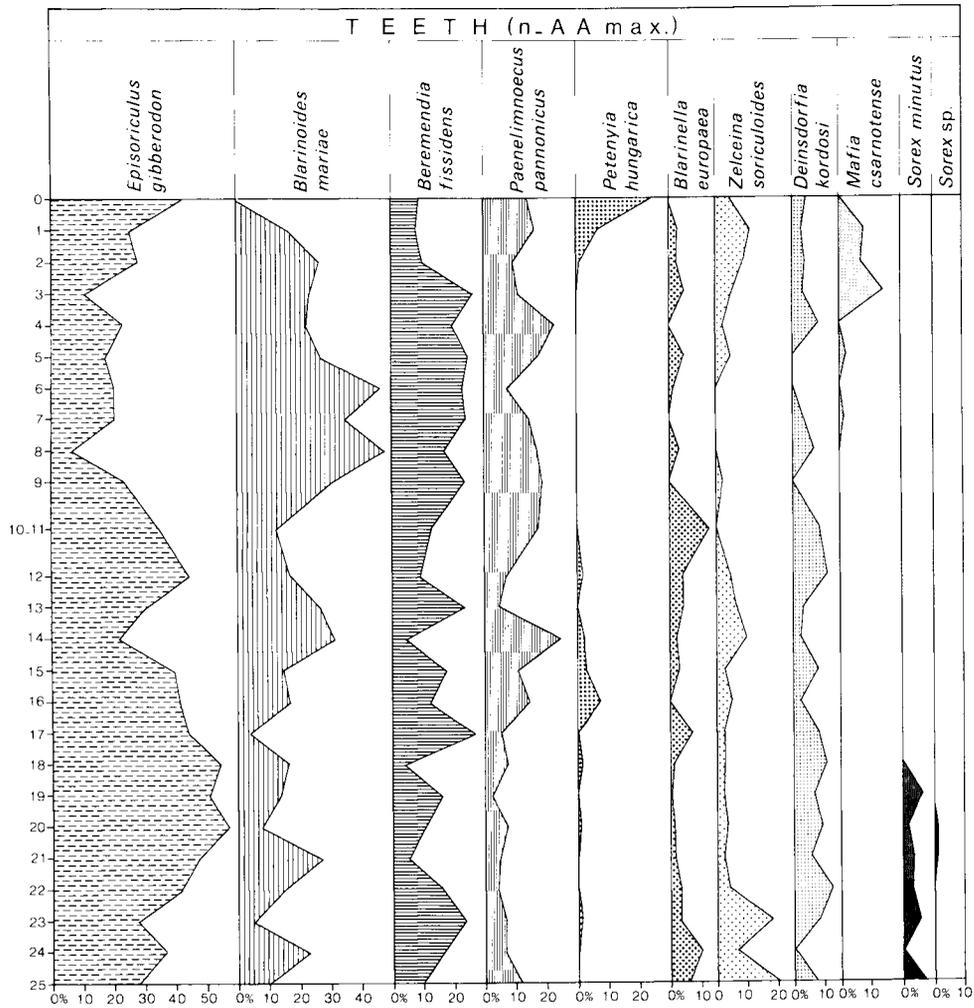


Fig. 19. Shrew spectrum of Csarnóta 2, based on the number of teeth (n-AA sup.).

Osztramos 7	n-AA	%	n _{cond}	%
<i>Blarinoides mariae</i>	390	23.6	22	21.6
<i>Beremendia fissidens</i>	370	22.4	16	15.7
<i>Deinsdorfia hibbardi</i>	338	20.5	19	18.6
<i>Petenyia hungarica</i>	267	16.2	28	27.5
<i>Episorculus gibberodon</i>	89	5.4	6	5.9
<i>Sorex minutus</i>	86	5.2	3	2.9
<i>Sorex bor</i>	30	1.8	4	3.9
<i>Sorex sp.</i>	29	1.8	1	1.0
<i>Paenelimnoecus pannonicus</i>	19	1.2	2	2.0
<i>Beremendia minor</i>	17	1.0	1	1.0
<i>Blarinella europaea</i>	8	0.5	—	—
<i>Sulimskia kretzoi</i>	5	0.3	—	—
<i>Amblycoptus sp.</i>	0(1)	0.1	—	—
Soricinae indet. 1	1	0.1	—	—
Soricinae indet. 3	1	0.1	—	—

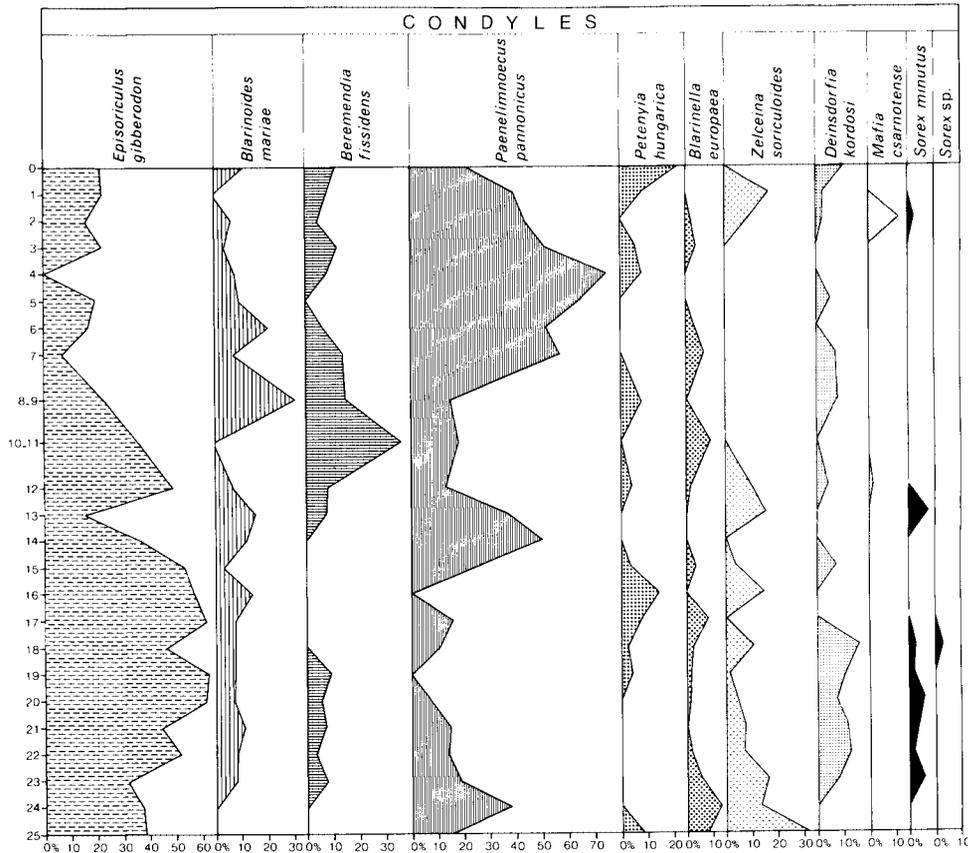


Fig. 20. Shrew spectrum of Csarnóta 2, based on the number of condyles.

Osztramos 7 has many species in common with Csarnóta 2, but their relative frequency is quite different. The fauna is strongly dominated by opportunists: *Blarinoides*, *Beremendia* and *Petenyia*. *Deisdorfia* is abundantly present. Species indicating a wet or moist and wooded biotope (*Episoriculus* and *Sorex*) are poorly represented. It can therefore be concluded that the general climatic picture of Osztramos 7 is somewhat drier and perhaps cooler than that of Csarnóta 2 (note the presence of *Lemmus!*).

The accompanying mammal fauna gives a mixed impression; sylvan elements (*Pliopetaurista*, *Pliopetes*, *Muscardinus*, *Apodemus*, Cervidae) are present as well as steppe indicators (*Hystrix*, *Cricetinus*, *Hypolagus*). It cannot be stated with certainty to what extent this may be due to the supposed long sedimentary history of Osztramos 7; it is quite possible that a change in environments, like that observed in Csarnóta 2, is represented in the Osz7 section as well.

A rather similar combination occurs in Weże (Sulimski, 1962). The most abundant genera of shrews in Weże are *Blarinoides*, *Beremendia*, *Zelceina*, and *Petenyia*. For this locality, Sulimski (1962) suggested a subtropical climate like that presently prevailing in Asia Minor and Northern Africa. We do not agree with this suggestion, as the warmth-loving *Episoriculus* is absent, and *Sorex* is more abundant than in Osztramos 7 or Csarnóta 2. Therefore, a moderate and somewhat forested environment seems more appropriate for Weże.

Villány 3	n-AA sup.	%	n _{cond}	%
<i>Crocidura kornfeldi</i>	158	70.2	21	67.8
<i>Beremendia fissidens</i>	41	18.2	4	12.9
<i>Petenya hungarica</i>	17	7.6	5	16.1
<i>Sorex minutus</i>	9	4.0	1	3.2
<i>Episoriculus gibberodon</i>	—	—	—	—
<i>Drepanosorex praeearaneus</i>	—	—	—	—

Villány 3 alsó	n-AA sup.	%	n _{cond}	%
<i>Crocidura kornfeldi</i>	122	65.6	21	65.6
<i>Beremendia fissidens</i>	35	18.8	4	12.5
<i>Petenya hungarica</i>	22	11.8	5	15.6
<i>Sorex minutus</i>	—	—	—	—
<i>Episoriculus gibberodon</i>	7	3.8	2	6.3
<i>Drepanosorex praeearaneus</i>	—	—	—	—

Villány 3 felső	n-AA sup.	%	n _{cond}	%
<i>Crocidura kornfeldi</i>	152	41.2	19	47.5
<i>Beremendia fissidens</i>	139	37.7	12	30.0
<i>Petenya hungarica</i>	56	15.2	5	12.5
<i>Sorex minutus</i>	6	1.7	—	—
<i>Episoriculus gibberodon</i>	14	3.7	3	7.5
<i>Drepanosorex praeearaneus</i>	2	0.6	1	2.5

Villány 3 total	n-AA sup.	%	n _{cond}	%
<i>Crocidura kornfeldi</i>	432	55.5	61	59.2
<i>Beremendia fissidens</i>	215	27.6	20	19.4
<i>Petenya hungarica</i>	95	12.2	15	14.6
<i>Sorex minutus</i>	15	1.9	1	1.0
<i>Episoriculus gibberodon</i>	21	2.8	5	4.9
<i>Drepanosorex praeearaneus</i>	2	0.3	1	1.0

Villány 3 is dominated entirely by shrews from the 'steppe' and from the 'opportunist' groups (over 90% in all samples). Animals from the 'wet' and 'forest' groups are present, but in very low frequencies. The accompanying fauna is suggestive of a steppe-like environment: *Citellus*, numerous Arvicolidae, *Hystrix*, Lagomorpha, and several Bovidae, although some wet or sylvan elements are present (*Glis*, Cervidae, *Desmana*) (Jánossy, 1979).

Other Villányian localities from the southern part of Hungary show a remarkably similar picture. The soricid fauna from Villány 5 (slightly younger than Villány 3) is strongly dominated by *Crocidura kornfeldi*, even more so than in Villány 3. Other dominant faunal elements in Villány 5 are (apart from snakes) *Rhinocricetus*, *Mimomys* and *Citellus* (Jánossy, 1979; Kretzoi, 1956).

Tegelen	n-AA sup.	%	n _{cond}	%
<i>Drepanosorex praeearaneus</i>	247	55.6	15	55.6
<i>Sorex minutus</i>	79	17.8	5	18.5
<i>Petenya hungarica</i>	64	14.4	3	11.1
<i>Beremendia fissidens</i>	54	12.2	4	14.8

The fauna of Kisláng, which is void of Soricidae, is dominated by steppe-dwellers (ostriches, horses and even a camel); there are some open water animals (*Castor*, *Trogontherium*), but sylvan elements are virtually absent.

The most abundant species in Tegelen, *Drepanosorex praeareneus*, is supposed to indicate a rather wet environment, because of its snail-eating habits. Meijer (in: Freudenthal et al., 1976) described 57 species of terrestrial and fresh-water molluscs, many of which could have formed part of the shrew's diet. *Sorex minutus* suggests the presence of woody covering. The two other species are opportunists. The assemblage shows remarkable resemblance to the one from Osztramos 3/2; the frequencies are different, due to a somewhat moister situation in Tegelen. This is reflected also in facies differences (a karstic terra rossa in Osz3/2 versus a fluvial clay in Tegelen).

The accompanying fauna (Bernsen, 1930-1934; Schreuder, 1945; Kortenbout van der Sluijs & Zagwijn, 1962; Freudenthal et al., 1976; Gaudant, 1979) and flora (van der Hammen, 1951; Zagwijn, 1963; van der Burgh, 1974) doubtlessly typify the Tegelen environment as warm and forested, with open water.

Van der Burgh (1974) described the climate during the second climatic optimum (corresponding to the TC5 pollen zone of Zagwijn, 1963) as having a mean annual temperature of about 10°C, a mean temperature in the warmest month of c. 20°C, a mean temperature of 4-6°C for the coldest month, and an annual precipitation of over 1200 mm.

Osztramos 3/2	n-AA sup.	%	n _{cond}	%
<i>Sorex minutus</i>	133	39.2	27	58.7
<i>Drepanosorex praeareneus</i>	72	21.2	4	8.7
<i>Ptenyia hungarica</i>	64	18.9	9	19.6
<i>Beremendia fissidens</i>	59	17.4	5	10.9
<i>Crocidura kornfeldi</i>	11	3.2	1	2.2

The fauna of Osztramos 3/2 is the exact opposite of that of Villány 3 and 5. Here elements prevail that favour a moist and wooded biotope (*Sorex* and *Drepanosorex*), followed by the apparently inevitable opportunists *Ptenyia* and *Beremendia*. *Crocidura* is present, but only with a very low percentage. The accompanying fauna is suggestive of a rather mixed environment of forest and open terrain. The only available larger mammals are *Cervus* and *Sus* (Jánosy, 1979), both typical forest-dwellers.

