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CUPRINS**CONTENT****Palaeontology****Paleontologie**

ZOLTÁN CZIER: The Genus <i>Zamites</i> Brongniart 1828 emend. Harris 1969 (Bennettitales) in the fossil flora of Romania.....	5
JÁNOS HÍR & MÁRTON VENCZEL: A preliminary report on the first results of the re-excavation of the middle Miocene palaeovertebrate locality Szentendre, Cseresznyés-árok (Hungary, Pest County).....	35
ERIKA POSMOȘANU, RADU HUZA, GAVRIL BOBȘE & IOAN JUDEA: Bioerosion and encrustation on a middle Miocene <i>Gigantopecten</i> <i>nodosiformis</i> shell from Tășad, Bihor, Romania.....	81
MÁRTON VENCZEL: The type material of <i>Parahynobius betfianus</i>	99

NYMPHAEA Folia naturae Bihariae	XLV	5 - 34	Oradea, 2018
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The Genus *Zamites* Brongniart 1828 emend. Harris 1969 (Bennettitales) in the fossil flora of Romania

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Abstract. New Bennettitalean foliage originating from the Konservat-Lagerstätte Anina (Banat region, Romania, eastern Central-Europe) is presented. Although the cuticular analysis by Light- and Scanning Electron Microscopy reveals many details of the epidermal structure, the leaves described and figured herein are attributed just to cf. *Zamites* sp. 1, cf. *Zamites* sp. 2, and aff. *Zamites* sp., because the absence of the adaxial cuticle in the microscope preparations does not allow creating new species. The occurrences of these taxa are in the limits of the Hettangian *pro parte* – Sinemurian interval of the Steierdorf Formation, Valea Terezia Sandstone Member; all of them come from the *Clathropteris meniscioides* Biozone, the *Banatozamites chlamydstomus* Subzone. The Romanian *Zamites* material is completely revised. It is known from the Early Jurassic continental deposits of the Eastern Carpathians (Cristian) and Southern Carpathians (Crivi valley, Berzasca, Buschmann mine, Pietrele Albe, Dragosella, Cozla, Mehadia, Viezuroi mine, Crasna, Baia de Aramă, Anina, Doman, Vulcan, Holbav). No one formerly known species of *Zamites* is recognised in the Romanian fossil flora. Moreover, the usage of “cf.”, “aff.”, or even of “?” before the *Zamites* generic name is necessary.

Keywords. Bennettitales, Jurassic, cuticular analysis, Macroflora, Romania, *Zamites*.

Introduction

During the history of palaeobotany, the always trendy Bennettitalean genus *Zamites* Brongniart 1828, was and still is frequently cited as being present with a lot of species in all the regions of the Mesophytic world. The type species selected by Andrews (1955) is *Zamia gigas* Lindley and Hutton 1835, a species that Morris (1843) transferred later to *Zamites*. Enumeration of the vast international literature dealing with this genus is not subject of the present paper; just the still valid discussion of Seward (1917) and the emended generic diagnosis of Harris (1969) are mentioned on this occasion.

The Romanian literature abounds in *Zamites* citations. Many authors mention in a way or other data in this respect but the majority of those data are based on old papers that seldom contain a description or figuration, and those few that exist are incomplete. Only Andrae (1855), Thomas (1930), Langer (1947), Semaka (1962c, 1970), Mateescu (1964), Givulescu (1989, 1991, 1998), and Berg (1996) published descriptions and figurations of some specimens. However, all those are exclusively based on macro-morphological features or on incomplete cuticular characters if mentioned any. A complete revision of the Romanian material is necessary, not only because of this incompleteness, but also owing to the usually ignored emendation of the genus.

Apart from the presentation of new specimens that are kept at Budapest (Hungary) in the Palaeobotanical Collection of the Hungarian Natural History Museum (HNHM-BP), a scope of this research is the revision of the Romanian *Zamites* material. This is part of the author's project regarding the description and revision of the Jurassic macroflora and localities of the Carpathian-Pannonian area (Czier & Popescu 1988; Givulescu & Czier 1990; Czier 1989, 1990, 1991, 1992, 1993, 1994, 1995a, 1995b, 1995c, 1995d, 1996a, 1996b, 1997a, 1997b, 1997c, 1998a, 1998b, 1998c, 1999a, 1999b, 1999c, 2000a, 2000b, 2000c, 2000d, 2001, 2002, 2003a, 2003b, 2004, 2005, 2006, 2008, 2009, 2010, 2011, 2014, 2016a, 2016b, 2017). A planned goal to attain also is to determine the stratigraphic distribution of the specimens, in the context of the new scheme (Czier 2017) containing the litho- and biostratigraphical units of their origin.

Geographic distribution

The study of the literature mentioning Romanian *Zamites* material, allows drawing a map of geographical distribution, which is a necessary first evidence for any research detailing this subject (Fig. 1).



Figure 1. Geographical map of Romania, indicating the fossiliferous localities with *Zamites* material. 1. Cristian; 2. Crivi valley; 3. Berzasca; 4. Buschmann mine; 5. Pietrele Albe; 6. Dragosella; 7. Cozla; 8. Mehadia; 9. Vierzuroi mine; 10. Crasna; 11. Baia de Aramă; 12. Anina; 13. Doman; 14. Vulcan; 15. Holbav.

The Romanian *Zamites* material is known from the continental Early Jurassic deposits of the Eastern Carpathians (Cristian) and Southern Carpathians (Crivi valley, Berzasca, Buschmann mine, Pietrele Albe, Dragosella, Cozla, Mehadia, Vierzuroi mine, Crasna, Baia de Aramă, Anina, Doman, Vulcan, Holbav).

Geology and stratigraphy

The new material presented herein originates from Konservat-Lagerstätte Anina (Banat region, South-west Romania). The geology and stratigraphy of this locality already being extensively presented, and problems concerning the age intervals of the fossil flora occurrences, the lithostratigraphic and the biostratigraphic units also being clarified (Czier 1999a, 1999b, 2000a, 2016b, 2017), these data are not repeated here.

Material and methods

A plant fossil specimen (HNHM-BP-602141) is preserved as compression of three fragments of a leaf, on a slab of fine-grained clastic sedimentary rock. The specimen was collected between the last decade of the 19th Century and before the end of the WW II.

A leaf compression of another plant fossil specimen (HNHM-BP-602231-1) is preserved on a face of another slab consisting from the same type of rock. A leaf impression of a third specimen (HNHM-BP-602231-2) is preserved on the other face of this slab. The slab containing these two specimens was collected in the second half of the 19th Century.

Although the specimens were collected from unknown sampling points around Anina, based on the label's information and the rock's aspect it is clear that the entire material comes from the Anina coal-bearing sequence of the Valea Terezia Sandstone Member of the Steierdorf Formation, from the *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, but the names of the collectors are unknown.

After macroscopical study, the material was analysed under light microscope (LM) and scanning electron microscope (SEM). Cuticles were prepared trying to use the method already described in details (Czier 2014, 2017). However, the adaxial cuticle of all specimens was so thin and delicate, that it has been lost during the preparation process, despite the maximal carefulness of the preparation by the author himself. Only the abaxial cuticle of the specimens was obtained in preparations, therefore this study is limited by the absence of the adaxial cuticle. Such circumstances rather commonly may appear when researchers prepare benettitalean cuticles of Anina specimens, and probably this is why Givulescu (1989, 1991, 1998) also was unable to describe and figure any adaxial cuticle of the material he had studied.

Nomenclature, taxonomy, and revision principles

The emended diagnosis that Harris (1969, p. 5) gives for the genus *Zamites* stipulates: „Leaf simply pinnate, pinnae attached to upper side of rachis; pinnae lanceolate; base of pinna symmetrically contracted and attached by a small area in middle of basal margin; apex of pinna acute; veins diverging from pinna base, dichotomising but not anastomosing; ending in pinna margins and apex. Cuticle developed, stomata syndetocheilic with one subsidiary cell beside each guard

cell; confined to under surface; epidermal cell walls sinuous.” Therefore, before attributing any specimen to *Zamites*, we should not forget that diagnostic features of this Bennettitalean genus include both morphologic and epidermal characters. Without denying the importance of the macromorphological characters of the leaf, the epidermal characters of the lamina are among the most important diagnostic features. However, the diagnostic epidermal characters can be proved only when both the adaxial cuticle and the abaxial cuticle are preserved and both are present in the microscope preparations, furthermore if both cuticles are described and figured. No sure generic determination is possible when any of these evidences is missing. Determinations of specimens assigned as sure to *Zamites* are susceptible to revision whenever the diagnostic characters are unproved. In such cases the generic attribution is unsure, and evidently, no specific assignment is possible.

The revision method (Czier 2011) used herein already was applied on *Ptilophyllum*, which is another Bennettitalean genus that frequently is cited in the Romanian literature. The essence of the method applied here consists in revisions as “cf. *Zamites* sp.” (hand specimen and one cuticle: description + figuration; the other cuticle not described and/or not figured), “aff. *Zamites* sp.” (only macroscopic or only microscopic description and/or figuration), and “? *Zamites* sp.” (no description, no figuration). In this context, the Romanian *Zamites* material is revised below, and the specimens described and figured in this paper are determined as cf. *Zamites* sp. 1 (macroscopic and abaxial cuticle description and figuration), cf. *Zamites* sp. 2 (macroscopic and abaxial cuticle description and figuration), and aff. *Zamites* sp. (macroscopic description and figuration, no cuticle preserved).