PALAEOGEOGRAPHY

Some palaeogeographical remarks can be made. Two of the studied genera (*Episoriculus* and *Crocidura*) suggest interesting migrations, related to their respective ecological preferences.

In the Ruscinian, *Episoriculus gibberodon* was widespread in Europe; it is known from for instance Podlesice (Poland, Kowalski, 1956; Rzebik-Kowalski, 1981), Osztramos 1 and 7, Csarnóta 2 (Hungary), Maritsa, and Apolakkia (Rhodes, Greece, de Bruijn et al., 1970; van de Weerd et al., 1982). However, it is absent in late Ruscinian Polish faunas. Weże 1 contains an abundance of Soricidae, but *Episoriculus* is lacking (Sulimski, 1959, 1962; Rzebik-Kowalska, 1981). The youngest Polish locality with *Episoriculus* is Podlesice, from the early Ruscinian.

In the Hungarian/Czechoslovakian area, *Episoriculus* persists until the beginning of the Biharian. The youngest locality from which the genus is recorded in Czechoslova-

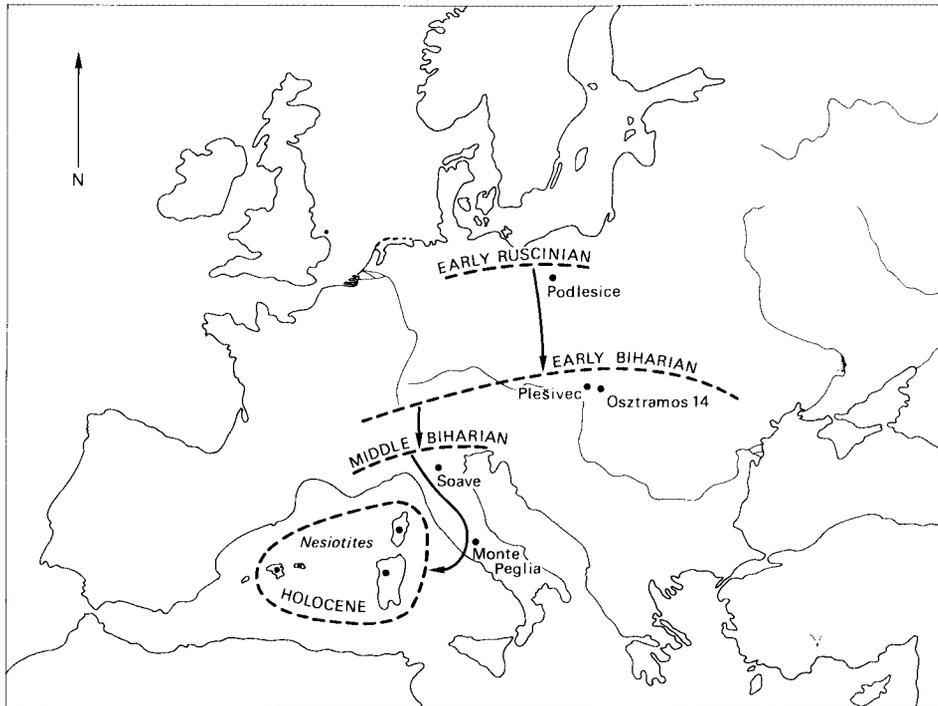


Fig. 21. Map showing the assumed migration of *Episoriculus*.

via is Plešivec; in Hungary it is Osztramos 14 (Fejfar, 1961; Jánossy, 1979). After the early Biharian the genus has disappeared from the Carpathian basin, but it persists in Italy and in some Western Mediterranean islands.

Two of the middle Biharian localities in Italy that contain *Episoriculus* (the species *castellarini*) are the Cava Sud near Soave (Pasa, 1947) and Monte Peglia (van der Meulen, 1973).

After the middle Biharian, the genus has disappeared from the continent and is thereafter extinct in Europe. It is still extant in Asia (Repenning, 1967).

However, in Europe it has a direct descendant: the genus *Nesiotites* Bate, 1944, known from Corsica: *N. corsicanus* Bate, 1944; from Sardinia: *N. similis* (Hensel, 1955) and from the Balearic Islands: *N. ponsi* Reumer, 1979 and *N. hidalgo* Bate, 1944 (see Bate, 1944; Reumer, 1979, 1980). This genus is present in the islands presumably from the late Pliocene onwards; it persists into the Holocene.

The picture of the southwards retreat of *Episoriculus* is shown in Fig. 21.

For *Crociodura* we can also reconstruct some migratory movements, in this case a northwards invasion (Fig. 22). The subfamily Crocidurinae originates from Africa. It is still the only soricid subfamily living there; it shows a large radiation of species including the smallest and the largest known shrews (*Suncus etruscus* and *Praesorex goliath*, respectively).

Several Crocidurinae are known from the Oligocene and Miocene of Europe (e.g. from Wintershof-West, Vieux Collonges, La Grive, see Repenning, 1967), but these do not belong to the genus *Crociodura*.

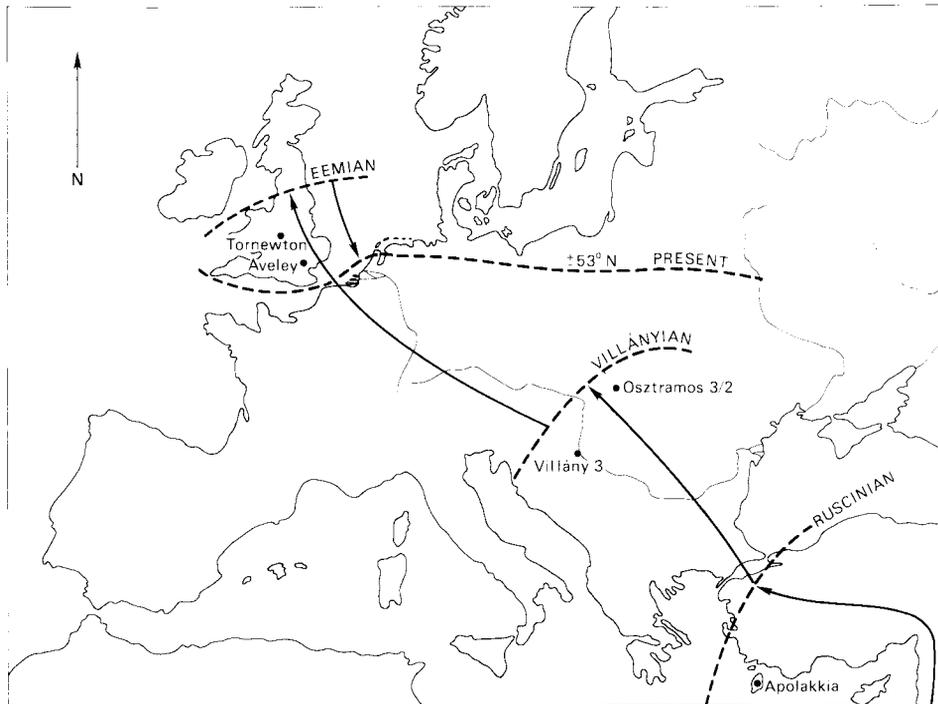


Fig. 22. Map showing the assumed migration of *Crocidura*.

The oldest record of *Crocidura* in Europe is Apolakkia, Rhodes (van de Weerd et al., 1982), which is of middle Ruscinian age (MN15). In the literature one encounters stratigraphically older reports, but these concern either other Crocidurinae or something completely different. For example, Sulimski (1959) mentions *Crocidura* sp. from the lower levels of Węże 1, of probably early Ruscinian age. His description and figures (pl. IV, fig. 4) clearly show that this species does not belong to the Crocidurinae, as it possesses a soricine condyle with a lingually emarginated interarticular area (Sulimski, 1959, p. 156).

During the late Villányian, *Crocidura* had reached the Carpathian basin; it is known from Villány 3 and Osztramos 3 (*C. kornfeldi*).

In the middle Biharian the genus is present in Northern Italy: *C. zorzii* from the Cava Sud near Verona (Pasa, 1947).

It is then a long time until further movements are recorded, apparently due to the harsher climate in NW Europe.

Then we have two recordings from England, both from sediments that are correlated to the Ipswichian/Eemian interglacial. The first is from the Vivian Vault of Tornewton Cave, Devon (Rzebik, 1968), a large species determined as *Crocidura* sp. The second is from Aveley, Essex, a smaller species described as *C. cf. suaveolens* (Stuart, 1976). The presence of the genus in England lasted only till the onset of the Weichselian, when it had to retreat. Nowadays it is absent from Britain (except for the Scilly Islands, where it has probably been introduced by man, Stuart, 1976). On the continent the genus does not live at latitudes above c. 53° (van den Brink, 1978); it apparently avoids low temperatures.

CONCLUSION

Summarizing, we can sketch the following picture of the palaeoenvironments from the early Ruscinian onwards.

In the early Ruscinian of northern Hungary (Osz9) a wooded environment prevailed, with considerable patches of open water. Later in the early Ruscinian (Osz1) the environment remains forested, but some steppe-elements appear in the fauna. The early Ruscinian in Hungary shows an apparent drying of the climate. This goes together with the expansion of hypsodont Cricetidae and Arvicolidae (see van de Weerd & Daams, 1978).

In the late Ruscinian (Csarnótian) we are able to observe some ecological differentiation. In Csarnóta 2 the environment is quite humid and forested, with a gradual change to a more open and less wooded environment in the higher part of the section. In Osztramos 7, as well in Węże, the climate must have been cooler and drier. In Węże the warmth-loving *Episoriculus* is lacking and in Osztramos 7 it is far less abundant than in Csarnóta 2 (5% vs. 38%).

Within the later part of the Ruscinian a differentiation of biotopes can be noted. The southern localities (Apolakkia, Csarnóta 2) seem to have been somewhat more humid and warmer than the northern localities (Węże, Osztramos 7); within SE Europe, some differentiation in humidity can be noted too (van de Weerd et al., 1982).

A cooling trend at the end of the Csarnótian is noted in several parts of Europe, e.g. in Spain by the extinction of many Muridae and the increase in Arvicolidae (van de Weerd & Daams, 1978). In Hungary it is well marked by the first appearance of *Lemmus* in Osztramos 7 (Jánossy, 1973a). This cooling may correspond to the Praetiglian in the Netherlands. In Hungary this cool period is not very well marked. The early Villányian faunas of Beremend 5 and 11 are not typically cool, although the lack of *Episoriculus* in the 'wet' fauna of Beremend 11 may give an indication.

The localities from the Beremend phase (Beremend 5 and 11) have yielded faunas with a rather humid character. In Beremend 5 the Soricidae fauna consists of: *Beremendia fissidens* (77 specimens); *Episoriculus gibberodon* (11); *Sorex runtonensis* (1) and *Petenya hungarica* (1), together with e.g. *Lagothidium beremendense* (93), *Miomys mehelyi* (35), *Dolomys milleri* (26), but also with *Desmana kormosi* (7) and numerous amphibians (Kretzoi, 1956). Kretzoi suggests a 'Busch-Steppen-Vegetation, mit wenigen von Wasser bedeckten Stellen'.

Beremend 11 contains *Beremendia fissidens* (7 specimens), *Petenya hungarica* (2), two *Sorex* species (4), and an indeterminate shrew. The most abundant accompanying faunal element is *Desmana* aff. *nehringi* (71); also abundant are some fish and amphibians. Steppe-elements are also present (antelope, *Prospalax*, *Sicista*) as well as some forest indicators (*Estramomys*).

A strong climatic differentiation occurs in the late Villányian. Tegelen exhibits a warm and humid, forested environment, whereas the south Hungarian Villány 3 fauna indicates a dry, savanna-like environment. This dry environment can also be noted in Villány 5 and Kisláng.

It is interesting to note the continuous drying trend in the south Hungarian localities, starting with the above-mentioned changes in the moist and forested environment of Csarnóta 2, via the forest-steppe vegetation of the Beremend phase to the dry steppe of Villány 3 and 5.

Osztramos 3, which is placed a bit later in the Villányian than Villány 3 and 5, shows a completely different environment: a humid forest. For the most part this will have been caused by the geography. At present, there is quite a difference between the

south of Hungary (a sub-Mediterranean climate with a rather dry and open terrain) and the north (a rather moist hilly to mountainous area with large deciduous forests). Jánosy's suggestion (1973a), that a rather similar differentiation occurred during the Villányian is here confirmed.

The faunas of Villány 3 and 5 represent the dry and open circumstances of the south, and Osztramos 3/2 represent the more humid and forested situation in the Carpathian foothills.

The end of the Villányian is already indicated by the re-appearance of *Lemmus* in Osztramos 3 (Jánosy, 1979).