Even if the excellent preservation of a cuticle studied in LM- and SEM microscopy suggests new species, no new species should be created when the other cuticle is unknown. The absence of the adaxial cuticle makes both the LM slides and SEM micrographs useless for specific determination, despite the excellent preservation of the abaxial cuticle.

Remark: The used nomenclature and the discussions below are in the style of a previous paper (Czier 2010). The segments improperly are called “pinnae” in the generic diagnosis of *Zamites*, because the meaning of “pinnae” is that of the leaf, when leaves appear as simply pinnate. In addition, the classification of the stomatal apparati follows the recommendations of Sincock and Watson (1988) for plant fossils (cyclocytic instead of haplocheilic, paracytic instead of syndetocheilic).

Systematic palaeontology

This section comprises the Romanian *Zamites* record and revision. Only the basic references are included in the lists of synonymies. Citations and refigurations, like those from the works of Schimper (1870), Stur (1872), Schréter (1912), Krasser (1921), Thomas (1930), Langer (1947), Oncescu (1951), Semaka (1954), Givulescu (1998) are omitted from the lists, to not increase them excessively, so to make them less complicated. However, previous nomenclatural revisions are considered, and finally, new revisions are done where necessary.

Class Cycadopsida Brongniart, 1843

Order Bennettitales Engler, 1892

Family Williamoniaceae (Carruthers, 1870) Nathorst, 1913

Genus *Zamites* Brongniart, 1828 emend. Harris, 1969

cf. ***Zamites*** sp. 1 Czier

(Figs. 2A, 3A–D, 4A–D, 5A–D)

Locality: Anina (coordinates 45°05'30"N 21°51'12"E), Caraş-Severin County, Banat region, Romania.

Lithostratigraphic units: Steierdorf Formation, Valea Terezia Sandstone Member.

Biostratigraphic units: *Clathropteris meniscioides* Biozone, *Banatozamites chlamydostomus* Subzone.

Age: Hettangian *pro parte* – Sinemurian.

Material: Hand specimen HNHM-BP-602141; Slides HNHM-BP-LM-ZC-11 and HNHM-BP-SEM-ZC-2.

Description and measurements: Medial-distal fragment of a pinnate leaf (Fig. 2A). Judging after the 75 mm maximal width measured in the middle of the fragment, its length of 144 mm, and the general aspect, the entire leaf initially was medium-sized and linear-lanceolate. The rachis is slightly curved, 3–5 mm wide, preserved on the whole length of the fragment. On its adaxial face there are attached alternately disposed segments at an angle of about 70°; they are closely set in the proximal part of the leaf, to slightly distant in its distal part. Segments are lanceolate, up to 40 mm long and 6 mm wide. They have symmetrically contracted slightly rounded base, being attached to rachis by a small callosity of insertion; in the rest the surface of lamina is flat. The margins of segments are entire, tapering gradually to an acute or even acuminate apex. The venation consists of about 18 crowded, hardly ever dichotomised, almost parallel veins that diverge from the segment base and end in the margins and in the apex. Veins density is 30 per cm.

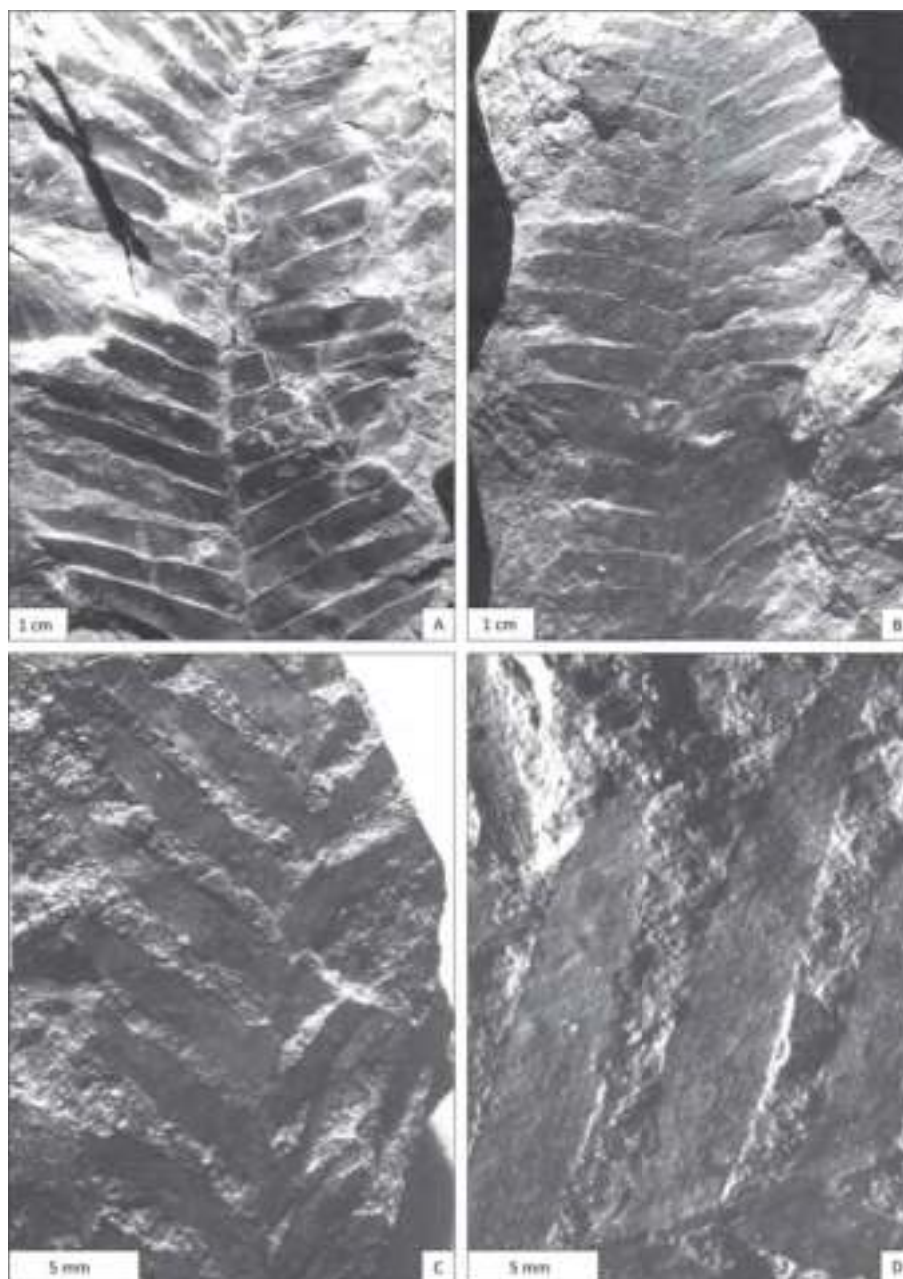


Figure 2. *Zamites* foliage. From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) cf. *Zamites* sp. 1 Czier. Leaf fragment (HNHM-BP-602141); (B) cf. *Zamites* sp. 2 Czier. Leaf fragment (HNHM-BP-602231-1); (C) aff. *Zamites* sp. Czier. Leaf fragment (HNHM-BP-602231-2); (D) aff. *Zamites* sp. Czier. Shape, attachment, and venation of a segment (HNHM-BP-602231-2).

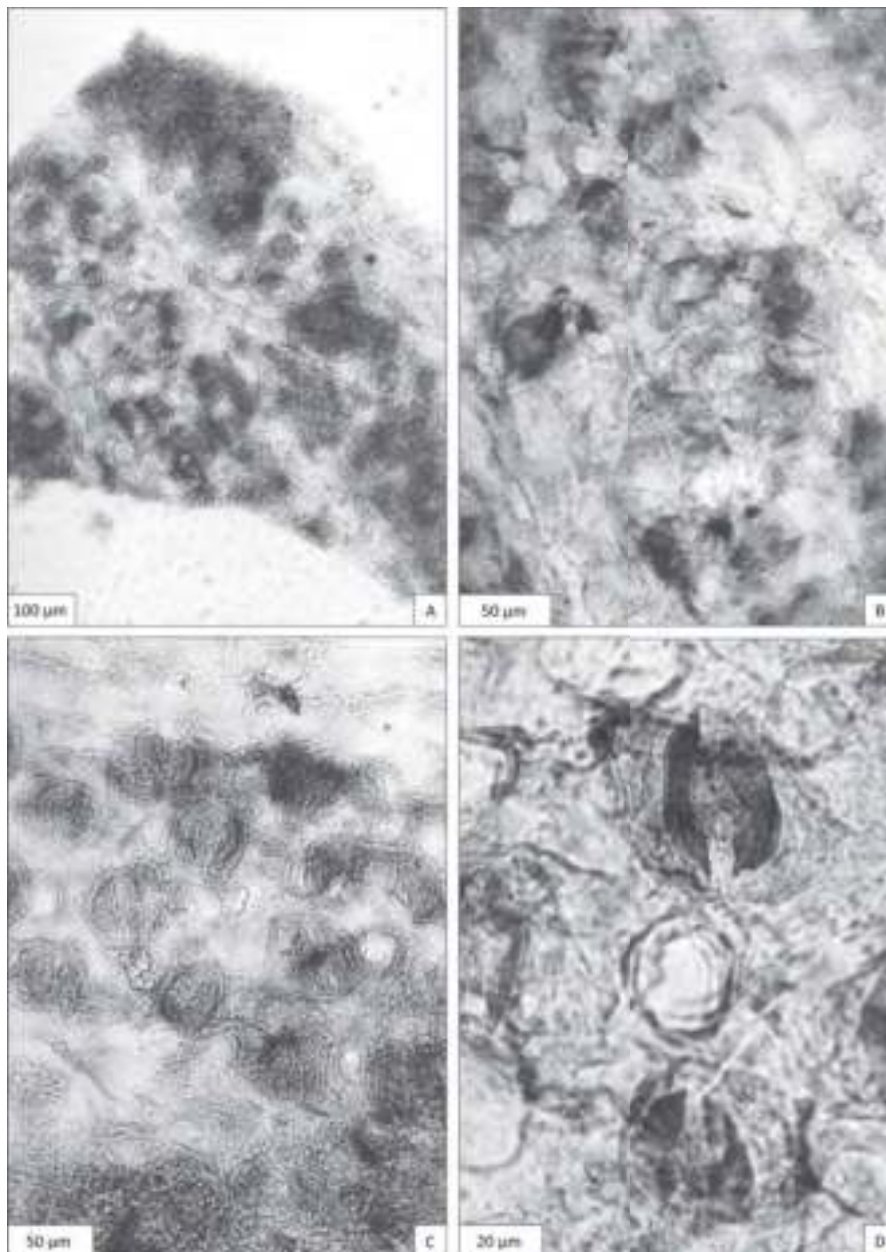


Figure 3. cf. *Zamites* sp. 1 Czier. Abaxial cuticle (HNHM-BP-LM-ZC-11). From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydotostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Stomatal and non-stomatal bands; (B) Stomatal band showing stomata with regular transverse orientation, between two bands of ordinary epidermal cells; (C) Heavily papillate cuticle, showing a stomatal band between two non-stomatal bands. Stomata transversely oriented to the veins, typically disposed in four rows; (D) Portion of a stomatal band, showing large developed papilla between each pair of stomata.

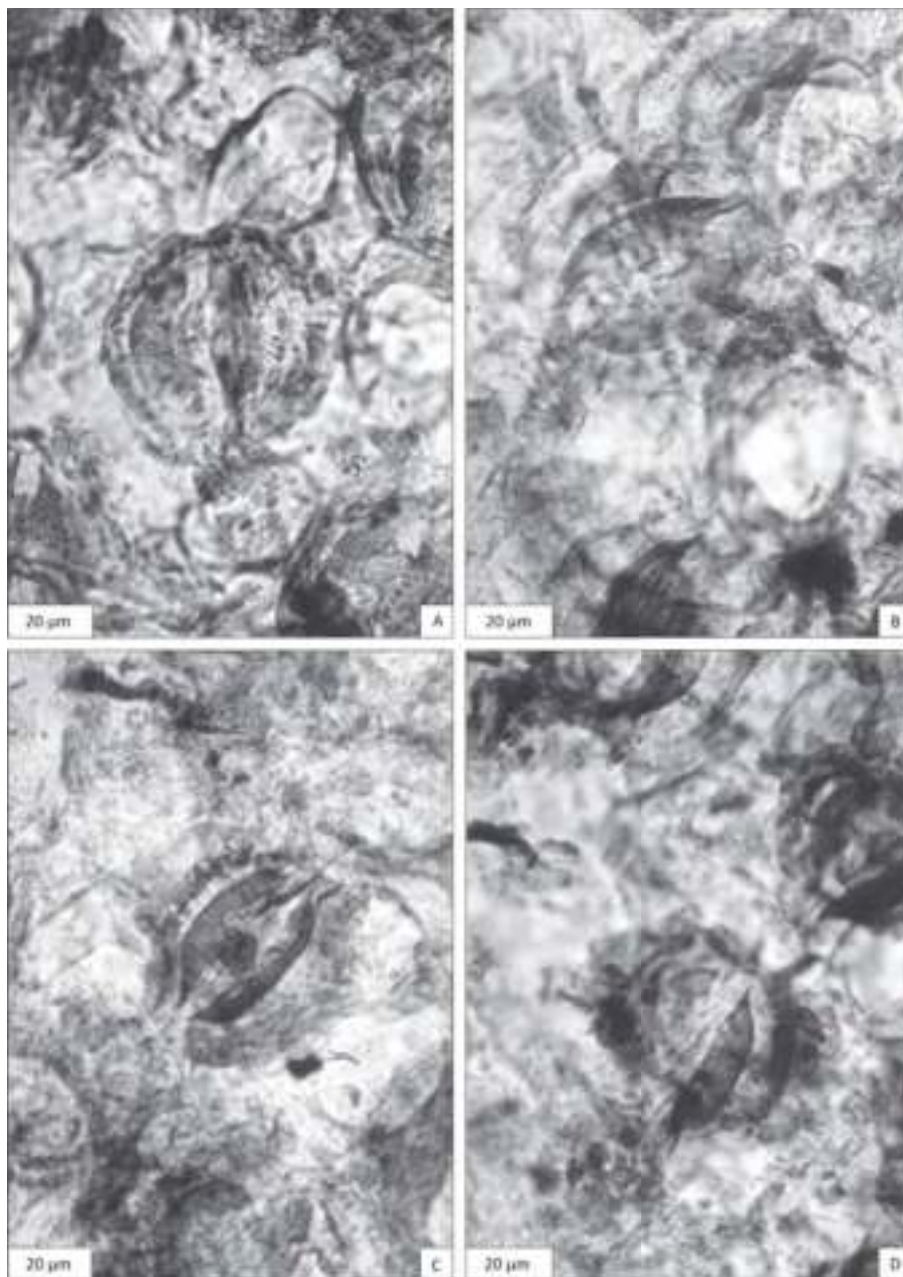


Figure 4. cf. *Zamites* sp. 1 Czier. Abaxial cuticle (HNHM-BP-LM-ZC-11). From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Stomatal apparatus and epidermal cells; (B) Stomata and epidermal cells; (C) Stomata and papillate epidermal cells; (D) Stomata and epidermal cells with large developed papillae.

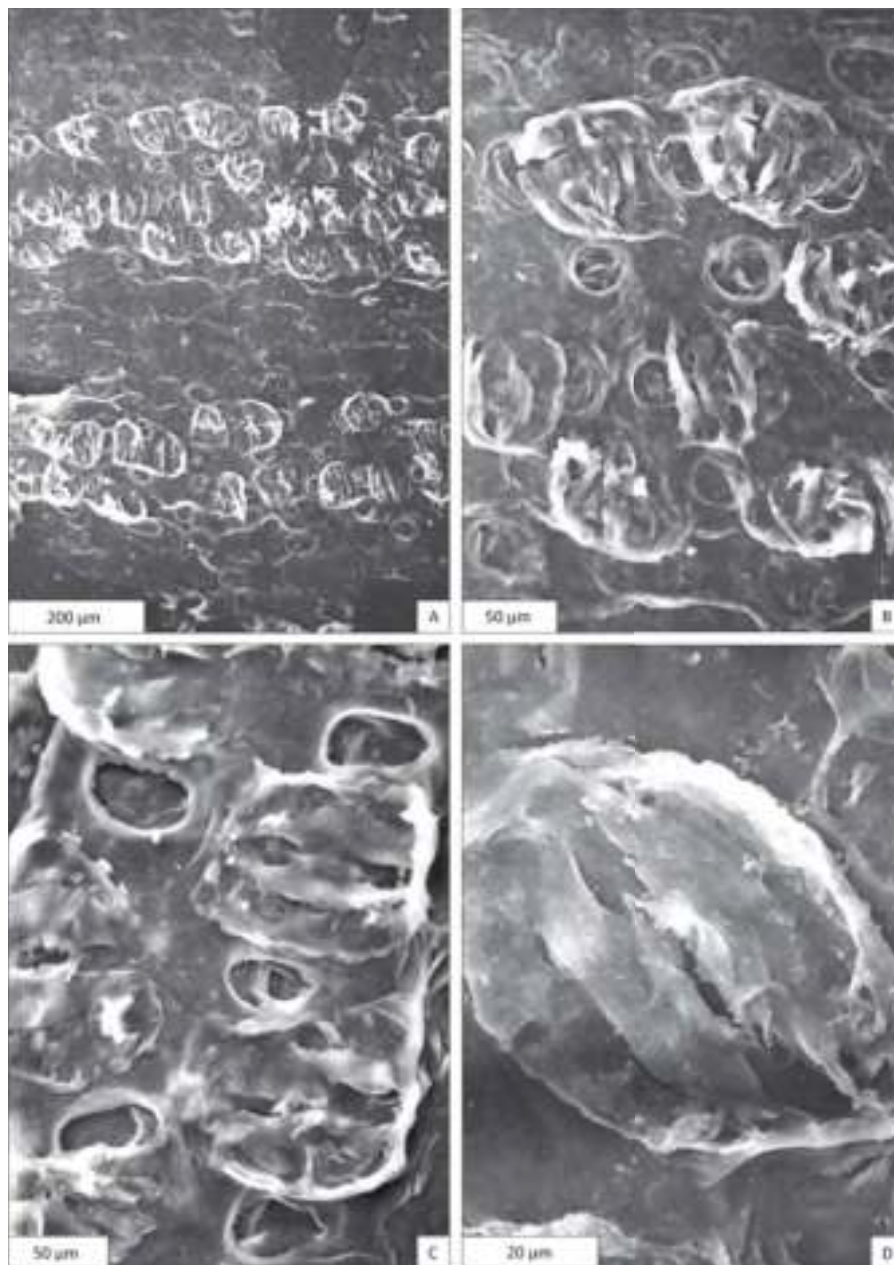


Figure 5. cf. *Zamites* sp. 1 Czier. Abaxial cuticle (HNHM-BP-SEM-ZC-2). From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydotomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Stomatal and non-stomatal bands; (B) Stomatal band showing epidermal cells and rows of stomata with regular transverse orientation; (C) Stomata surrounded by epidermal cells with large developed papillae; (D) Paracytic stomatal apparatus, showing details of guard cells, subsidiary cells, and stomatal aperture.