DISTRIBUTION IN TIME

The range-chart of Fig. 23 gives the stratigraphic ranges of the species under study. These ranges are inferred not only from the studied localities, but also from various literature sources on other localities (e.g. Bachmayer & Wilson, 1970, 1978; Heller, 1930, 1958,

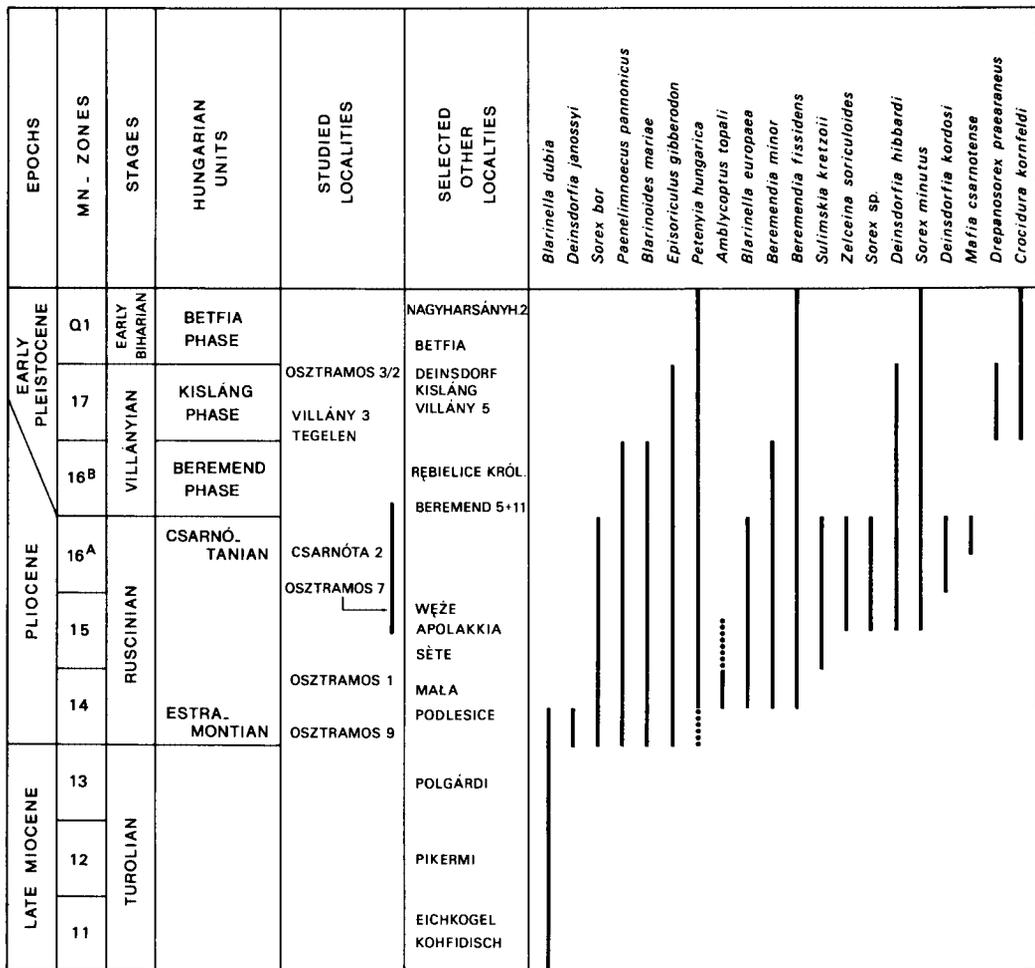


Fig. 23. Range-chart of the studied species of Soricidae.

1963; Jánossy, 1979; Kowalski, 1956, 1960; Kretzoi, 1941, 1956; van der Meulen, 1973; van der Meulen & Zagwijn, 1974; Rzebik-Kowalska, 1975, 1976, 1981; Sulimski, 1959, 1962; Sulimski et al., 1979).

The chart is therefore not exhaustive for all Soricidae within the depicted time-range (early Turolian through early Biharian). Several other Soricidae are known, especially from the lower part (Turolian) and from the upper part (Biharian). The picture from the early Ruscinian to the Villányian-Biharian boundary is fairly complete, give or take a few species (such as some *Sorex* species from Węże, Sulimski, 1962).

The most striking conclusion that can be drawn is that there was a considerable explosion in diversity during the Ruscinian. The Csarnótanian localities are all rich in Soricidae: 13 species in Węże 1 (Sulimski, 1962), 15 in Osztramos 7, and 12 in Csarnóta 2. Concerning this latter locality it should be noted that in the lower layers we have a maximum of 11 species occurring together, and a maximum of 9 species in the upper-levels. From Osztramos 7 and Węże 1 it is highly uncertain whether or not any sampling mixture has occurred, but still the numbers are very high.

Older localities are less diversified: 8 species in both Osztramos 9 and Osztramos 1. The younger localities are still poorer: 6 species in Villány 3, only 4 in Tegelen and 5 in Osztramos 3.

The radiation took place in the early/middle Ruscinian. The 'boom' was partly caused by new arrivals; for several genera, such as *Episoriculus* and *Beremendia* an ancestor is not known in Europe. Other taxa have ancestors in the Turolian: *Paenelimnoecus pannonicus* (*P. crouzeli* and *P. repenningi*); *Blarinella europaea* could be a descendant of *B. dubia*; perhaps *Petenyia hungarica* has also some relationship to *B. dubia* or they have a common ancestor. *Amblycoptus topali* is supposed to be a descendant of the late Turolian *A. oligodon*, which in turn is suggested to have descended from the early Turolian *Anourosorex kormosi* (see Jánossy, 1972).

During the Ruscinian a radiation in *Deinsdorfia* was found, with *D. janossyi* being ancestral to the other two species, *D. hibbardi* and *D. kordosi*.

All together at least 12 genera of Soricidae occur in the Ruscinian, many of which contain more than one species. Today, only four genera are living in Europe: *Sorex*, *Neomys*, *Crocidura*, and *Suncus* (van den Brink, 1978). Apparently there has been considerable impoverishment.

The genera *Blarinella*, *Sulimskia*, *Zelceina*, and *Mafia* became extinct at the Ruscinian-Villányian boundary; *Paenelimnoecus* and *Blarinoides* became extinct during the Villányian and *Episoriculus* (except in Italy) and *Deinsdorfia* at the Villányian-Biharian boundary. Of the other Ruscinian genera, *Petenyia* lives on till the early Biharian (Kövesvarad being its youngest locality), *Beremendia* till the late Biharian (Tarkó, see Jánossy, 1979); only *Sorex* is still extant.

These extinctions are insufficiently counterbalanced by entries. In the Villányian, two new genera appear: *Drepanosorex* (which becomes extinct in the late Biharian) and *Crocidura*, which is still extant. Later in the Pleistocene, two aberrant, monospecific and exoedaenodont genera occur for a short period: *Dimylosorex* in Deutsch-Altenburg 2 (early Biharian, Rabeder, 1972a, 1981) and *Macroneomys* in Cave C718, Koneprusy (late Biharian, Fejfar, 1966b).

Neomys has its entry in the early Biharian (Monte Peglia, van der Meulen, 1973), *Suncus* in the Holocene.

The deterioration of the climate at the onset of the Villányian apparently caused the decline; the diversity of the Ruscinian has never been equalled.

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Tables

In Tables 1-53 the following abbreviations are used, in addition to the ones designating the parameters described above and the codes for dental elements:

prm = parameter

n = number of observations

min = minimum, smallest measurement

\bar{x} = mean of the observations

max = maximum, largest measurement

sd = standard deviation (only given if n = 7 or more).

In the tables, the sizes are given in 0.1 mm units.

Table 1. Measurements of *Crocidura kornfeldi* Kormos, 1934 from Villány 3.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	19	6.5	7.7	9.5	0.82
	L	19	15.4	17.4	19.7	1.16
	H	21	11.4	12.5	13.6	0.72
P ⁴	PE	21	6.6	7.8	8.7 (10.2)	0.83
	LL	20	7.3	8.5	9.3	0.60
	BL	21	16.1	17.7	19.1	0.80
	W	19	14.8	16.0	17.6	0.72
M ¹	PE	19	8.7	10.1	11.0	0.64
	LL	19	11.6	13.2	14.9	0.73
	BL	18	12.9	14.6	15.3	0.75
	AW	19	14.8	16.2	17.4	0.74
	PW	18	17.7	19.6	21.6	0.99
M ²	PE	12	8.6	9.5	10.2	0.51
	LL	13	10.7	11.7	12.8	0.68
	BL	13	11.2	12.2	13.6	0.66
	AW	12	16.6	18.2	19.2	0.84
	PW	12	14.6	15.6	17.0	0.80
M ³	L	2	6.0	6.2	6.3	
	W	2	11.5	12.1	12.6	
I inf.	L	33	28.3	30.8	34.8	1.45
M ₁	TRW	94	7.9	9.2	10.7	0.45
	TAW	94	9.2	10.1	11.8	0.44
	L	91	12.9	15.1	17.5	0.84
M ₂	TRW	93	7.3	8.7	9.6	0.35
	TAW	92	7.5	8.9	10.1	0.40
	L	92	13.1	14.3	15.8	0.64
M ₃	W	67	5.5	6.4	7.0	0.29
	L	67	10.0	11.1	12.2	0.47
M ₁ -M ₃	L	45	34.5	37.4	39.2	1.07
ramus	L	37	48.3	53.7	58.9	2.52
	H	47	36.5	42.2	46.8	2.38
	LUF	37	4.9	6.7	8.1	0.64
	LLF	54	9.7	11.8	13.6	0.83
	HC	39	13.6	15.3	17.3	0.93

Table 2. Measurements of *Crocidura kornfeldi* Kormos, 1934 from Osztramos 3/2.

element	prm	n	min	\bar{x}	max
I sup.	LT	1		7.5	
	L	1		17.1	
	H	1		12.5	
P ⁴	PE	1		9.3	
	LL	1		10.4	
	BL	1		18.4	
	W	1		16.3	
M ¹	PE	1		10.2	
	LL	1		14.1	
	BL	1		15.5	
	AW	1		17.0	
M ₁	PW	1		19.6	
	TRW	2	9.7	9.8	9.8
	TAW	2	10.6	10.8	11.0
M ₂	L	2	16.3	16.9	17.4
	TRW	2	8.8	9.0	9.1
	TAW	2	9.1	9.2	9.3
M ₃	L	2	14.0	14.9	15.7
	W	2	6.3	6.5	6.6
	L	2	11.3	11.5	11.7
M ₁ -M ₃	L	2	39.2	39.3	39.3
ramus	L	1		59.0	
	H	1		45.9	
	LUF	1		7.3	
	LLF	1		13.1	
	HC	1		16.5	

Table 3. Measurements of *Sorex minutus* L., 1766 from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
P ⁴	PE	6	6.4	7.6	8.5	
	LL	6	7.3	8.6	9.6	
	BL	6	11.3	11.8	12.7	
	W	6	11.0	11.4	12.8	
M ¹	PE	9	8.2	9.0	9.4	0.37
	LL	8	10.6	11.2	11.7	0.34
	BL	9	10.3	10.9	11.7	0.41
	AW	8	10.1	11.0	11.7	0.56
	PW	7	11.5	12.2	13.4	0.68
M ²	PE	6	7.7	8.3	8.6	
	LL	4	9.3	9.8	10.6	
	BL	4	9.5	10.0	10.1	
	AW	6	10.4	10.9	11.5	
	PW	3	11.0	11.5	12.4	
M ³	L	2	6.0	6.2	6.3	
	W	2	9.7	10.0	10.3	
M ₁	TRW	17	5.1	5.9	6.5	0.37
	TAW	17	5.5	6.5	7.2	0.45
	L	17	10.6	12.1	13.3	0.81
M ₂	TRW	16	5.3	5.8	6.1	0.23
	TAW	16	5.3	5.9	6.7	0.31
	L	16	10.0	10.9	11.8	0.54
M ₃	W	11	4.6	4.9	5.2	0.24
	L	11	8.1	8.9	9.6	0.47
M ₁ -M ₃	L	6	28.8	30.1	31.9	
ramus	H	2	28.1	28.8	29.4	
	LUF	2	4.4	4.5	4.6	
	LLF	3	7.8	8.2	8.4	
	HC	2	11.6	11.8	12.0	

Table 4. Measurements of *Sorex minutus* L., 1766 from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	2	6.1	6.3	6.4	
	L	2	11.8	12.0	12.1	
	H	2	8.6	8.6	8.6	
P ⁴	PE	1		6.9		
	LL	1		8.5		
	BL	2	10.5	11.3	12.0	
	W	1		10.1		
M ₁	TRW	16	5.5	6.0	6.4	0.28
	TAW	16	5.9	6.7	7.1	0.31
	L	15	11.0	12.4	13.5	0.60
M ₂	TRW	15	5.6	6.0	6.5	0.26
	TAW	15	5.7	6.3	6.8	0.33
	L	15	10.2	11.1	12.2	0.49
M ₃	W	7	4.6	5.0	5.3	0.29
	L	7	8.3	8.8	9.3	0.35
M ₁ -M ₃	L	5	29.0	30.3	32.5	
	L	3	37.0	41.6	46.6	
ramus	H	9	29.6	31.4	33.8	1.32
	LUF	8	6.3	6.5	7.2	0.32
	LLF	8	8.6	9.4	10.2	0.52
	HC	8	13.9	14.5	15.2	0.53

Table 5. Measurements of *Sorex minutus* L., 1766 from Tegelen.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	3	6.2	7.3	7.9	
	L	3	12.0	12.7	13.1	
	H	3	8.5	8.6	8.7	
P ⁴	PE	9	7.8	8.3	8.8	0.40
	LL	9	9.2	9.7	10.7	0.56
	BL	11	11.7	12.7	13.7	0.49
	W	9	11.5	12.2	13.5	0.61
M ¹	PE	14	9.0	9.6	10.3	0.32
	LL	13	11.4	12.1	12.8	0.45
	BL	14	11.3	12.0	12.3	0.31
	AW	13	10.8	12.0	12.5	0.45
	PW	12	12.2	13.4	14.2	0.50
M ²	PE	9	8.2	8.8	9.2	0.32
	LL	9	9.9	10.3	11.0	0.33
	BL	9	9.5	10.3	11.0	0.43
	AW	8	10.8	12.1	12.7	0.60
	PW	8	11.3	11.9	12.6	0.52
I inf.	L	5	27.9	28.7	29.3	
M ₁	TRW	13	5.8	6.2	6.8	0.28
	TAW	13	6.5	6.8	7.1	0.23
	L	13	12.3	13.3	14.1	0.63
M ₂	TRW	14	5.8	6.3	6.6	0.28
	TAW	14	5.9	6.4	6.8	0.30
	L	14	11.3	11.9	12.6	0.43
M ₃	W	7	4.7	5.2	5.6	0.32
	L	8	9.3	9.5	9.7	0.15
M ₁ -M ₃	L	4	31.7	32.4	33.7	
	L	9	42.0	44.1	46.1	1.24
ramus	H	7	31.4	33.1	34.3	1.11
	LUF	5	5.1	6.0	6.6	
	LLF	6	8.3	9.1	9.4	
	HC	6	12.5	13.8	14.7	

Table 6. Measurements of *Sorex minutus* L., 1766 from Villány 3.

element	prm	n	min	\bar{x}	max
P ⁴	PE	2	7.3	8.2	9.0
	LL	2	8.4	9.1	9.7
	BL	2	12.9	13.0	13.0
	W	2	11.6	11.9	12.1
M ₁	TRW	2	7.0	7.5	7.9
	TAW	2	7.3	7.9	8.5
	L	2	14.2	14.4	14.5
M ₂	TRW	4	6.3	7.1	7.5
	TAW	4	6.4	7.1	7.6
	L	4	12.2	13.0	13.6
M ₃	W	3	5.5	5.6	5.8
	L	4	9.6	9.9	10.1
M ₁ -M ₃	L	2	33.8	34.5	35.1
	L	1		41.9	
ramus	H	1		32.7	
	LUF	1		6.0	
	LLF	1		9.0	
	HC	1		13.7	

Table 7. Measurements of *Sorex minutus* L., 1766 from Osztramos 3/2.

element	prm	n	min	\bar{x}	max	sd
P ⁴	PE	1		7.3		
	LL	1		8.4		
	BL	1		12.3		
	W	1		12.1		
M ¹	PE	3	9.3	9.7	10.2	
	LL	3	11.3	11.6	11.9	
	BL	2	10.8	11.4	11.9	
	AW	3	10.9	11.8	12.7	
	PW	2	12.1	12.3	12.4	
M ²	PE	1		8.5		
	LL	1		10.0		
	BL	1		9.6		
	AW	1		10.6		
	PW	1		11.2		
I inf.	L	3	28.9	29.4	30.2	
M ₁	TRW	28	5.8	6.6	7.2	0.39
	TAW	28	6.2	7.0	7.6	0.33
	L	26	12.4	13.6	14.5	0.46
M ₂	TRW	33	5.6	6.5	7.1	0.37
	TAW	33	5.8	6.5	7.1	0.30
	L	33	11.0	11.9	12.9	0.48
M ₃	W	25	4.7	5.3	5.7	0.23
	L	25	8.8	9.5	10.3	0.36
M ₁ -M ₃	L	13	30.2	32.8	34.4	1.12
	L	26	40.3	42.7	45.6	1.31
ramus	H	23	30.1	33.5	36.1	1.43
	LUF	21	5.8	6.6	7.8	0.54
	LLF	25	8.5	9.7	11.0	0.60
	HC	22	13.3	14.5	15.9	0.70

Table 8. Measurements of *Sorex bor* sp. nov., from Osztramos 9.

element	prim	n	min	\bar{x}	max
I sup.	LT	1		7.0	
	L	1		13.8	
	H	1		8.9	
P ⁴	PE	3	7.2	8.0	9.0
	LL	3	8.0	8.6	9.5
	BL	3	12.0	12.3	12.9
	W	3	11.4	11.8	12.2
M ¹	PE	3	9.5	9.8	10.3
	LL	3	11.1	11.7	12.9
	BL	3	11.3	11.9	12.9
	AW	3	11.8	12.2	12.7
	PW	3	12.6	13.0	13.3
M ²	PE	2	8.6	8.8	8.9
	LL	2	10.2	10.2	10.2
	BL	1		10.6	
	AW	2	12.1	12.1	12.1
	PW	1		11.9	
I inf.	L	2	23.4	24.1	24.8
M ₁	TRW	2	6.4	6.5	6.6
	TAW	2	7.2	7.2	7.2
	L	2	12.5	12.8	13.1
M ₂	TRW	2	6.4	6.5	6.6
	TAW	2	6.5	6.7	6.8
	L	2	11.8	11.9	12.0
M ₃	W	2	5.3	5.4	5.4
	L	2	9.3	9.3	9.3
M ₁ -M ₃	L	1		32.1	
ramus	L	1		43.2	
	H	2	32.4	33.3	34.1
	LLF	1		7.9	
	LLF	2	9.4	9.6	9.8
	HC	2	13.9	15.2	16.4

Table 9. Measurements of *Sorex bor* sp. nov., from Osztramos 1.

element	prim	n	min	\bar{x}	max
I sup.	LT	1		5.8	
	L	1		13.2	
	H	1		10.3	
P ⁴	PE	1		7.1	
	LL	1		8.2	
	BL	1		12.8	
	W	1		11.6	
M ¹	PE	4	9.5	10.0	11.3
	LL	4	11.8	12.4	13.6
	BL	4	11.5	12.3	13.9
	AW	4	11.4	12.3	13.0
	PW	4	13.2	13.6	14.4
M ²	PE	3	8.9	9.5	10.0
	LL	3	11.0	11.6	12.1
	BL	3	10.1	10.9	11.6
	AW	3	11.3	12.2	13.8
	PW	2	11.6	12.2	12.7
M ³	L	2	5.9	6.0	6.0
	W	2	10.3	10.4	10.5
M ₁	TRW	6	5.7	6.2	6.5
	TAW	6	5.8	6.8	7.4
	L	6	11.5	12.0	13.4
M ₂	TRW	5	5.9	6.2	6.4
	TAW	5	5.8	6.3	6.7
	L	5	10.7	11.2	11.6
M ₃	W	3	4.8	5.0	5.2
	L	3	9.3	9.5	9.8
M ₁ -M ₃	L	3	30.9	31.5	32.0

Table 10. Measurements of *Sorex bor* sp. nov., from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
P ⁴	BL	1		14.6		
I inf.	L	1		30.2		
M ₁	TRW	7	6.4	7.0	7.5	0.43
	TAW	7	7.0	7.5	8.0	0.38
	L	7	12.9	14.0	15.2	0.82
M ₂	TRW	7	6.4	6.9	7.3	0.33
	TAW	7	6.4	7.0	7.5	0.37
	L	6	11.9	12.4	13.0	
M ₃	W	3	5.4	5.7	5.8	
	L	3	9.5	9.8	10.0	
ramus	L	1		47.1		
	H	2	35.8	35.8	35.9	
	LUF	2	6.1	6.8	7.5	
	LLF	3	10.1	10.3	10.7	
	HC	2	14.9	15.8	16.6	

Table 11. Measurements of *Sorex* sp. from Osztramos 7.

element	prm	n	min	\bar{x}	max
P ⁴	PE	2	10.8	11.1	11.4
	LL	2	11.7	12.0	12.2
	BL	2	16.0	16.3	16.6
	W	2	13.9	14.2	14.4
M ¹	PE	1		11.8	
	LL	1		14.8	
	BL	1		14.5	
	AW	1		17.4	
	PW	1		18.2	
M ²	PE	1		10.1	
	LL	1		12.7	
	AW	1		17.3	
M ³	L	1		5.6	
	W	1		11.2	
M ₁	TRW	5	7.5	8.2	8.9
	TAW	5	7.7	8.7	9.7
	L	5	15.6	16.2	17.0
M ₂	TRW	6	7.0	7.9	8.9
	TAW	6	7.1	8.0	8.7
	L	5	12.9	13.7	14.6
M ₃	W	2	6.2	6.3	6.3
	L	2	10.2	10.6	11.0
M ₁ -M ₃	L	1		37.6	
ramus	L	1		42.2	
	LUF	1		8.7	
	LLF	1		14.3	
	HC	1		18.3	

Table 12. Measurements of *Sorex* sp. from Csarnóta 2.

element	prm	n	size
M ₁	TRW	1	8.5
	TAW	1	8.7
	L	1	15.2
M ₂	TRW	1	8.0
	TAW	1	8.4
	L	1	13.6
ramus	H	1	40.9
	LUF	1	8.0
	LLF	1	12.3
	HC	1	19.0

Table 13. Measurements of *Drepanosorex praeareneus* (Kormos, 1934) from Villány 3.

element	prm	n	size
M ₁	TRW	1	8.9
	TAW	1	9.6
	L	1	16.1
ramus	L	1	56.0
	H	1	49.1
	LUF	1	8.7
	LLF	1	13.4
	HC	1	21.2

Table 14. Measurements of *Drepanosorex praeareneus* (Kormos, 1934) from Osztramos 3/2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	3	10.9	11.3	11.8	
	L	3	17.9	19.0	19.8	
	H	3	11.5	11.9	12.6	
P ⁴	PE	4	10.1	10.4	10.6	
	LL	4	11.0	11.2	11.4	
	BL	4	15.7	16.0	16.6	
	W	4	14.5	15.0	16.1	
M ¹	PE	4	12.2	12.7	13.0	
	LL	5	13.9	14.6	15.1	
	BL	5	13.5	14.5	15.2	
	AW	5	15.0	15.4	16.3	
	PW	5	15.5	16.3	17.8	
M ²	PE	5	10.9	11.2	11.4	
	LL	5	12.2	12.7	13.2	
	BL	3	12.2	12.4	12.8	
	AW	5	14.9	15.6	17.3	
	PW	3	13.5	14.2	14.7	
M ³	L	2	6.7	6.9	7.1	
	W	1		11.8		
I inf.	L	2	40.4	40.8	41.2	
M ₁	TRW	2	8.7	8.8	8.8	
	TAW	2	9.5	9.6	9.6	
	L	2	16.4	16.4	16.4	
M ₂	TRW	2	8.2	8.4	8.5	
	TAW	2	8.2	8.4	8.6	
	L	1		14.0		
M ₃	W	1		6.5		
	L	1		11.2		
ramus	L	5	55.0	55.9	57.5	
	H	6	47.2	48.4	50.2	
	LUF	2	9.7	10.3	10.8	
	LLF	3	13.0	13.5	14.2	
	HC	2	21.5	22.0	22.4	

Table 15. Measurements of *Drepanosorex praeareneus* (Kormos, 1934) from Tegelen.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	28	8.9	9.9	11.1	0.53
	L	27	15.8	17.1	18.5	0.55
	H	24	9.6	10.8	11.9	0.69 ¹⁾
P ⁴	PE	24	9.0	9.8	10.8	0.47
	LL	21	10.2	11.0	12.1	0.60
	BL	26	13.9	15.2	16.2	0.55
	W	22	13.4	14.2	15.3	0.55
M ¹	PE	42	10.5	11.2	12.5	0.44
	LL	35	12.7	13.5	14.9	0.46
	BL	39	12.8	13.8	14.5	0.36
	AW	39	13.0	14.6	16.5	0.57
	PW	30	14.8	16.1	17.0	0.58
M ²	PE	19	9.6	10.2	11.2	0.29
	LL	18	11.3	12.2	13.1	0.48
	BL	17	11.4	12.0	12.6	0.35
	AW	19	14.2	14.9	16.7	0.35
	PW	15	14.0	14.9	15.8	0.52
I inf.	L	21	34.2	36.0	40.3	1.08
M ₁	TRW	48	7.0	7.6	8.8	0.26
	TAW	48	7.6	8.3	9.3	0.29
	L	49	13.9	15.1	16.8	0.62
M ₂	TRW	29	6.9	7.5	8.2	0.28
	TAW	27	7.1	7.6	8.2	0.30
	L	29	12.5	13.5	14.4	0.44
M ₃	W	10	5.3	6.0	6.4	0.32
	L	10	9.9	10.4	10.9	0.31
M ₁ -M ₃	L	2	35.1	36.7	38.2	
ramus	L	7	49.1	53.5	55.8	2.23
	H	10	41.3	43.6	45.3	1.31
	LUF	11	6.4	8.5	10.4	1.21
	LLF	10	10.5	11.6	12.9	0.84
	HC	11	17.7	19.2	20.9	1.14
¹⁾ in unworn specimens only:						
I sup.	H	14	10.8	11.3	11.9	0.32

Table 16. Measurements of *Deinsdorfia janossyi* sp. nov. from Osztramos 9.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	6	9.5	10.0	10.5	
	L	4	18.8	19.1	19.4	
	H	6	11.4	12.0	13.5	
p ⁴	PE	6	10.9	11.9	12.6	
	LL	5	12.9	13.7	15.2	
	BL	6	16.2	17.0	17.9	
	W	5	12.8	13.3	13.7	
M ¹	PE	4	10.7	10.9	11.1	
	LL	3	12.3	13.0	13.8	
	BL	4	13.4	13.7	13.9	
	AW	4	12.5	13.0	13.4	
	PW	4	12.5	13.4	14.6	
M ²	PE	3	9.4	9.7	9.8	
	LL	3	11.7	12.1	12.6	
	BL	2	11.3	11.9	12.4	
	AW	3	14.0	14.3	14.8	
	PW	2	13.0	13.6	14.1	
M ³	L	1		5.9		
	W	1		11.6		
I inf.	L	1		39.4		
M ₁	TRW	7	7.4	8.0	8.5	0.40
	TAW	7	8.3	8.5	9.4	0.41
	L	7	14.9	15.4	16.4	0.48
M ₂	TRW	3	7.4	7.6	8.0	
	TAW	4	6.7	7.4	7.7	
	L	3	13.1	13.8	14.5	
M ₃	W	2	5.4	5.7	6.0	
	L	2	9.3	9.5	9.6	
M ₁ -M ₃	L	1		36.0		
ramus	LUF	2	9.0	9.3	9.6	
	LLF	2	12.6	12.8	12.9	
	HC	2	20.0	20.5	21.0	

Table 17. Measurements of *Deinsdorfia hibbardi* (Sulimski, 1962) from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	32	9.1	10.1	11.5	0.64
	L	25	18.9	20.1	21.5	0.74
	H	36	12.4	13.2	13.9	0.43
P ⁴	PE	9	10.2	10.9	12.3	0.68
	LL	8	11.5	12.3	13.6	0.71
	BL	12	15.9	16.9	17.5	0.51
	W	8	13.2	13.7	14.1	0.29
M ¹	PE	27	9.9	10.7	11.5	0.44
	LL	23	12.2	13.5	14.4	0.56
	BL	26	13.0	14.1	15.0	0.54
	AW	26	13.5	14.0	14.8	0.34
	PW	23	14.0	15.3	16.3	0.51
M ²	PE	16	8.7	9.3	10.6	0.43
	LL	13	10.6	11.5	12.6	0.61
	BL	12	10.8	11.6	12.8	0.52
	AW	18	13.0	14.2	14.9	0.54
	PW	9	12.3	13.0	13.8	0.45
M ³	L	2	5.1	5.2	5.2	
	W	2	10.8	11.0	11.2	
I inf.	L	5	43.2	43.8	44.4	
M ₁	TRW	75	7.4	8.0	8.8	0.32
	TAW	76	8.0	8.5	9.3	0.28
	L	75	14.2	15.8	17.5	0.61
M ₂	TRW	62	7.0	7.4	8.0	0.23
	TAW	63	6.9	7.3	8.0	0.25
	L	61	12.5	13.3	14.7	0.41
M ₃	W	36	5.0	5.5	6.2	0.29
	L	35	8.9	9.7	10.3	0.33
M ₁ -M ₃	L	13	35.8	36.7	38.2	0.72
ramus	L	7	41.2	43.9	47.2	2.05
	H	17	36.8	39.0	41.8	1.33
	LUF	13	9.7	10.8	12.0	0.61
	LLF	15	12.7	14.0	14.9	0.55
	HC	13	21.4	23.1	25.0	1.14