No adaxial cuticle is preserved in the obtained preparations, but only some abaxial cuticle fragments that, however, are well developed. These indicate an abaxial epidermis that was composed by 150 μm wide costal fields (non-stomatal bands corresponding to the veins), and 200–260 μm wide intercostal fields (stomatal bands corresponding to the regions between the veins) (Figs. 3A, 5A). The costal fields are composed by more or less conspicuous rows of epidermal cells rectangular to irregular in shape, of 40–100 / 30–50 μm , oriented with the longest side along the vein courses. These cells show slightly to medium sinuous walls; the sinuosities are relatively large, though not exceeding 10 μm in length (wave length) and 12 μm in width (amplitude). The intercostal fields consist of typically four rows (occasionally 2 or 3 rows) of stomata transversely oriented to the veins, and epidermal cells the most often polygonal or irregular in shape (Figs. 3B, 3C, 5B), shorter than the cells of the costal fields. The stomatal apparatus is of paracytic ('syndetocheilic') type (Figs. 5C–D). Stomata are elliptical, sunken, with two rather elongated guard cells. Each of the guard cells is 45–50 μm long and 12–18 μm wide (typically of 48/16 μm), showing simple thickenings at the margins and pointed ends, as well large polar spaces. The two subsidiary cells are semicircular, of about 30 μm wide, having smooth walls. The stomatal aperture is large, with maximal diameter of 28 μm . It is bordered by an ovale space in the centre of the stoma, ending at its terminations in a sharp point. Densely scattered stomata, of 50–100 per sq. mm reported to the costal and intercostal fields together, but in the stomatal bands alone even twice as much. Stomatic index of about 15 %. The epidermal cells both in the stomatal and in the non-stomatal bands present large developed papillae bases. These latter usually are circular, sometimes triangular or hexagonal, each of about 20 μm in diameter. In the stomatal bands they typically are disposed one between each neighbored pairs of stomata (Figs. 3D, 4A–D).

Discussion: Based on the macro-morphology, and on the paracytic stomatal apparatus that according to Florin (1933) is essential character of Bennettitales, the material undoubtedly belongs to this order. The characters of the specimen suggest that it is a *Zamites*; however, the lack of the adaxial cuticle does not allow a sure statement regarding the lamina, so the amphistomatic character cannot be excluded, and the hypostomatic character stipulated in the generic diagnosis cannot be firmly confirmed. Therefore, the absence of the adaxial cuticle does not allow sure assignment to this genus. At the same time, no specific assignment is done, because specific determination has sense only when the generic attribution is perfectly reliable. Consequently, the material is attributed to *Zamites* with "cf".

Remark: The lack of the adaxial cuticle does not allow pronouncing if the lamina is hypostomatic or amphistomatic, therefore, the generic assignment in such cases is unsure, and the specimens are not proper for specific determination. This situation, when the adaxial cuticle is unknown, noted here for *Zamites*, is analogue with that of *Ptilophyllum*, which became well known from the Romanian literature. *Ptilophyllum acifolium*, *P. curvatum*, *P. grandis*, and *P. romanicum* are good examples of incompletely documented species, which were revised by the author (Czier 2011) as cf. *Ptilophyllum* sp.

cf. ***Zamites*** sp. 2 Czier
(Figs. 2B, 6A–D, 7A–D)

Locality: Anina (coordinates 45°05'30"N 21°51'12"E), Caraş-Severin County, Banat region, Romania.

Lithostratigraphic units: Steierdorf Formation, Valea Terezia Sandstone Member.

Biostratigraphic units: *Clathropteris meniscioides* Biozone, *Banatozamites chlamydotomus* Subzone.

Age: Hettangian *pro parte* – Sinemurian.

Material: Hand specimen HHNM-BP-602231-1; Slides HHNM-BP-LM-ZC-15 and HHNM-BP-SEM-ZC-3.

Description and measurements: Small-sized pinnate leaf preserved on a length of 116 mm, with maximal width in its medial portion of 51 mm (Fig. 2B). Although its base is not entirely preserved and the apex is not exactly known, the shape of the leaf may be estimated to elliptical, as it gradually narrows both in the proximal and distal part of the fragment. The rachis is slender and thin, of 1–2 mm wide, slightly curved in its proximal third. It is almost completely concealed by the closely set and alternately disposed segments attached on its upper side at an insertion angle generally of about 80°, but angle reducing proximally and distally to about 50°. The preserved segments, 21 pairs in number, are disposed alternately, while the whole leaf supposing had 25–30 pairs. The segments are lanceolate, typically of 30 mm long and 6 mm wide, decreasing near the extremities of the fragment even to about half of these dimensions. They possess entire margins, symmetrically contracted and slightly rounded base attached in the middle of the basal margin, and acute apex. The veins are very thin, apparently diverging from the segment base. Macroscopically they are almost indistinguishable, but microscopically the cuticle sometimes shows dichotomous veins.

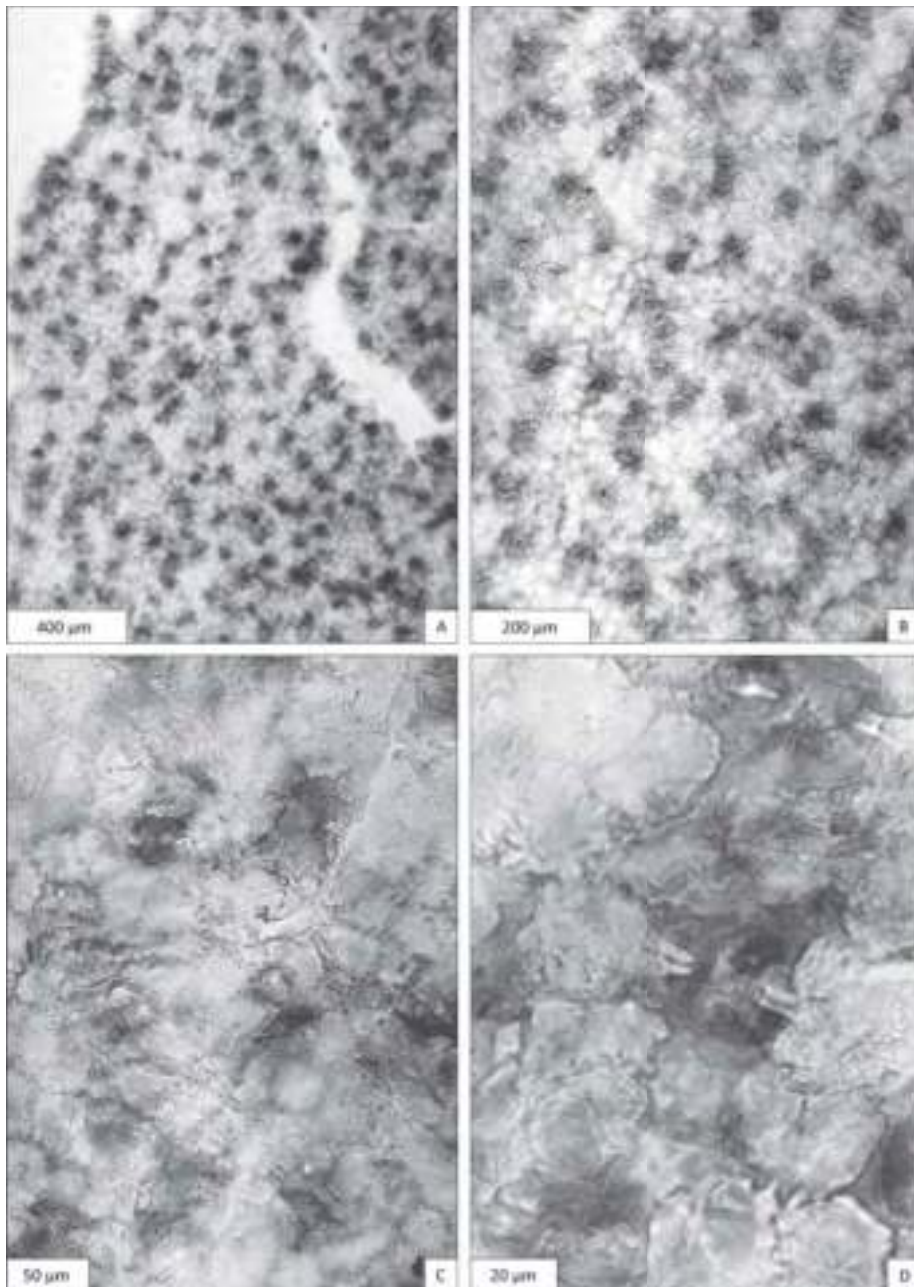


Figure 6. cf. *Zamites* sp. 2 Czier. Abaxial cuticle (HNHM-BP-LM-ZC-15). From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydotomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) General view of the cuticle; (B) Stomatal and non-stomatal bands; (C) Portion of a stomatal band; (D) Stomata and epidermal cells.