Table 18. Measurements of *Deinsdorfia kordosi* sp. nov. from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	43	9.7	11.2	12.7	0.82
	L	38	20.0	21.6	23.6	0.89
	H	45	11.1	13.1	14.5	0.61
P ⁴	PE	7	11.2	12.6	13.6	0.75
	LL	7	13.4	14.6	16.2	1.01
	BL	8	18.5	19.1	19.9	0.48
	W	7	15.0	15.3	15.9	0.36
M ¹	PE	10	10.6	11.6	12.3	0.55
	LL	10	13.3	13.9	15.5	0.67
	BL	8	13.9	14.8	15.7	0.66
	AW	9	13.9	15.9	16.7	0.84
	PW	8	15.6	16.8	17.7	0.68
M ²	PE	3	8.4	8.7	8.9	
	LL	3	9.8	10.1	10.3	
	BL	3	10.5	10.7	10.8	
	AW	3	15.7	16.2	16.5	
	PW	3	11.3	11.5	11.8	
I inf.	L	15	42.5	45.3	47.9	1.45
M ₁	TRW	24	8.0	8.9	10.0	0.54
	TAW	24	8.2	9.0	10.2	0.50
	L	23	15.3	17.0	18.1	0.73
M ₂	TRW	19	7.4	7.9	8.7	0.35
	TAW	19	6.9	7.4	7.7	0.25
	L	19	12.9	13.8	14.4	0.40
M ₃	W	6	5.4	5.8	6.2	
	L	6	8.3	9.3	10.7	
M ₁ -M ₃	L	5	36.2	37.2	38.2	
ramus	L	7	42.2	44.6	46.7	1.57
	H	21	37.6	42.5	46.9	2.63
	LUF	31	9.2	11.1	13.1	0.94
	LLF	35	13.0	14.4	16.2	0.86
	HC	31	21.7	24.4	28.1	1.31

Table 19. Measurements of *Petenyia hungarica* Kormos, 1934 from Osztramos I.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	5	10.5	10.8	11.2	
	L	4	22.5	22.7	23.0	
	H	6	12.7	12.9	13.0	
P ⁴	PE	1		10.1		
	LL	1		10.1		
	BL	2	13.8	14.1	14.3	
	W	1		13.9		
M ¹	PE	3	11.9	12.6	13.3	
	LL	3	12.8	13.5	14.2	
	BL	3	13.1	13.7	14.4	
	AW	3	13.1	13.4	13.7	
	PW	3	14.2	14.3	14.6	
M ²	PE	1		11.4		
	LL	1		12.8		
	BL	1		11.7		
	AW	1		14.0		
	PW	1		13.6		
I inf.	L	2	40.2	40.6	41.0	
M ₁	TRW	3	8.0	8.3	8.6	
	TAW	3	9.1	9.3	9.6	
	L	3	14.5	14.7	14.9	
M ₂	TRW	3	7.5	8.1	8.8	
	TAW	3	8.1	8.5	9.3	
	L	3	12.9	13.6	14.9	
M ₃	W	1		7.3		
	L	1		12.1		

Table 20. Measurements of *Petenyia hungarica* Kormos, 1934 from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	15	11.7	13.1	14.3	0.66
	L	9	23.2	24.3	25.3	0.75
	H	18	12.3	13.3	14.2	0.54
P ⁴	PE		not measurable			
	LL		not measurable			
	BL	11	13.4	14.0	14.5	0.35
	W	12	11.9	12.4	12.9	0.29
M ¹	PE	23	11.2	11.9	12.3	0.28
	LL	21	12.3	12.9	13.4	0.31
	BL	23	12.5	13.1	14.2	0.47
	AW	23	12.8	13.4	14.1	0.35
	PW	21	13.4	14.1	14.7	0.37
M ²	PE	15	10.7	11.1	11.7	0.34
	LL	14	11.6	12.2	13.0	0.39
	BL	13	11.5	12.1	12.8	0.41
	AW	14	13.5	13.9	14.5	0.26
	PW	11	12.9	13.4	14.2	0.44
M ³	L	3	5.4	5.7	6.3	
	W	3	11.3	11.5	11.8	
I inf.	L	8	36.2	37.7	39.1	0.91
M ₁	TRW	38	7.3	7.9	8.7	0.29
	TAW	39	8.3	8.8	9.3	0.24
	L	38	13.1	14.2	15.0	0.41
M ₂	TRW	54	7.0	7.6	8.3	0.29
	TAW	53	7.5	8.0	8.5	0.25
	L	51	11.9	13.1	13.9	0.41
M ₃	W	43	5.7	6.3	6.8	0.29
	L	41	10.1	10.5	11.1	0.25
M ₁ -M ₃	L	17	34.0	35.2	36.7	0.63
ramus	L	10	40.5	42.1	45.2	1.67
	H	22	39.9	42.7	45.2	1.29
	LUF	20	8.3	9.1	10.2	0.53
	LUF	25	11.5	12.6	13.8	0.54
	HC	20	17.8	19.5	21.7	0.96

Table 21. Measurements of *Petenyia hungarica* Kormos, 1934 from Csarnóta 2.

element	prim	n	min	x	max	sd
I sup.	LT	7	10.7	11.5	12.4	0.75
	L	6	21.6	22.7	24.6	
	H	7	12.5	13.6	15.1	
M ¹	PE	1		12.1		
	LL	1		12.6		
	BL	1		13.5		
	AW	1		12.3		
	PW	1		13.6		
I inf.	L	4	36.8	38.0	38.6	
	TRW	2	8.6	9.0	9.4	
M ₁	TAW	3	7.9	9.1	10.3	
	L	2	14.5	16.2	17.8	
	TRW	5	6.9	8.5	9.4	
M ₂	TAW	5	7.3	8.5	9.4	
	L	5	12.8	14.4	16.2	
	W	5	6.1	6.8	7.6	
M ₃	L	5	10.3	11.2	12.4	
	L	2	34.4	37.9	41.2	
ramus	L	3	41.5	43.6	45.4	2.07
	H	12	42.7	45.2	49.8	
	LUF	15	9.2	10.9	12.2	
	LLF	18	13.3	14.6	16.3	
	HC	14	22.7	24.6	27.0	

Table 22. Measurements of *Petenyia hungarica* Kormos, 1934 from Villány 3.

element	prim	n	min	x	max	sd
I sup.	LT	4	12.5	12.8	13.2	
	L	4	24.1	25.1	25.9	
	H	4	13.4	13.8	14.2	
P ¹	PE		not measurable			
	LL	6	not measurable			
	BL	6	15.2	15.8	16.6	
	W	6	13.0	13.7	14.6	
	PE	7	12.7	13.1	13.6	0.35
M ¹	LL	6	13.3	13.9	14.4	
	BL	7	13.8	14.5	14.8	
	AW	7	14.0	14.6	15.6	
	PW	5	14.2	15.0	15.7	
	PE	5	11.6	11.9	12.1	
M ²	LL	5	12.6	13.0	13.3	
	BL	4	12.8	13.1	13.2	
	AW	5	14.4	15.0	15.5	
	PW	4	13.5	13.8	14.1	
	L	4	6.0	6.1	6.5	
M ³	W	4	11.5	11.6	11.8	
	L	5	37.4	38.6	39.8	
M ₁	TRW	15	8.6	9.1	9.6	0.32
	TAW	15	9.3	9.8	10.2	
	L	15	14.8	15.6	16.4	
M ₂	TRW	15	7.9	8.6	9.1	0.37
	TAW	15	8.3	8.8	9.2	
M ₃	L	15	13.0	14.0	14.8	0.47
	W	15	6.0	6.8	7.5	
M ₁ -M ₃	L	15	10.5	11.1	11.6	0.31
	L	11	36.8	38.0	39.1	
ramus	L	12	41.4	44.8	47.3	1.72
	H	12	42.8	45.0	46.5	
	LUF	13	8.9	9.9	10.9	
	LLF	13	12.4	13.6	14.5	
	HC	13	18.5	20.5	22.0	

Table 23. Measurements of *Petenya hungarica* Kormos, 1934 from Tegelen.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	8	11.9	12.7	13.4	0.49
	L	7	23.7	24.4	25.2	0.59
	H	12	11.7	13.1	14.3	0.80
P ⁴	PE		not measurable			
	LL		not measurable			
	BL	4	14.2	14.9	15.2	
	W	4	12.9	13.4	13.6	
M ¹	PE	6	12.3	12.9	13.3	
	LL	5	13.6	14.0	14.5	
	BL	5	13.4	13.9	14.3	
	AW	5	14.0	14.4	14.8	
	PW	3	14.6	15.2	16.0	
M ²	PE	9	11.4	11.9	12.3	0.32
	LL	9	12.7	13.3	13.7	0.38
	BL	6	12.6	13.0	13.3	
	AW	6	14.5	14.9	15.2	
	PW	6	13.2	13.7	14.3	
M ³	L	1		6.6		
	W	1		12.0		
I inf.	L	1		39.5		
M ₁	TRW	8	7.5	8.2	9.2	0.55
	TAW	8	8.3	9.0	9.9	0.50
	L	8	14.1	14.7	15.1	0.37
M ₂	TRW	14	7.3	8.0	8.3	0.24
	TAW	14	7.7	8.2	8.7	0.24
	L	14	12.9	13.9	14.6	0.45
M ₃	W	6	5.5	6.4	7.0	
	L	5	10.9	11.2	11.4	
ramus	L	3	43.9	44.1	44.3	
	H	3	43.4	44.1	45.2	
	LUF	3	7.8	8.5	8.9	
	LLF	3	13.8	13.8	13.9	
	HC	3	18.5	19.1	20.0	

Table 24. Measurements of *Petenya hungarica* Kormos, 1934 from Osztramos 3/2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	3	12.5	13.0	13.8	
	L	3	24.7	25.4	26.4	
	H	3	13.3	13.9	14.5	
P ⁴	PE		not measurable			
	LL	6	15.1	15.6	16.3	
	BL	5	13.5	13.8	14.0	
M ¹	PE	5	12.7	12.9	13.0	
	LL	5	13.9	14.3	14.8	
	BL	5	13.7	13.9	14.1	
	AW	5	14.1	14.4	14.7	
	PW	5	15.0	15.4	15.7	
M ²	PE	3	11.4	11.6	11.9	
	LL	3	12.5	12.9	13.2	
	BL	2	12.4	12.6	12.7	
	AW	3	15.3	15.5	15.8	
M ³	PW	2	14.2	14.3	14.3	
	L	1		5.7		
I inf.	L	2	35.2	37.0	38.7	
M ₁	TRW	10	8.6	8.9	9.2	0.24
	TAW	10	9.2	9.8	10.4	0.36
	L	10	15.3	15.6	16.3	0.28
M ₂	TRW	11	8.0	8.5	9.0	0.31
	TAW	11	8.5	8.8	9.4	0.27
	L	11	13.5	14.0	14.4	0.33
M ₃	W	9	6.5	6.9	7.3	0.30
	L	9	10.7	11.0	11.6	0.28
M ₁ -M ₃	L	7	36.9	37.9	38.8	0.80
ramus	L	10	42.9	44.4	46.0	1.05
	H	9	42.6	43.9	45.2	0.78
	LUF	7	8.0	9.4	10.1	0.85
	LLF	8	13.1	13.6	14.4	0.42
	HC	7	19.3	20.2	21.7	0.82

Table 25. Measurements of *Petenya* aff. *hungarica* Kormos, 1934 from Osztramos 9.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	1		9.6		
	L	1		19.3		
	H	1		11.5		
P ⁴	PE	3	8.9	9.6	10.0	
	LL	3	8.9	9.6	10.0	
	BL	3	13.0	13.4	13.7	
M ¹	W	3	11.9	12.5	12.9	
	PE	3	11.4	11.9	12.8	
	LL	3	12.6	12.9	13.3	
	BL	4	12.5	12.8	13.1	
	AW	3	12.9	13.3	13.9	
M ²	PW	3	14.2	14.4	14.8	
	PE	1		11.0		
	LL	1		12.1		
M ₁	BL	1		11.7		
	AW	1		13.9		
	PW	1		13.8		
M ₂	TRW	2	6.8	7.1	7.3	
	TAW	2	7.5	7.9	8.3	
M ₃	L	2	13.1	13.2	13.3	
	TRW	2	6.9	7.0	7.0	
	TAW	3	7.4	7.6	7.8	
M ₁ -M ₃	L	2	12.1	12.1	12.1	
	W	6	5.1	5.7	6.3	
M ₁ -M ₃	L	6	9.2	9.8	10.3	
	L	1		33.8		

Table 26. Measurements of *Blarinella dubia* (Bachmayer & Wilson, 1970) from Osztramos 9.

element	prm	n	min	\bar{x}	max	sd
P ⁴	PE	2	10.5	11.0	11.5	
	LL	2	10.5	11.2	11.8	
	BL	2	13.9	14.0	14.0	
	W	2	13.1	13.2	13.3	
M ¹	PE	2	13.1	13.2	13.2	
	LL	1		13.5		
	BL	2	14.1	14.2	14.2	
	AW	2	13.1	13.6	14.1	
	PW	1		14.0		
M ²	PE	1		12.2		
	LL	1		13.4		
	BL	1		13.6		
	AW	1		15.3		
	PW	1		14.5		
I inf.	L	1		39.3		
M ₁	TRW	2	9.9	10.0	10.0	
	TAW	2	11.2	11.3	11.3	
	L	2	15.5	15.7	15.8	
M ₂	TRW	3	9.9	10.2	10.4	
	TAW	3	10.2	10.3	10.4	
	L	2	15.8	15.9	16.0	
M ₃	W	2	7.8	8.1	8.3	
	L	2	13.1	13.2	13.3	
M ₁ -M ₃	L	1		40.9		
ramus	L	1		56.8		
	H	1		45.9		
	LLUF	1		12.7		
	LLF	1		13.5		
	HC	1		24.4		

Table 27. Measurements of *Blarinella europaea* sp. nov. from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	5	12.0	13.0	13.8	
	L	6	25.8	27.0	27.8	
	H	5	15.2	15.7	16.6	
P ⁴	PE		not measurable			
	LL	4	14.9	15.2	15.6	
	BL	3	12.3	12.7	13.0	
	W					
M ¹	PE	5	13.1	13.4	13.7	
	LL	5	13.7	13.9	14.1	
	BL	5	14.3	14.8	15.6	
	AW	5	13.8	14.5	15.0	
	PW	5	15.6	16.2	16.8	
M ²	PE	8	13.3	13.5	13.7	0.16
	LL	8	14.1	14.4	14.9	0.27
	BL	7	14.3	14.8	15.6	0.43
	AW	8	15.8	16.3	16.9	0.36
	PW	7	15.2	15.6	16.0	0.32
I inf.	L	2	40.7	42.6	44.4	
M ₁	TRW	10	8.1	8.8	9.2	0.39
	TAW	10	9.8	10.4	11.1	0.46
	L	10	14.5	15.7	16.8	0.57
M ₂	TRW	11	9.2	9.6	10.2	0.31
	TAW	11	9.8	10.0	10.5	0.22
	L	11	15.0	15.8	16.8	0.52
M ₃	W	8	7.8	8.2	8.7	0.34
	L	8	12.7	13.2	14.0	0.44
M ₁ -M ₃	L	4	40.4	41.3	42.4	
ramus	L	8	46.6	49.2	50.7	1.41
	H	12	42.4	44.7	48.9	1.81
	LLUF	14	9.4	10.6	11.9	0.76
	LLF	15	13.0	14.1	15.3	0.71
	HC	14	20.0	21.4	24.3	1.13

Table 28. Measurements of *Blarinella europaea* sp. nov. from Osztramos 7.

element	prm	n	min	\bar{x}	max
I sup.	LT	1		14.1	
	H	2	14.3	14.4	14.4
I inf.	L	1		40.5	
M ₁	TRW	2	8.5	9.0	9.4
	TAW	2	10.5	10.8	11.1
	L	2	14.7	15.4	16.0
M ₂	TRW	2	9.2	9.5	9.8
	TAW	2	10.0	10.2	10.3
	L	2	14.5	15.2	15.9
M ₃	W	1		8.5	
	L	1		13.7	

Table 29. Measurements of *Blarinella europaea* sp. nov. from Osztramos 1.

element	prm	n	min	\bar{x}	max
I sup.	LT	2	15.9	16.0	16.0
	L	2	26.7	27.0	27.3
	H	2	13.8	13.9	14.0
M ¹	PE	1		13.4	¹⁾
	LL	1		13.7	¹⁾
	BL	2	14.4	14.7	15.0
	AW	2	13.8	14.2	14.5
	PW	2	14.9	15.0	15.0
M ²	PE		not measurable		
	LL	1		13.4	
	BL	1		14.8	
	AW	1		15.4	
M ³	PW	1		14.7	
	L	1		7.5	
ramus	W	1		13.7	
	H	1		50.2	
	LUF	2	9.5	10.9	12.3
	LLF	2	16.7	16.8	16.8
	HC	2	24.2	26.0	27.8

¹⁾ not measurable in another specimen

Table 30. Measurements of *Zelceina soriculoides* Sulimski, 1959 from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
P ⁴	PE	6	11.4	12.0	12.6	
	LL	6	12.1	12.5	12.9	
	BL	6	14.7	15.6	16.0	
	W	7	13.7	14.4	15.3	0.56
M ¹	PE	18	11.5	12.9	13.5	0.57
	LL	16	13.4	14.5	15.9	0.57
	BL	18	13.5	14.6	15.3	0.46
	AW	16	13.5	15.3	16.8	0.78
	PW	16	14.5	15.8	17.1	0.61
M ²	PE	13	10.7	11.1	11.8	0.35
	LL	11	11.8	12.6	13.9	0.57
	BL	10	12.1	12.7	13.7	0.43
	AW	10	14.4	15.3	15.8	0.47
	PW	9	13.3	14.0	14.8	0.54
I inf.	L	18	34.4	37.4	40.1	1.25
M ₁	TRW	26	7.9	8.6	9.8	0.44
	TAW	29	8.4	9.0	9.7	0.32
	L	25	15.2	15.9	17.1	0.53
M ₂	TRW	16	7.2	7.9	8.4	0.39
	TAW	16	7.4	7.9	8.4	0.36
	L	17	13.0	13.7	14.5	0.39
M ₃	W	4	5.5	5.8	6.2	
	L	4	9.3	10.2	10.8	
ramus	L	10	40.9	43.3	46.2	1.69
	H	33	38.1	41.1	44.0	1.26
	LUF	35	8.6	9.9	11.4	0.73
	LLF	43	12.8	14.0	15.6	0.67
	HC	36	20.2	22.0	23.6	0.94

Table 31. Measurements of Soricini indet. from Osztramos 1.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	7	8.2	9.5	10.8	0.78
	L	7	17.4	18.1	18.9	0.48
	H	7	10.7	11.1	11.7	0.45
M ¹	PE	1		11.1		
	LL	1		13.2		
	BL	1		15.3		
	AW	1		14.9		
	PW	1		16.0		
M ²	PE	1		9.6		
	LL	1		11.6		
	BL	1		11.4		
	AW	1		14.9		
	PW	1		13.0		
I inf.	L	8	34.5	35.3	36.2	0.76
M ₁	TRW	7	6.8	7.7	8.4	0.47
	TAW	7	7.6	8.4	8.9	0.40
	L	7	14.5	14.9	15.5	0.26
M ₂	TRW	9	7.1	7.4	7.6	0.20
	TAW	9	7.4	7.6	7.9	0.26
	L	9	13.0	13.5	13.9	0.26
M ₃	W	4	5.4	5.6	5.8	
	L	4	10.2	10.4	10.6	
ramus	L	1		40.5		
	H	1		36.1		
	LUF	1		7.0		
	LLF	1		11.1		
	HC	1		19.1		

Table 32. Measurements of *Mafia csarnotensis* gen. et sp. nov. from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	7	10.7	11.9	13.0	0.79
	L	6	21.5	24.0	25.3	
	H	6	15.2	16.0	16.8	
P ⁴	PE	4	11.6	12.1	12.8	
	LL	3	12.1	12.2	12.3	
	BL	2	17.7	17.8	17.9	
	W	2	15.1	15.8	16.5	
M ¹	PE	5	12.9	13.6	14.1	
	LL	3	15.9	16.3	16.8	
	BL	5	15.2	15.9	16.5	
	AW	4	15.9	16.3	16.7	
M ²	PW	3	17.6	18.0	18.6	
	PE	1		12.4		
	LL	1		14.8		
M ₁	AW	1		17.8		
	TRW	5	9.1	9.9	11.0	
	TAW	5	9.7	10.4	11.0	
M ₂	L	5	16.7	17.5	18.5	
	TRW	8	8.9	9.5	10.1	0.41
	TAW	8	8.7	9.2	9.9	0.44
ramus	L	8	15.4	16.0	17.0	0.50
	H	1		49.8		
	LUF	4	44.9	49.6	51.5	
	LLF	5	11.7	12.7	13.3	
	HC	6	15.1	15.9	17.1	
		6	24.2	26.4	27.2	

Table 33. Measurements of *Blarinoides mariae* Sulimski, 1959 from Osztramos 9.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	3	11.4	13.4	15.4	
	L	3	28.4	31.3	32.4	
	H	3	19.1	19.3	19.7	
P ⁴	PE	1		18.5		
	LL	1		17.8		
	BL	1		26.3		
	W	1		22.1		
M ¹	PE	1		18.8		
	LL	1		20.0		
	BL	1		22.9		
	AW	1		c. 23.0		
M ²	PW	1		c. 23.5		
	PE	1		15.5		
	LL	1		16.6		
I inf.	BL	1		17.1		
	L	1		69.8		
ramus	LUF	1		14.1		

Table 34. Measurements of *Blarinoides mariae* Sulimski, 1959 from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	46	12.3	14.6	16.7	1.02
	L	36	29.3	32.5	35.1	1.38
	H	55	18.3	20.3	23.3	1.07
P ⁴	PE	22	18.4	20.5	22.8	1.13
	LL	21	18.4	20.7	23.5	1.19
	BL	32	25.9	28.6	30.9	1.28
	W	22	22.5	24.2	27.4	1.34
M ¹	PE	48	18.7	20.6	22.8	0.81
	LL	45	19.8	22.4	24.3	0.98
	BL	45	21.4	23.2	25.7	0.94
	AW	44	23.1	25.6	27.8	1.14
	PW	39	22.6	25.2	28.3	1.19
M ²	PE	29	13.9	15.5	17.1	0.74
	LL	26	15.5	17.3	19.2	1.04
	BL	29	16.2	17.6	19.1	0.75
	AW	26	22.0	24.3	27.1	1.28
	PW	26	15.1	18.0	20.0	1.21
M ³	L	1		7.5		
	W	1		13.4		
I inf.	L	18	64.8	70.5	75.3	2.76
M ₁	TRW	63	13.6	15.5	17.1	0.80
	TAW	66	14.5	16.1	17.6	0.77
	L	62	24.1	26.7	29.6	1.25
M ₂	TRW	42	11.9	13.4	15.2	0.72
	TAW	43	11.8	13.3	14.8	0.73
	L	42	19.0	20.8	23.3	0.87
M ₃	W	17	8.4	8.8	9.8	0.40
	L	17	12.4	13.5	14.7	0.59
M ₁ -M ₃	L	5	54.2	55.8	58.0	
ramus	L	8	57.7	60.8	63.9	2.17
	H	31	60.9	66.4	71.1	2.89
	LUF	42	15.3	18.4	20.6	1.34
	LLF	48	25.5	28.3	31.3	1.32
	HC	39	28.8	32.8	40.2	2.16

Table 35. Measurements of *Blarinoides mariae* Sulimski, 1959 from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	15	12.8	14.0	17.0	1.15
	L	11	29.2	31.4	34.0	1.65
	H	18	17.5	19.9	22.3	1.01
P ⁴	PE		not measurable			
	LL		not measurable			
	BL	24	25.4	27.6	29.3	1.08
	W	26	21.1	22.6	24.4	0.89
M ¹	PE	28	19.0	20.4	22.9	1.01
	LL	30	20.0	21.9	23.7	0.99
	BL	24	21.1	23.1	24.8	0.98
	AW	29	23.2	24.9	27.6	1.08
	PW	22	22.4	24.5	26.2	0.78
M ²	PE	21	13.6	15.3	16.5	0.75
	LL	21	14.6	16.8	18.1	0.99
	BL	20	16.0	17.7	19.2	0.91
	AW	19	21.9	24.2	26.3	0.98
	PW	18	15.6	17.4	18.9	0.96
M ³	L	2	7.7	7.9	8.0	
	W	3	13.4	13.8	14.1	
I inf.	L	4	69.7	71.3	73.1	
M ₁	TRW	80	12.7	14.5	16.5	0.72
	TAW	80	13.3	15.1	16.8	0.66
	L	75	23.3	26.2	29.1	1.49
M ₂	TRW	68	11.0	12.8	14.1	0.80
	TAW	67	11.1	12.8	14.4	0.77
	L	69	18.2	20.2	22.2	0.93
M ₃	W	34	7.1	8.8	9.9	0.66
	L	34	12.1	13.3	15.5	0.82
M ₁ -M ₃	L	22	50.2	54.7	58.0	1.73
ramus	L	13	54.2	59.0	64.4	3.12
	H	14	60.2	64.8	71.8	2.91
	LUF	16	14.8	17.2	19.5	1.15
	LLF	20	26.1	27.9	30.4	1.25
	HC	14	26.8	31.4	34.7	2.13

Table 36. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Osztramos 9.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	16	5.9	6.5	7.4	0.38
	L	15	13.1	14.6	15.6	0.67
	H	16	10.4	11.5	12.8	0.72
P ⁴	PE	13	8.3	9.6	10.8	0.77
	LL	13	9.4	10.5	11.6	0.76
	BL	13	14.2	14.9	16.0	0.50
	W	13	12.2	14.2	16.6	1.06
M ¹	PE	11	11.4	12.0	12.6	0.41
	LL	11	13.1	14.3	15.6	0.65
	BL	11	13.7	14.9	15.9	0.60
	AW	12	13.1	13.9	14.8	0.44
	PW	10	14.5	15.8	16.5	0.55
M ²	PE	7	10.0	10.4	10.9	0.31
	LL	7	11.8	12.5	13.1	0.57
	BL	6	11.8	12.9	14.0	
	AW	5	13.7	14.5	15.1	
	PW	5	12.7	14.1	16.0	
M ³	L	3	5.3	6.0	6.6	
	W	3	9.9	11.0	12.3	
I inf.	L	4	29.6	31.8	33.3	
M ₁	TRW	15	7.2	7.7	8.5	0.36
	TAW	16	7.7	8.6	9.4	0.47
	L	13	14.1	14.9	15.8	0.48
M ₂	TRW	13	7.0	7.6	8.0	0.29
	TAW	13	7.3	7.9	8.3	0.29
	L	13	12.7	13.9	15.6	0.70
M ₃	W	8	5.6	6.3	6.8	0.46
	L	8	10.2	10.8	11.5	0.45
M ₁ -M ₃	L	3	36.5	37.8	38.7	
ramus	H	3	40.2	41.4	42.3	
	LUF	5	6.6	7.5	8.3	
	LLF	5	12.6	13.5	14.4	
	HC	5	20.9	21.8	23.6	