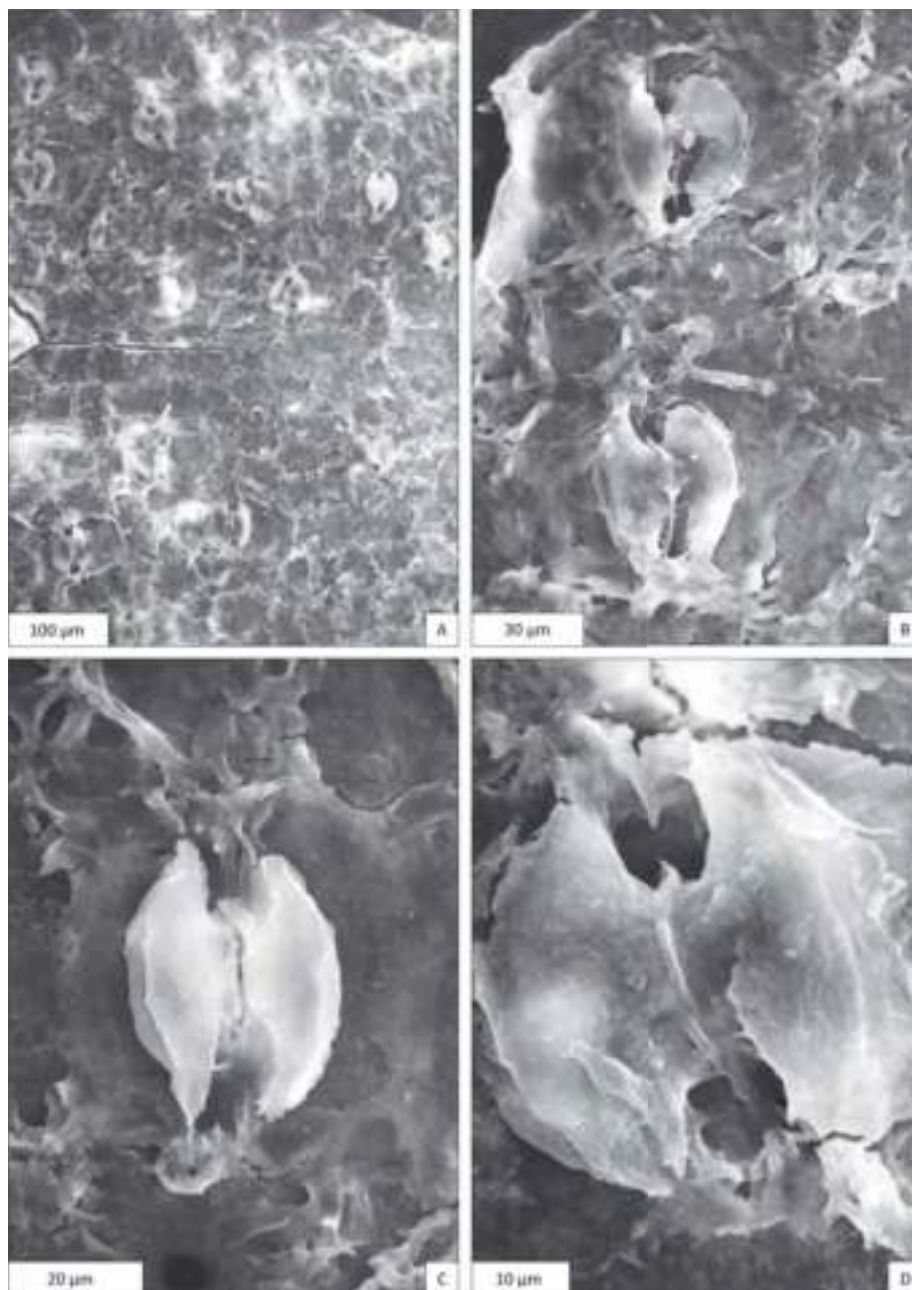


Figure 7. cf. *Zamites* sp. 2 Czier. Abaxial cuticle (HNHM-BP-SEM-ZC-3). From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Non-stomatal band between two stomatal bands; (B) Stomata and epidermal cells; (C) Stomatal apparatus; (D) Stoma with distinct polar spaces.

Adaxial cuticle unfortunately not present in the slides, but the abaxial cuticle is well developed (Fig. 6A). It indicates an epidermis composed by narrow, just about 80 μm wide costal fields (non-stomatal bands corresponding to the veins) alternating with much wider, about 250 μm wide intercostal fields (stomatal bands corresponding to the regions between the veins) (Fig. 6B). The costal fields usually consist of two rows of squarish, rectangular to elliptical epidermal cells typically of 30 / 30 μm (range 20–100 / 20–40 μm), which possess marked sinuous walls; the sinuosities are thick, of about 10 μm long (wave-length) and 10 μm wide (amplitude) (Fig. 7A). The intercostal fields contain somehow alike but more rounded or even polygonal ordinary epidermal cells, and irregularly disposed stomata that usually are transversely oriented to the direction of the bands (Fig. 7B); just some of them may have the pore oriented in any direction (Fig. 6C). The stomatal apparatus is paracytic, showing circular stoma typically of 35 μm diameter (Fig. 7C). The guard cells possess semicrescent thickenings and distinct polar spaces (Fig. 7D), so at the end of their margins they appear as having four endings resembling with some horns (Fig. 6D). The subsidiary cells are small to medium-sized, of about 30 μm wide, with almost smooth walls. The maximal diameter of the stomatal aperture is of 22 μm . The stomata are densely scattered, about 100 per sq.mm, the stomatic index being 6–8 %. The periclinal wall of any epidermal cell may possess circular trichome bases, each of about 8 μm in diameter.

Discussion: Reported to cf. *Zamites* sp. 1, this specimen presents marked differences, rendered in a table of comparison (Tab. 1). These differences make necessary a clearly distinction, therefore, the specimen is determined as cf. *Zamites* sp. 2. Otherwise, the discussion already given is effectual here too.

Table 1. The main differences between the characters of cf. *Zamites* sp. 1 Czler, and cf. *Zamites* sp. 2 Czler.

Character	cf. <i>Zamites</i> sp. 1	cf. <i>Zamites</i> sp. 2
<i>Macro-morphology</i>		
Size of the leaf	Medium	Small
Shape of the leaf	Linear-lanceolate	Elliptic
Segment apex	Acute or acuminate	Acute
<i>Abaxial epidermis</i>		
General aspect and width of the costal fields	Wide, about 150 μm	Narrow, about 80 μm
Disposition of stomata in the intercostal fields	In rows	Irregular
Shape and length/width of typical stoma	Elliptic, 48/32 μm	Circular, 35/35 μm
Maximal diameter of the stomatal aperture	28 μm	22 μm
Stomatic index	15 %	6–8 %
Ornamentation of the epidermal cells	Papilla	Trichome

cf. *Zamites* sp.

1. 1989 *Zamites andraeanus* (Semaka) Giv. Givulescu and Farcaşiu, p. 139 (part)
2. 1989 *Zamites aninaensis* (Semaka) Giv. Givulescu and Farcaşiu, p. 139 (part)
3. 1989 *Zamites* sp. Givulescu and Farcaşiu, p. 139 (part)
4. 1989 *Zamites* sp. Givulescu and Farcaşiu, p. 139 (part)
5. 1989 *Zamites aninaensis* (Semaka) Giv. Givulescu, p. 30
6. 1989 *Zamites* sp. 2. Givulescu, p. 30
7. 1989 *Zamites schmiedeli* Stbg. Givulescu, p. 30, plate 1, fig. 1
8. 1991 *Zamites vachrameevii* Doludenko. Givulescu, p. 17, plate 1, figs. 1, 2

Localities: Anina (1, 2, 3, 4, 5, 6, 7); Vulcan (8).

Lithostratigraphic units: Steierdorf Formation, Valea Terezia Sandstone Member (1, 2, 3, 4, 5, 6, 7); Codlea-Vulcan Formation, Vulcan Sandstone Member (8).

Biostratigraphic units: *Clathropteris meniscioides* Biozone, *Banatozamites chlamydomostomus* Subzone (1, 2, 3, 4, 5, 6, 7, 8).

Age: Hettangian *pro parte* – Sinemurian (1, 2, 3, 4, 5, 6, 7, 8).

Discussion: Adaxial cuticle not figured (1, 2, 3, 4, 5, 6, 7, 8).

aff. *Zamites* sp. Czier

(Fig. 2C–D)

Locality: Anina (coordinates 45°05'30"N 21°51'12"E), Caraş-Severin County, Banat region, Romania.

Lithostratigraphic units: Steierdorf Formation, Valea Terezia Sandstone Member.

Biostratigraphic units: *Clathropteris meniscioides* Biozone, *Banatozamites chlamydomostomus* Subzone.

Age: Hettangian *pro parte* – Sinemurian.

Material: Hand specimen HNHM-BP-602231-2.

Description and measurements: Fragment of a pinnate leaf (Fig. 2C), preserved on a length of 56 mm and width of 30 mm, representing a portion not far from its hypothetical apex. The rachis, preserved along the whole fragment, is straight and very narrow, of only 0.6 mm wide. On its upper side, at 50° angle of insertion, there are attached alternate segments, distantly disposed, with gaps of 2.5 mm between them. The segments are lanceolate, possessing entire margins and acute to acuminate apex (Fig. 2D). Their length is about 27 mm, and their width of 4 mm. The venation is hardly seen as the specimen is rather poorly preserved, but on some better preserved portions the segments show 14 apparently parallel veins.

Discussion: The very narrow rachis of this specimen does not allow clear statement regarding the attachment of the segments, so it is not clear enough if they are attached by a small area in middle of the basal margin or not. The macroscopic generic determination needs, therefore, at least a "cf.", however, owing to the absence of any cuticle finally is needed "aff."

aff. ***Zamites*** sp.