Table 37. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Osztramos 1.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	1		5.5		
	L	1		14.9		
	H	1		10.3		
P ⁴	PE	2	8.9	9.8	10.6	
	LL	1		12.5		
	BL	2	13.9	14.8	15.7	
	W	2	12.5	12.9	13.3	
M ¹	PE	3	11.0	11.2	11.5	
	LL	3	13.7	13.8	13.9	
	BL	2	14.3	14.5	14.6	
	AW	3	12.6	13.5	14.7	
M ²	PW	2	15.4	15.6	15.7	
	PE	2	9.8	9.9	9.9	
	LL	2	11.7	11.9	12.0	
	BL	2	11.9	12.6	13.2	
AW	AW	2	13.3	13.6	13.9	
	PW	2	12.3	12.9	13.4	
I inf.	L	9	28.0	29.7	31.5	1.23
M ₁	TRW	4	7.1	7.4	7.6	
	TAW	4	7.8	8.0	8.2	
	L	4	13.8	14.6	15.0	
M ₂	TRW	6	6.2	6.9	7.5	
	TAW	7	6.7	7.2	7.5	0.28
	L	6	13.3	13.8	14.3	
M ₃	W	2	5.2	5.5	5.8	
	L	2	10.0	10.5	10.9	
ramus	L	1		43.5		
	H	1		39.2		
	LUF	1		9.2		
	LLF	1		14.0		
	HC	1		22.4		

Table 38. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Osztramos 7: upper teeth of morphotype A.

element	prm	n	min	\bar{x}	max	sd
P ⁴	PE	1		9.9		
	LL	1		10.5		
	BL	1		16.8		
	W	1		15.1		
M ¹	PE	7	11.3	12.7	13.7	0.78
	LL	6	14.3	15.0	15.5	
	BL	5	14.7	15.0	15.7	
	AW	5	14.5	15.6	16.2	
	PW	4	17.2	17.6	18.2	
M ²	PE	4	11.2	11.5	11.7	
	LL	4	12.5	13.2	13.5	
	BL	3	12.9	13.1	13.3	
	AW	4	16.1	16.9	17.5	
	PW	3	15.1	15.7	16.4	
M ³	L	1		7.2		
	W	1		13.2		

Table 39. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Osztramos 7: upper teeth of morphotype B.

element	prm	n	min	\bar{x}	max
P ⁴	PE	5	8.3	9.4	10.5
	LL	5	9.9	11.2	12.3
	BL	5	15.5	16.2	16.6
	W	5	14.1	14.7	15.2
M ¹	PE	4	11.9	12.2	12.8
	LL	4	14.0	14.9	15.4
	BL	4	15.6	16.1	16.6
	AW	4	14.1	15.1	15.7
	PW	4	17.2	17.8	18.7
M ²	PE	3	11.0	11.3	11.6
	LL	3	13.2	13.3	13.5
	BL	3	13.8	14.1	14.8
	AW	3	14.9	15.6	16.3
	PW	3	15.0	15.4	15.7

Table 40. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Osztramos 7: other dental elements and the ramus.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	7	7.0	8.0	8.8	0.60
	L	5	17.2	18.2	19.7	
	H	7	12.8	13.5	14.1	0.46
I inf.	L	1		36.2		
M ₁	TRW	16	8.1	8.7	9.4	0.44
	TAW	16	8.9	9.6	10.2	0.44
	L	15	14.6	16.4	18.1	0.82
M ₂	TRW	18	7.4	8.0	8.6	0.36
	TAW	20	7.5	8.3	9.1	0.40
	L	17	13.3	15.0	16.3	0.73
M ₃	W	10	6.0	6.4	6.8	0.24
	L	10	10.6	11.4	12.4	0.49
ramus	L	2	44.5	44.8	45.0	
	H	2	38.4	40.6	42.8	
	LUF	5	8.7	9.2	9.7	
	LLF	5	14.5	15.2	16.3	
	HC	3	20.0	22.4	23.8	

Table 41. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	114	6.4	8.0	10.3	0.67
	L	105	14.3	18.2	21.3	1.11
	H	115	10.3	12.6	14.0	0.62
P ⁴	PE	30	7.5	8.8	10.3	0.60
	LL	30	8.3	10.4	11.6	0.68
	BL	29	14.1	16.1	17.0	0.62
	W	31	12.5	13.9	15.0	0.69
M ¹	PE	71	10.6	12.3	13.5	0.49
	LL	68	13.2	14.4	15.5	0.48
	BL	57	13.1	14.8	15.8	0.46
	AW	63	13.0	15.2	16.9	0.56
M ²	PW	51	15.2	16.9	18.6	0.61
	PE	47	9.7	11.0	11.8	0.41
	LL	46	11.3	12.6	13.5	0.52
	BL	45	11.5	12.7	13.6	0.45
I inf.	AW	35	13.8	16.0	17.3	0.74
	PW	42	13.5	14.7	15.8	0.56
M ₁	L	75	31.0	33.7	38.9	1.47
	TRW	173	7.0	8.4	9.7	0.39
	TAW	180	8.0	9.2	10.2	0.44
M ₂	L	167	13.9	15.7	17.6	0.65
	TRW	179	6.9	7.9	9.3	0.36
	TAW	186	7.1	8.3	9.2	0.38
M ₃	L	177	12.7	14.4	15.9	0.59
	W	48	5.8	6.4	7.3	0.34
M ₁ -M ₃	L	47	9.4	11.2	12.3	0.51
	L	19	36.4	38.5	40.4	0.97
ramus	L	25	43.7	46.2	49.0	1.45
	H	97	36.7	42.4	45.8	1.59
	LUF	187	6.7	9.0	10.8	0.76
	LLF	201	12.3	14.6	17.4	0.85
	HC	167	18.7	22.6	25.5	1.24

Table 42. Measurements of *Episoriculus gibberodon* (Petényi, 1864) from Villány 3.

element	prm	n	min	\bar{x}	max
M ¹	PE	1		10.6	
	LL	1		13.6	
	BL	1		13.8	
	AW	1		13.5	
	PW	1		16.1	
I inf.	L	2	30.5	30.6	30.7
M ₁	TRW	4	7.8	8.1	8.6
	TAW	4	8.4	8.7	8.8
	L	4	14.5	15.1	15.5
M ₂	TRW	5	7.5	7.8	8.2
	TAW	5	7.6	7.9	8.3
	L	5	13.3	13.6	13.8
M ₃	W	4	5.6	6.1	6.8
	L	4	10.3	10.7	11.2
M ₁ -M ₃	L	3	34.6	35.6	36.4
ramus	L	4	41.0	41.5	42.0
	H	4	38.8	39.1	39.3
	LUF	5	7.3	8.4	9.6
	LLF	5	12.4	12.9	13.6
	HC	5	18.5	21.0	22.6

Table 43. Measurements of *Beremendia minor* Rzebik-Kowalska, 1976 from Osztramos 1.

element	prm	n	min	\bar{x}	max
P ⁴	BL	1		21.0	
M ₁	TRW	6	8.5	9.8	11.0
	TAW	6	9.7	10.8	11.7
	L	6	17.9	19.3	21.2
M ₂	TRW	4	8.4	8.9	9.2
	TAW	4	8.6	9.2	9.5
	L	4	15.9	16.5	16.8
M ₃	W	2	6.8	7.2	7.6
	L	2	11.7	12.4	13.0

Table 44. Measurements of *Beremendia minor* Rzebik-Kowalska, 1976 from Osztramos 7.

element	prm	n	min	\bar{x}	max
I sup.	LT	2	10.2	10.7	11.1
	L	1		26.5	
	H	2	18.8	19.1	19.3
P ⁴	PE	1		14.9	
	LL	1		15.9	
	BL	1		22.8	
	W	1		18.0	
M ¹	PE	1		16.6	
	LL	1		19.3	
	BL	1		20.2	
	AW	1		21.1	
	PW	1		21.9	
M ²	PE	1		14.1	
	AW	1		21.2	
I inf.	L	1		48.8	
M ₁	TRW	3	11.7	11.8	11.9
	TAW	2	11.9	12.2	12.4
	L	2	21.1	21.8	22.4
M ₂	TRW	2	10.0	10.3	10.6
	TAW	2	9.8	9.9	10.0
	L	2	16.9	17.7	18.4
M ₃	W	1		7.4	
	L	1		11.9	
ramus	LUF	1		13.1	
	LLF	1		24.7	
	HC	1		26.4	

Table 45. Measurements of *Beremendia fissidens* (Petényi, 1864) from Osztramos 7.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	20	14.5	16.2	19.2	1.15
	L	12	32.0	35.5	39.5	2.48
	H	26	19.7	22.6	24.1	1.15
P ⁴	PE	26	16.4	18.5	20.1	0.85
	LL	26	18.7	20.3	21.9	0.91
	BL	28	24.1	27.1	30.3	1.46
	W	29	20.9	23.3	25.5	1.20
M ¹	PE	33	17.9	19.4	21.9	0.79
	LL	32	21.0	23.5	27.2	1.21
	BL	28	23.9	25.1	26.2	0.62
	AW	30	22.3	24.8	26.8	1.14
	PW	27	23.8	26.2	27.6	0.89
M ²	PE	28	16.0	17.2	18.7	0.61
	LL	25	17.6	20.3	22.6	1.16
	BL	14	19.3	21.2	23.3	1.22
	AW	24	22.8	25.1	27.0	1.02
	PW	13	18.4	21.2	22.5	1.00
M ³	L	16	7.9	8.9	9.6	0.55
	W	13	15.8	17.3	18.6	0.81
I inf.	L	6	58.9	62.3	65.0	
M ₁	TRW	54	13.1	14.6	16.2	0.72
	TAW	58	13.0	15.0	16.9	0.76
	L	49	24.2	27.4	29.5	1.25
M ₂	TRW	54	12.2	13.6	15.1	0.64
	TAW	55	12.1	13.4	15.1	0.75
	L	50	21.4	23.3	25.3	0.99
M ₃	W	48	8.5	9.7	11.4	0.63
	L	47	14.9	17.1	19.4	1.00
M ₁ -M ₃	L	17	59.6	62.7	66.1	1.82
ramus	L	6	70.1	73.7	81.6	
	H	11	61.4	65.7	69.0	2.67
	LUF	14	16.9	18.8	22.2	1.68
	LLF	15	26.2	29.8	33.0	1.76
	HC	12	36.3	38.4	42.0	1.94

Table 46. Measurements of *Beremendia fissidens* (Petényi, 1864) from Csarnóta 2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	25	13.3	15.6	18.7	1.17
	L	20	31.9	34.6	38.0	1.37
	H	27	20.8	22.5	24.9	1.02
P ⁴	PE	21	16.6	18.5	21.2	1.16
	LL	19	18.5	20.0	22.6	1.21
	BL	25	25.3	27.0	28.8	0.90
	W	19	21.7	23.7	25.1	1.11
M ¹	PE	24	18.4	19.5	21.0	0.76
	LL	21	20.7	22.6	24.8	1.20
	BL	20	23.0	24.4	26.5	0.88
	AW	22	23.3	25.0	26.7	0.96
	PW	15	24.5	25.3	26.9	0.63
M ²	PE	21	15.5	16.8	18.2	0.68
	LL	19	17.6	19.6	22.1	1.12
	BL	19	19.2	21.0	23.1	0.95
	AW	20	22.7	24.5	26.2	1.04
	PW	16	18.4	20.6	22.1	1.04
I inf.	L	17	60.1	63.5	68.4	2.23
M ₁	TRW	47	12.8	14.7	16.5	0.88
	TAW	47	13.8	15.2	16.9	0.71
	L	44	23.7	26.6	29.9	1.34
M ₂	TRW	51	12.2	13.6	15.8	0.72
	TAW	51	11.9	13.4	15.1	0.72
	L	47	19.9	23.0	24.7	0.95
M ₃	W	28	8.4	9.5	10.5	0.65
	L	27	13.8	17.0	18.4	1.09
M ₁ -M ₃	L	7	57.8	61.5	65.5	2.53
ramus	L	7	68.9	72.1	75.7	2.47
	H	20	59.3	64.4	68.8	2.67
	LUF	44	15.6	19.4	22.8	1.71
	LLF	44	25.5	28.7	30.8	1.29
	HC	41	29.9	36.5	41.7	2.75

Table 47. Measurements of *Beremendia fissidens* (Petényi, 1864) from Villány 3.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	14	12.1	14.0	15.6	1.05
	L	11	29.2	31.8	34.8	1.96
	H	14	22.0	23.8	25.6	1.05
P ⁴	PE	7	17.7	20.2	21.2	1.28
	LL	7	18.9	21.1	22.2	1.29
	BL	10	26.2	29.1	32.1	1.77
	W	7	24.8	25.7	27.5	0.92
M ¹	PE	14	17.9	20.7	22.1	1.02
	LL	13	21.1	24.7	26.6	1.40
	BL	13	23.0	26.2	28.5	1.51
	AW	14	23.8	26.1	29.0	1.49
	PW	13	25.1	27.1	29.2	1.08
M ²	PE	16	16.4	17.7	19.3	0.73
	LL	13	18.6	20.8	21.8	0.94
	BL	12	20.5	21.8	23.9	0.83
	AW	15	24.2	26.1	27.7	0.96
	PW	10	19.5	21.2	22.6	1.05
M ³	L	5	9.5	10.0	10.5	
	W	5	17.1	17.7	18.9	
I inf.	L	19	59.8	64.6	69.0	2.98
M ₁	TRW	24	15.6	16.8	18.3	0.64
	TAW	24	16.2	17.8	19.2	0.77
	L	24	25.2	29.2	30.6	1.25
M ₂	TRW	30	13.4	15.1	16.5	0.71
	TAW	30	13.1	14.8	15.9	0.77
	L	31	22.4	24.5	25.7	0.81
M ₃	W	19	9.6	10.3	11.3	0.40
	L	20	15.7	17.1	18.2	0.65
M ₁ -M ₃	L	13	62.1	64.2	65.8	1.15
ramus	L	12	71.0	76.3	80.8	3.05
	H	17	61.6	68.4	74.8	3.42
	LUF	17	16.4	19.4	21.8	1.41
	LLF		not measurable			
	HC	17	33.7	38.1	41.5	2.27

Table 48. Measurements of *Beremendia fissidens* (Petényi, 1864) from Tegelen.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	5	14.7	15.9	17.4	
	L	6	31.9	34.6	37.2	
	H	5	22.0	22.6	23.3	
P ⁴	PE	5	16.4	17.9	19.5	
	LL	5	18.1	19.4	21.2	
	BL	7	25.5	27.4	29.0	1.39
	W	5	21.4	23.1	24.1	
M ¹	PE	9	18.0	19.6	20.7	1.09
	LL	9	21.5	23.5	25.0	1.23
	BL	9	21.8	24.5	25.8	1.17
	AW	10	21.8	25.2	26.9	1.50
	PW	9	22.7	25.5	26.9	1.28
M ²	PE	3	14.8	16.0	17.2	
	LL	3	18.2	18.7	19.6	
	BL	2	19.3	19.7	20.0	
	AW	3	23.3	24.4	25.1	
	PW	2	19.0	19.8	20.6	
M ³	L	2	9.3	9.8	10.3	
	W	2	16.2	17.0	17.7	
I inf.	L	1		61.1		
M ₁	TRW	7	13.7	14.5	15.3	0.59
	TAW	8	14.8	15.3	16.2	0.51
	L	7	25.8	26.9	28.8	1.07
M ₂	TRW	4	13.1	13.7	14.5	
	TAW	5	12.5	13.1	14.0	
	L	4	21.2	22.1	22.9	
M ₃	W	3	8.4	8.9	9.3	
	L	3	15.5	15.7	16.0	
ramus	L	1		76.5		
	H	3	62.5	63.2	63.9	
	LUF	3	17.4	18.2	18.6	
	LLF	3	27.5	28.5	29.7	
	HC	3	33.7	35.2	36.5	

Table 49. Measurements of *Beremendia fissidens* (Petényi, 1864) from Osztramos 3/2.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	3	16.1	16.4	16.7	
	L	3	37.4	38.9	40.5	
	H	3	20.4	23.3	24.9	
M ¹	PE	1		19.4		
	BL	1		24.5		
	AW	1		24.0		
	PW	1		23.9		
I inf.	L	2	62.7	63.5	64.2	
M ₁	TRW	13	13.9	15.0	15.9	0.62
	TAW	12	14.3	15.7	17.0	0.69
	L	12	25.0	27.6	29.7	1.33
M ₂	TRW	11	12.1	13.7	14.3	0.57
	TAW	11	11.9	13.3	14.2	0.58
	L	11	19.4	22.6	24.1	1.32
M ₃	W	11	8.0	9.4	10.1	0.59
	L	10	12.6	16.1	17.1	1.27
M ₁ -M ₃	L	7	53.3	61.1	65.1	3.73
ramus	L	3	69.0	72.9	76.0	
	H	3	59.6	64.6	68.1	
	LUF	5	17.0	18.7	20.2	
	LLF	5	27.5	29.9	31.7	
	HC	4	35.6	37.8	40.3	

Table 50. Measurements of *Amblycoptus topali* Jánossy, 1972 from Osztramos 1.

element	prm	n	min	\bar{x}	max	sd
I sup.	LT	6	10.6	11.6	12.8	
	L	6	26.6	28.1	29.5	
	H	6	19.3	21.6	22.8	
P ¹	PE	4	24.4	26.0	27.7	
	LL	4	24.8	27.2	28.9	
	BL	4	29.4	30.7	31.4	
	W	4	24.4	25.3	26.2	
M ¹	PE	6	19.2	21.0	22.0	
	LL	6	20.5	21.9	23.6	
	BL	6	23.7	24.8	25.4	
	AW	5	28.7	29.5	30.1	
	PW	6	17.7	18.4	19.3	
I inf.	L	4	68.9	71.5	74.3	
M ₁	TRW	10	14.4	15.8	16.6	0.75
	TAW	11	12.5	15.2	16.5	1.03
	L	11	31.7	32.9	35.6	1.12
M ₂	W	4	8.9	9.8	10.7	
	L	4	15.9	16.9	18.1	
M ₁ -M ₂	L	4	47.1	48.0	48.9	
ramus	L	4	45.6	47.6	49.1	
	H	4	65.8	68.6	71.9	
	LUF	5	9.6	12.3	13.8	
	LLF	6	21.9	23.5	26.6	
	HC	5	31.4	32.2	33.1	

Table 51. Measurements of *Paenelimnoecus pannonicus* (Kormos, 1934) from Osztramos 9.

element	prm	n	min	\bar{x}	max
I sup.	LT	3	6.2	6.6	7.0
	L	3	13.4	13.7	14.1
	H	3	8.1	8.4	8.5
I inf.	L	3	23.5	25.3	27.1
M ₁	TRW	1		6.3	
	TAW	1		6.9	
	L	3	10.4	11.1	11.7
M ₂	TRW	3	5.9	6.3	6.6
	TAW	3	6.1	6.3	6.5
	L	3	9.9	10.4	10.8
M ₃	W	2	4.3	4.8	5.2
	L	2	7.0	7.1	7.2
M ₁ -M ₃	L	1		27.3	
ramus	L	1		30.2	
	H	1		25.5	
	LUF	2	4.7	4.8	4.8
	LLF	2	8.7	9.1	9.4
	HC	2	12.2	12.6	13.0

Table 52. Measurements of *Paenelimoecus pannonicus* (Kormos, 1934) from Osztramos 7.

element	prim	n	min	\bar{x}	max	sd
P ⁴	PE	1		5.8		
	LL	1		7.2		
	BL	1		10.3		
	W	1		10.7		
M ¹	PE	3	7.2	7.6	8.2	
	LL	3	9.1	9.7	10.1	
	BL	3	10.1	10.6	10.9	
	AW	3	10.9	11.3	11.6	
	PW	3	11.8	12.4	13.0	
M ²	PE	3	6.6	6.8	7.1	
	LL	3	8.1	8.4	8.6	
	BL	2	8.5	9.0	9.4	
	AW	2	11.3	11.7	12.0	
	PW	2	10.2	10.7	11.1	
M ₁	TRW	3	4.9	5.9	6.7	
	TAW	3	5.0	6.0	6.8	
	L	3	10.0	11.2	12.0	
M ₂	TRW	4	5.2	6.0	6.8	
	TAW	4	5.1	5.8	6.4	
	L	4	8.5	9.8	10.4	
M ₃	W	4	4.3	4.5	4.9	
	L	3	5.9	6.6	7.1	
M ₁ -M ₃	L	2	23.0	24.7	26.3	
ramus	L	1		28.0		

Table 53. Measurements of *Paenelimoecus pannonicus* (Kormos, 1934) from Csarnóta 2.

element	prim	n	min	\bar{x}	max	sd
I sup.	LT	13	6.3	7.2	8.2	0.55
	L	13	13.3	14.0	15.0	0.53
	H	14	8.3	9.0	9.8	0.40
P ⁴	PE	7	5.6	6.3	7.6	0.67
	LL	6	7.1	7.9	9.0	
	BL	7	10.2	11.1	11.7	0.53
	W	7	10.7	11.6	12.5	0.66
M ¹	PE	24	7.9	8.4	9.0	0.33
	LL	21	10.5	11.2	11.9	0.39
	BL	25	10.4	11.1	12.1	0.41
	AW	24	10.9	12.0	13.1	0.55
	PW	21	12.8	13.4	14.4	0.40
M ²	PE	16	7.2	7.8	8.3	0.33
	LL	15	9.1	10.2	10.8	0.56
	BL	15	9.2	10.1	10.6	0.39
	AW	15	11.5	12.4	13.0	0.42
	PW	14	11.5	12.0	12.7	0.35
M ³	L	1		3.7		
	W	1		8.9		
I inf.	L	9	26.4	27.2	28.1	0.56
M ₁	TRW	30	5.4	6.2	6.9	0.39
	TAW	34	5.7	6.6	7.2	0.37
	L	27	11.1	12.0	13.1	0.55
M ₂	TRW	55	5.5	6.4	7.2	0.34
	TAW	56	5.4	6.3	7.2	0.33
	L	55	9.8	11.0	11.8	0.47
M ₃	W	27	4.7	5.2	5.6	0.29
	L	24	6.8	7.7	8.5	0.42
M ₁ -M ₃	L	7	27.8	28.6	29.4	0.57
ramus	L	13	29.9	31.4	34.7	1.41
	H	101	26.1	28.8	32.2	1.04
	LUF	125	4.5	5.8	7.2	0.52
	LLF	146	8.4	9.7	11.1	0.56
	HC	121	12.1	13.8	15.9	0.76

Table 54. Results of the calculations of the PE-index, given for each individual species of each locality; the numbers (left and right) correspond to those given in Fig. 18.

no.	species	loc.	M ¹			M ²			x̄	min	max	no.
			n	n	n	n	n	n				
1	<i>Petenya hungarica</i>	Cs2	1			0.08	0.08				1	
2	<i>Petenya hungarica</i>	Osz1	3			0.08	0.09	0.09	0.09	0.11	2	
3	<i>Petenya hungarica</i>	Osz3/2	5			0.07	0.09	0.10	0.09	0.14	3	
4	<i>Petenya hungarica</i>	Te	5			0.07	0.09	0.10	0.09	0.11	4	
5	<i>Petenya hungarica</i>	V13	5			0.05	0.09	0.10	0.07	0.12	5	
6	<i>Petenya hungarica</i>	Osz7	20			0.06	0.09	0.14	0.07	0.10	6	
7	<i>Petenya aff. hungarica</i>	Osz9	3			0.06	0.08	0.11		0.08	7	
8	<i>Blarinella dubia</i>	Osz9	1			0.05	0.05			0.11	8	
9	<i>Blarinella europaea</i>	Osz1	1			0.05	0.05				9	
10	<i>Blarinella europaea</i>	Cs2	5			0.05	0.08	0.10	0.06	0.11	10	
11	<i>Blarinoides mariae</i>	Cs2	38			0.04	0.11	0.16	0.09	0.19	11	
12	<i>Blarinoides mariae</i>	Osz7	22			0.05	0.11	0.15	0.08	0.17	12	
13	<i>Blarinoides mariae</i>	Osz9	1			0.14	0.14			0.09	13	
14	<i>Amblycoptus topali</i>	Osz1	6			0.08	0.11	0.15	0.10	0.17	14	
15	<i>Zelcena soriculoides</i>	Cs2	16			0.09	0.13	0.21	0.10	0.17	15	
16	<i>Mafia csarmolense</i>	Cs2	3			0.13	0.17	0.22			16	
17	<i>Drepanosorex praeareanus</i>	Osz3/2	4			0.12	0.16	0.19	0.10	0.15	17	
18	<i>Drepanosorex praeareanus</i>	Te	33			0.15	0.21	0.27	0.10	0.25	18	
19	<i>Episoriculus gibberodon</i>	Cs2	51			0.15	0.19	0.24	0.10	0.22	19	
20	<i>Episoriculus gibberodon</i>	Osz7(A)	4			0.13	0.17	0.20	0.13	0.15	20	
21	<i>Episoriculus gibberodon</i>	Osz7(B)	4			0.25	0.27	0.29	0.18	0.24	21	
22	<i>Episoriculus gibberodon</i>	Osz9	11			0.17	0.22	0.26	0.18	0.31	22	
23	<i>Episoriculus gibberodon</i>	Osz1	2			0.24	0.26	0.27	0.19	0.29	23	
24	<i>Episoriculus gibberodon</i>	V13	1			0.29	0.29				24	
25	<i>Beremendia minor</i>	Osz7	1			0.19	0.19				25	
26	<i>Beremendia fissidens</i>	Cs2	16			0.15	0.21	0.26	0.16	0.25	26	
27	<i>Beremendia fissidens</i>	V13	11			0.21	0.23	0.27	0.16	0.27	27	
28	<i>Beremendia fissidens</i>	Te	9			0.19	0.23	0.28	0.16	0.27	28	
29	<i>Beremendia fissidens</i>	Osz7	26			0.20	0.26	0.30	0.15	0.24	29	
30	<i>Deinsdorffia janossyi</i>	Osz9	3			0.22	0.23	0.24	0.15	0.28	30	
31	<i>Deinsdorffia kardosi</i>	Cs2	8			0.19	0.24	0.31	0.17	0.24	31	
32	<i>Deinsdorffia hibbardi</i>	Osz7	23			0.20	0.28	0.36	0.17	0.31	32	
33	<i>Sorex bor</i>	Osz9	3			0.18	0.20	0.25	0.17	0.25	33	
34	<i>Sorex bor</i>	Osz1	4			0.21	0.23	0.26	0.19	0.19	34	
35	<i>Sorex minutus</i>	Osz3/2	2			0.19	0.21	0.22	0.16	0.23	35	
36	<i>Sorex minutus</i>	Osz7	8			0.19	0.23	0.29	0.16	0.23	36	
37	<i>Sorex minutus</i>	Te	12			0.20	0.26	0.32	0.13	0.26	37	
38	<i>Sorex sp.</i>	Osz7	1			0.24	0.24				38	
39	<i>Paenelimoecus pannonicus</i>	Cs2	21			0.25	0.33	0.40	0.25	0.35	39	
40	<i>Paenelimoecus pannonicus</i>	Osz7	3			0.27	0.33	0.44	0.26	0.27	40	
41	<i>Soricini</i> gen. et sp. indet.	Osz1	1			0.30	0.28		0.20	0.26	41	
42	<i>Crocidura kornfeldi</i>	V13	15			0.30	0.36	0.47	0.20	0.31	42	
43	<i>Crocidura kornfeldi</i>	Osz3/2	1			0.45	0.45				43	