1. 1855 *Zamites Schmiedelii* Sternb. Andrae, p. 39, plate 9, fig. 1 (part)
2. 1855 *Zamites Schmiedelii* Sternb. Andrae, p. 39, plate 9, figs. 1 (part), 2, 3
3. 1855 *Zamites Schmiedelii* Sternb. Andrae, p. 39 (part), plate 9, fig. 4
4. 1855 *Zamites Schmiedelii* Sternb. Andrae, p. 39 (part), plate 11, fig. 7
5. 1855 *Zamites* oder *Pterophyllum*. Andrae, p. 42, plate 8, fig. 1a
6. 1921 *Zamites Andraei* Stur. Krasser, p. 362 (part)
7. 1921 *Zamites Andraei* Stur. Krasser, p. 362 (part)
8. 1930 *Zamites Schmiedelii* Andrae. Thomas, p. 399, text-figs. 9, 10
9. 1947 *Zamites schmiedeli* Sternb. Langer, p. 25, plate 3, fig. a
10. 1958 *Zamites schmiedelii* Sternberg. Semaka, p. 414, tab. 3
11. 1962 *Otozamites schmiedelii* (Sternberg) Semaka. Oarcea and Semaka, p. 241 (part)
12. 1962 *Otozamites schmiedelii* (Sternberg) Semaka. Oarcea and Semaka, p. 241 (part)
13. 1962 *Otozamites andraeanus* Semaka. Oarcea and Semaka, p. 241 (part)
14. 1962 *Otozamites andraeanus* Semaka. Oarcea and Semaka, p. 241 (part)
15. 1962 *Otozamites andraeanus* Semaka. Oarcea and Semaka, p. 241 (part)
16. 1962a *Otozamites* div. sp. n. Semaka, p. 532 (part)
17. 1962a *Otozamites* div. sp. n. Semaka, p. 532 (part)
18. 1962a *Otozamites* div. sp. n. Semaka, p. 532 (part)
19. 1962a *Zamites schmiedelii* Sternberg. Semaka, p. 533 (part), 542 (part), 550 (part), 554 (part), tab. 1 (part)
20. 1962c *Otozamites andreanus* n. p. Semaka, p. 95 (part)
21. 1962c *Otozamites andreanus* Semaka. Semaka, p. 95 (part), plate 1, text-figs. 2, 3
22. 1964 *Zamites* sp. Mateescu, p. 100, plate 3, fig. 1
23. 1966 *Zamites* sp. Zborea et al., p. 50
24. 1970 *Otozamites schmiedelii* (Sternberg) Semaka. Semaka, p. 28, 50, plate 21 (part), tab. 14
25. 1989 *Zamites schmiedeli* Presl in Stbg. Givulescu and Farcașiu, p. 139

26. 1989 *Zamites aninaensis* (Semaka) Giv. Givulescu and Farcașiu, p. 139 (part)
27. 1996 *Zamites andraeanus*. Berg, p. 54, tab. 1 (part)
28. 1996 *Zamites andraeanus* (Semaka) Givulescu. Berg, p. 54 (part), 56 (part), tab. 1 (part)
29. 1996 *Zamites andraeanus* (Semaka) Givulescu. Berg, p. 54 (part), 56 (part), tab. 1 (part)
30. 1996 *Zamites andraeanus* (Semaka) Givulescu. Berg, p. 54 (part), 56 (part), plate 2, fig. 7, tab. 1 (part)
31. 1996 *Zamites aninaensis*. Berg, p. 54 (part), 56 (part), plate 2, fig. 5, tab. 1 (part)
32. 1996 *Zamites schmiedeli* Sternberg. Berg, p. 55 (part), pl. 1, figs. 4, 6
33. 1996 *Zamites schmiedeli* Sternberg. Berg, p. 55 (part)

Localities: Anina (1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 14, 15, 16, 17, 18, 19, 21, 25, 26, 27, 28, 29, 30, 31, 32, 33); Cristian (6); Doman (13); Anina and/or Doman (20); Vulcan (22); Crasna (23); Berzasca (24).

Lithostratigraphic units: Steierdorf Formation or Dealul Zânei Formation (1, 2, 4, 5, 8, 9, 20); Steierdorf Formation, Valea Terezia Sandstone Member (3, 10, 12, 15, 16, 18, 19, 21, 25, 26, 27, 28, 29, 30, 31, 32, 33); Cristian Formation, Valea Schneebrich Sandstone Member (6); Steierdorf Formation, Dealul Budinic Conglomerate Member or Valea Terezia Sandstone Member (7, 11, 13, 14, 17); Codlea-Vulcan Formation, Vulcan Sandstone Member (22); Baia de Aramă Formation, Valea Sunătorii Argillaceous Member (23); Svinița Formation, Ogașul Murguceva Limestone Member (24).

Biostratigraphic units: *Clathropteris meniscioides* Biozone or *Carpolithes liasinus* Biozone or *Anomozamites spectabilis* assemblage (1, 2, 4, 5, 8, 9, 20); *Clathropteris meniscioides* Biozone, *Banatozamites chlamydostomus* Subzone (3, 10, 12, 15, 18, 19, 21, 22, 25, 26, 27, 28, 29, 30, 32, 33); *Anomozamites marginatus* Biozone (6); *Carpolithes liasinus* Biozone (7, 11, 13, 14, 16, 17, 23, 24); *Clathropteris meniscioides* Biozone (31).

Ages: Hettangian – Toarcian (1, 2, 4, 5, 8, 9, 20); Hettangian *pro parte* – Sinemurian (3, 10, 12, 15, 16, 18, 19, 21, 22, 25, 26, 27, 28, 29, 30, 31, 32, 33); Sinemurian *pro parte* (6, 23); Hettangian – Sinemurian (7, 11, 13, 14, 17); Pliensbachian *pro parte* (24).

Discussions: The material is only macroscopically described and figured (1, 2, 3, 4, 5, 9, 10, 16, 21, 24, 30, 31, 32); the material is only macroscopically described and is not figured (6, 7, 11, 12, 13, 14, 15, 17, 18, 19, 20, 23, 25, 26, 27, 28, 29, 33);

the material is only microscopically described and figured, both cuticles are known, but the hand specimen is unidentifiable (8); the material is only macroscopically figured and is not described (22).

? *Zamites* sp.

1. 1850 *Zamites*. Foetterle, p. 357
2. 1860a *Zamites Schmiedelii* Strnbg. Stur, p. 57 (part)
3. 1860a *Zamites Schmiedelii* Strnbg. Stur, p. 57 (part)
4. 1860b *Zamites* sp.? oder *Pterophyllum* sp.? Stur, p. 58
5. 1871 *Podozamites* cf. *Schmiedelii* Sternb. Stur, p. 464
6. 1878 *Zamites Schmiedelii* Presl. Hantken, p. 64 (spelling error for *schmiedelii*)
7. 1878 *Zamites Schmiedelii* Presl. Hantken, p. 65
8. 1878 *Zamites Barrei* St. n. sp. Hantken, p. 69
9. 1878 *Zamites Barrei*. Hantken, p. 69
10. 1878 *Cyclopteris Barrei*. Hantken, p. 69
11. 1878 *Cyclopteris barrei*. Hantken, p. 70
12. 1878 *Pterophyllum Barrei*. Hantken, p. 71
13. 1878 *Zamites meriani*. Hantken, p. 70
14. 1878 *Zamites* sp. Hantken, p. 71
15. 1890 *Zamites Schmiedelii* Sternb. Telegdi Roth, p. 96
16. 1891 *Zamites Schmiedelii* Sternb. Telegdi Roth, p. 89 (part)
17. 1891 *Zamites Schmiedelii* Sternb. Telegdi Roth, p. 89 (part)
18. 1891 *Zamites gracilis* Kurr. Telegdi Roth, p. 93
19. 1891 *Zamites*. Bene, p. 329
20. 1906 *Zamites gracilis* Kurr. Telegdi Roth, p. 25
21. 1911 *Nilssonina polymorpha* Schenk. Toula, p. 17
22. 1951 *Z. schmideli*. Barbu, p. 130
23. 1957 *Zamites banaticus* Stur. Mateescu, p. 9
24. 1957 *Zamites rigidus* Andrae. Mateescu, p. 9
25. 1961 *Otozamites* typus. Semaka, p. 392, tab. 1
26. 1961 Unbestimmbare Reste. Semaka, p. 393 (part)
27. 1962 *Zamites gracilis* Kurr. Oarcea & Semaka, p. 241 (part)
28. 1962 *Zamites gracilis* Kurr. Oarcea & Semaka, p. 241 (part)
29. 1962 *Zamites* sp. Oarcea & Semaka, p. 241
30. 1962 *Zamites* sp. Oarcea & Semaka, p. 241 (part)
31. 1962 *Zamites* sp. Oarcea & Semaka, p. 241 (part)
32. 1962b *Zamites gracilis* Kurr. Semaka, p. 217

33. 1962 *Folia zamitoides*, *Folia zamitoidea*. Iliescu & Semaka, p. 115, 116
34. 1962 *Zamites* sp. Iliescu & Semaka, p. 116, 117
35. 1962 *Zamites* sp. Drăghici & Semaka, p. 41
36. 1963 *Zamites* sp. Humml, p. 194
37. 1963 *Otozamites schmiedelii* (Sternberg) Semaka. Humml, p. 195 (part)
38. 1963 *Otozamites schmiedelii* (Sternberg) Semaka. Humml, p. 195 (part)
39. 1963 *Zamites* sp. (typus *Otozamites*). Humml, p. 195
40. 1963 *Zamites* sp. Humml, p. 195
41. 1963 *Otozamites schmiedelii* (Sternberg) Semaka. Humml, p. 196 (part)
42. 1963 *Otozamites schmiedelii* (Sternberg) Semaka. Humml, p. 196 (part)
43. 1963 *Otozamites andraeanus* Semaka. Humml, p. 196
44. 1963 *Otozamites aninaensis* Semaka. Humml, p. 196 (part)
45. 1963 *Otozamites aninaensis* Semaka. Humml, p. 196 (part)
46. 1963 *Otozamites schmiedelii* (Sternberg) Semaka. Humml, p. 196 (part), 197
47. 1963 *Zamites* sp. Humml, p. 196
48. 1963 *Zamites* sp. Humml, p. 197 (part)
49. 1963 *Zamites* sp. Humml, p. 197 (part), 198 (part)
50. 1963 *Zamites* sp. Humml, p. 197 (part), 198 (part)
51. 1963 *Zamites* sp. Humml, p. 198 (part)
52. 1963 *Zamites* sp. Humml, p. 199
53. 1970 *Zamites* sp. Semaka, p. 17, 50, tab. 7
54. 1970 *Zamites* sp. Semaka, p. 25, 50, tab. 10
55. 1970 *Zamites* sp. Semaka, p. 26, 50, tab. 11
56. 1970 *Zamites* sp. Semaka, p. 27, 50, tab. 12
57. 1972 *Zamites* sp. Semaka et al., p. 436, 439, tab. 1 (part)
58. 1972 *Zamites* sp. an sp. n. Semaka et al., p. 439, tab. 1
59. 1989 *Zamites andraeanus* (Semaka) Giv. Givulescu and Farcașiu, p. 139 (part)
60. 1996 *Zamites* Cf. *schmiedeli*. Berg, p. 54, tab. 1
61. 1996 *Zamites aninaensis*. Berg, p. 54, tab. 1 (part)
62. 1996 *Zamites aninaensis* (Semaka) Givulescu. Berg, p. 54 (part), 56 (part), tab. 1 (part)
63. 1996 *Zamites* sp. Berg, p. 54, 56, tab. 1 (part)

Localities: Anina (1, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 22, 27, 28, 29, 30, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 59, 60, 61, 62, 63); Holbav (2, 4); Cristian (3, 21); Doman (19, 23, 24, 31, 32, 36); Buschmann mine (25); Berzasca (26); Mehadia (33, 34); Baia de Aramă (35); Not exactly known (52); Co-

zla (53); Pietrele Albe (54); Dragosella (55); Crivi valley (56); Viezuroi mine (57, 58). *Lithostratigraphic units*: Steierdorf Formation, Valea Terezia Sandstone Member (1, 5, 6, 7, 17, 19, 23, 24, 28, 30, 32, 37, 39, 43, 45, 48, 49, 59, 60, 61, 62, 63); Codlea-Vulcan Formation, Vulcan Sandstone Member (2, 4); Cristian Formation, Valea Schneebrich Sandstone Member (3, 21); Dealul Zânei Formation *pro parte* (8, 9, 10, 11, 13); Dealul Zânei Formation, Valea Sodol Marl Member (12, 14); Steierdorf Formation, Dealul Budinic Conglomerate Member or Valea Terezia Sandstone Member (15, 16, 27, 29, 31, 36, 38, 40, 41, 42, 44, 46, 47, 50, 51); Steierdorf Formation, Uteriş Argilitic Member (18, 20); Steierdorf Formation or Dealul Zânei Formation (22, 52); Sviniţa Formation, Ogaşul Vodânischi Sandstone Member (25, 53, 54, 55, 56); Sviniţa Formation, Ogaşul Murguceva Limestone Member (26); Mehadia Formation, Valea Ciumoasa Conglomerate Member (33, 34); Baia de Aramă Formation, Dealul Spineni Marl Member (35); Schela Formation (57, 58). *Biostratigraphic units*: *Clathropteris meniscioides* Biozone, *Banatozamites chlamydotomus* Subzone (1, 2, 4, 5, 6, 7, 17, 19, 23, 24, 28, 30, 32, 37, 39, 43, 45, 48, 49, 59, 60, 61, 62, 63); *Anomozamites marginatus* Biozone (3, 21); Not defined, "Layers with *Gryphaea*" (8, 9, 10, 11, 13); Not defined, "*Anomozamites spectabilis* assemblage" (12, 14); *Clathropteris meniscioides* Biozone (15, 16, 25, 27, 29, 31, 35, 36, 38, 40, 41, 42, 44, 46, 47, 50, 51, 54, 55, 56, 57, 58); *Carpolithes liasinus* Biozone (18, 20, 26); *Clathropteris meniscioides* Biozone or *Carpolithes liasinus* Biozone or *Anomozamites spectabilis* assemblage (22, 52); *Clathropteris meniscioides* Biozone, *Leptostrobus laxiflora* Subzone (33, 34); *Clathropteris meniscioides* Biozone, *Neocalamites carcinooides* Subzone (53). *Ages*: Hettangian *pro parte* – Sinemurian (1, 2, 4, 5, 6, 7, 17, 19, 23, 24, 25, 28, 30, 32, 37, 39, 43, 45, 48, 49, 54, 55, 56, 59, 60, 61, 62, 63); Sinemurian *pro parte* (3, 21); Aalenian *pro parte* (8, 9, 10, 11, 13); Toarcian (12, 14); Hettangian – Sinemurian (15, 16, 27, 29, 31, 35, 36, 38, 40, 41, 42, 44, 46, 47, 50, 51, 57, 58); Pliensbachian (18, 20); Hettangian – Toarcian (22, 52); Pliensbachian *pro parte* (26); Hettangian *pro parte* (33, 34); Hettangian *pro parte* - Sinemurian *pro parte* (53).

Discussion: The material is not described and not figured (1–63).

Stratigraphic distribution of the Romanian *Zamites* material

The revision of the Romanian *Zamites* material does not alter the map of geographical distribution presented at the beginning of this work. The map may be used together with the attached table (Tab. 2) containing the stratigraphic distribution of the taxa, which are present in the fossil flora of the localities.

Table 2. Chronostratigraphic, tectonostratigraphic, lithostratigraphic, and biostratigraphic distribution of the Romanian *Zamites* material.

Localities	Chronostratigraphy	Tectonostratigraphy	Lithostratigraphy	Biostratigraphy	Taxa
Cristian	Sinemurian <i>pro parte</i>	Leaota	Cristian Formation, Valea Schneebrich Sandstone Member	<i>Anomozamites marginatus</i> Biozone	aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
Crivi valley	Hettangian <i>pro parte</i> – Sinemurian	Danubian	Svinița Formation, Ogașul Vodănișchi Sandstone Member	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.
Berzasca	Pliensbachian <i>pro parte</i>	Danubian	Svinița Formation, Ogașul Murguceva Limestone Member	<i>Carpolithes liasinus</i> Biozone	aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
Buschmann mine	Hettangian <i>pro parte</i> – Sinemurian	Danubian	Svinița Formation, Ogașul Vodănișchi Sandstone Member	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.
Pietrele Albe	Hettangian <i>pro parte</i> – Sinemurian	Danubian	Svinița Formation, Ogașul Vodănișchi Sandstone Member	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.
Dragosella	Hettangian <i>pro parte</i> – Sinemurian	Danubian	Svinița Formation, Ogașul Vodănișchi Sandstone Member	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.
Cozla	Hettangian <i>pro parte</i> – Sinemurian <i>pro parte</i>	Danubian	Svinița Formation, Ogașul Vodănișchi Sandstone Member	<i>Ciathropteris meniscioides</i> Biozone, <i>Neocalamites carcinoides</i> Subzone	? <i>Zamites</i> sp.
Mehadia	Hettangian <i>pro parte</i>	Danubian	Mehadia Formation, Valea Ciomoasa Conglomerate Member	<i>Ciathropteris meniscioides</i> Biozone, <i>Leptostrobus laxiflora</i> Subzone	? <i>Zamites</i> sp.
Vieziuroi mine	Hettangian – Sinemurian	Danubian	Schela Formation	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.
Crasna	Sinemurian <i>pro parte</i>	Danubian	Baia de Aramă Formation, Valea Sunătorii Argillaceous Member	<i>Ciathropteris meniscioides</i> Biozone	aff. <i>Zamites</i> sp.
Baia de Aramă	Hettangian – Sinemurian	Danubian	Baia de Aramă Formation, Dealul Spineni Marl Member	<i>Ciathropteris meniscioides</i> Biozone	? <i>Zamites</i> sp.

	Hettangian <i>pro parte</i> – Sinemurian	Getic	Steierdorf Formation, Valea Terezia Sandstone Member	<i>Clathropteris meniscioides</i> Biozone, <i>Banatozamites chilamydostomus</i> Subzone	cf. <i>Zamites</i> sp. 1 Czter, cf. <i>Zamites</i> sp. 2 Czter, cf. <i>Zamites</i> sp., aff. <i>Zamites</i> sp. Czter, aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
Anina	Hettangian – Toarcian	Getic	Steierdorf Formation or Dealul Zânei Formation	<i>Clathropteris meniscioides</i> Biozone or <i>Carpolithes liasinus</i> Biozone or <i>Anomozamites spectabilis</i> assemblage	aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
	Hettangian – Sinemurian	Getic	Steierdorf Formation, Dealul Budinic Conglomerate Member or Valea Terezia Sandstone Member	<i>Clathropteris meniscioides</i> Biozone	aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
	Pliensbachian	Getic	Steierdorf Formation, Uteriş Ar-gilitic Member	<i>Carpolithes liasinus</i> Biozone	? <i>Zamites</i> sp.
	Toarcian	Getic	Dealul Zânei Formation, Valea Sodoi Marl Member	Not defined ("Anomozamites spectabilis assemblage")	? <i>Zamites</i> sp.
	Aalenian <i>pro parte</i>	Getic	Dealul Zânei Formation <i>pro parte</i>	Not defined ("Layers with <i>Gryphaea</i> ")	? <i>Zamites</i> sp.
Doman	Hettangian – Sinemurian	Getic	Steierdorf Formation, Dealul Budinic Conglomerate Member or Valea Terezia Sandstone Member	<i>Clathropteris meniscioides</i> Biozone	aff. <i>Zamites</i> sp., ? <i>Zamites</i> sp.
Vulcan	Hettangian <i>pro parte</i> – Sinemurian	Getic	Steierdorf Formation, Valea Terezia Sandstone Member	<i>Clathropteris meniscioides</i> Biozone, <i>Banatozamites chilamydostomus</i> Subzone	? <i>Zamites</i> sp.
	Hettangian <i>pro parte</i> – Sinemurian	Getic	Codlea-Vulcan Formation, Vulcan Sandstone Member	<i>Clathropteris meniscioides</i> Biozone, <i>Banatozamites chilamydostomus</i> Subzone	cf. <i>Zamites</i> sp., aff. <i>Zamites</i> sp.
Holbav	Hettangian <i>pro parte</i> – Sinemurian	Getic	Codlea-Vulcan Formation, Vulcan Sandstone Member	<i>Clathropteris meniscioides</i> Biozone, <i>Banatozamites chilamydostomus</i> Subzone	? <i>Zamites</i> sp.
Not exactly known	Hettangian – Toarcian	Getic	Steierdorf Formation or Dealul Zânei Formation	<i>Clathropteris meniscioides</i> Biozone or <i>Carpolithes liasinus</i> Biozone or <i>Anomozamites spectabilis</i> assemblage	? <i>Zamites</i> sp.

Results and Conclusions

The excellent preservation of bennettitalean abaxial cuticle is not enough to define new genera and species.

The absence of the adaxial cuticle makes even the best *Zamites* preparations useless for specific determination.

The revision of the published *Zamites* material, plus the herein described and figured new specimens, documents the presence of this genus in the Romanian fossil flora by cf. *Zamites* sp. 1 Czier, cf. *Zamites* sp. 2 Czier, cf. *Zamites* sp., aff. *Zamites* sp. Czier, aff. *Zamites* sp., and ? *Zamites* sp.

The usage of “cf.”, “aff.”, or even of “?” before the name *Zamites* is necessary for the entire so far published Romanian material attributed to this genus, because no one of the specimens is provided with complete thus diagnostically useful macro- and microscopical description and figuration.

There exists no evidence to prove the presence of any valid full species of *Zamites* in the fossil flora of Romania.

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NYMPHAEA Folia naturae Bihariae	XLV	35 - 80	Oradea, 2018
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A preliminary report on the first results of the re-excavation of the middle Miocene palaeovertebrate locality Szentendre, Cseresznyés-árok (Hungary, Pest County)

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Abstract. In 2018 the middle Miocene palaeovertebrate locality Szentendre, Cseresznyés-árok was re-excavated. New fossiliferous layers were unearthed, and rich microvertebrate material was collected. In this publication the elaboration of the amphibians, reptiles and rodents is given. From biochronological point of view the *Cricetodon aureus* population is the most important element of the fauna. In the Northern Alpine Foreland Basin the *C. aureus* faunas are situated between the “Brock horizon” and the Main bentonite horizon. In the Neogene vertebrate biochronology it is referable to the MN 6 zone. In the Paratethys stratigraphy it is equivalent to the middle Badenian, 15.0–14.9 Ma.

Key words. Miocene, Badenian, Microvertebrata, Carpathian Basin.

Introduction

Szentendre is a historical town North to Budapest. Sporadic Miocene palaeovertebrate finds have been collected from the vicinity of the settlement from the 19th century. The remains of *Listriodon splendens*, *Dorcatherium* sp. and *Mastodon*

arvernensis are stored in the Palaeontological Collection of the Hungarian National Museum (Kordos, 1985). A *Listriodon* tooth was found in 1860 and it was mentioned by Koch (1900). Freshwater mollusc shells were described from the surroundings of Szentendre by Szalai (1928). *Mastodon* bone fragments were mentioned by Wein (1939) from a well-digging close to the Serbian Calvary. As a result of different occasional collections *Testudo* sp., *Gomphotherium* sp. and Rhinocerotidae indet. finds are stored in the Collection of the Hungarian Mining and Geological Survey (earlier Hungarian Geological Institute). During the 1970's *Mastodon* and *Chalicotherium* bones were found during the course of a cellar digging in no. 66. of the Vörös Hadsereg Str. of Szentendre.

The fossiliferous diatomite of the "Cseresznyés-árok" ("Cherry Trench") was found by Mr. József László geologist assistant in 1979. First he reported it as a palaeobotanical locality. In 1980 a sampling activity was managed by Dr. László Kordos and Mr. Peter Solt. After the preparation Kordos (1982) published the following faunal list:

Salientia indet.

Testudo sp.

Cricetodon (*Cricetodon*) *albanensis* (Mein & Freudenthal)

Cricetodon sp. (s. l.)

Democricetodon minor (Lartet)

Suidae indet. (? *Listriodon*)

Lagomeryx seu *Palaeomeryx* sp.

Eocerus sp.

Chalicotherium grande (Blainville)

Aceratherium tetradactylum (Lartet)

Anchitherium aurelianense Cuvier

Later Kordos (1986) gave the detailed description of the cricetid material of the localities Hasznos and Szentendre and founded the taxa:

Deperetomys hagni hungaricus n. ssp.

Democricetodon hasznosensis n. sp.

The holotypes of both new species were chosen from the Hasznos material, because the number of the teeth from Szentendre were very limited (*Deperetomys*: 7 teeth, *Democricetodon*: 2 intact teeth + 1 fragment). De Bruijn et al (1993) verified that *Deperetomys hagni hungaricus* has a closer relationship to *Cricetodon*

and emended it as *Cricetodon hungaricus*. An *Anomalomys* M2 from Szentendre was described as *Anomalomys kowalskii* n. sp. by Kordos (1989). For a long time the locality was abandoned. Korpás (1998) edited a detailed explanation for the geological map of Börzsöny and Visegrád Mountains, where, unfortunately, the fossiliferous middle Miocene nonmarine sediments and the vertebrate finds are not mentioned.

Previous report on the frog remains of Szentendre has been provided by Venczel (2004) with the following taxa: *Latonia gigantea*, *Pelobates sanchizi* and *Pelophylax* (= *Rana*) *esculenta* synklepton.

The new field activity

In 2017 Lukács Mészáros and János Hír identified the locality on the field again (Fig. 1). GPS: N 47° 41.119', E 18° 41.617'.

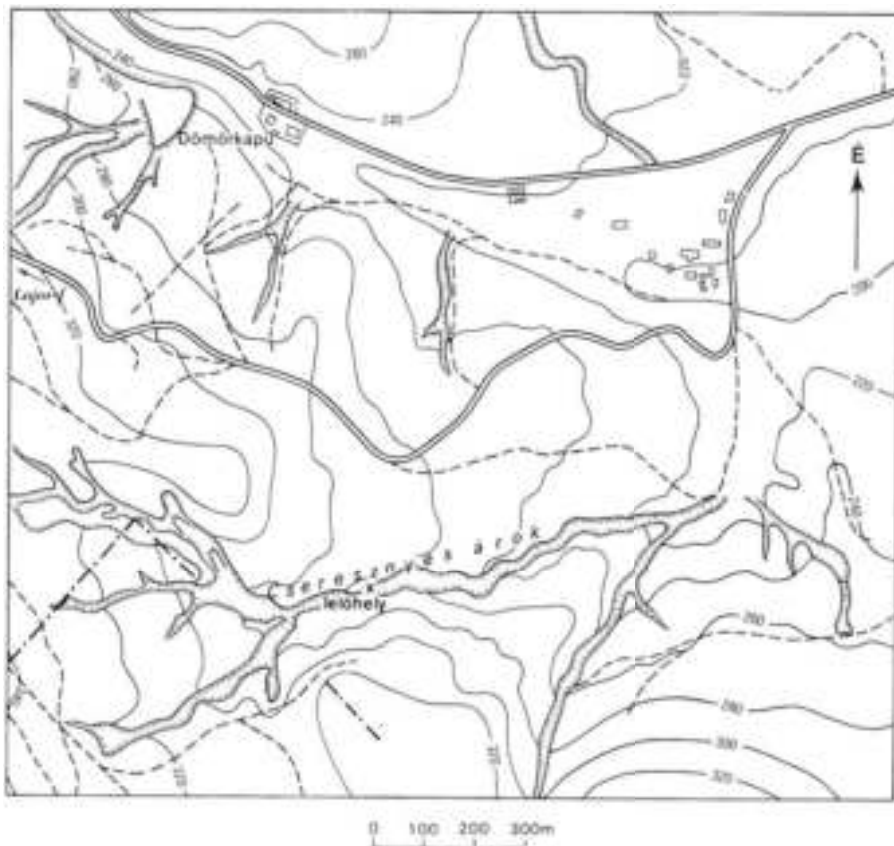
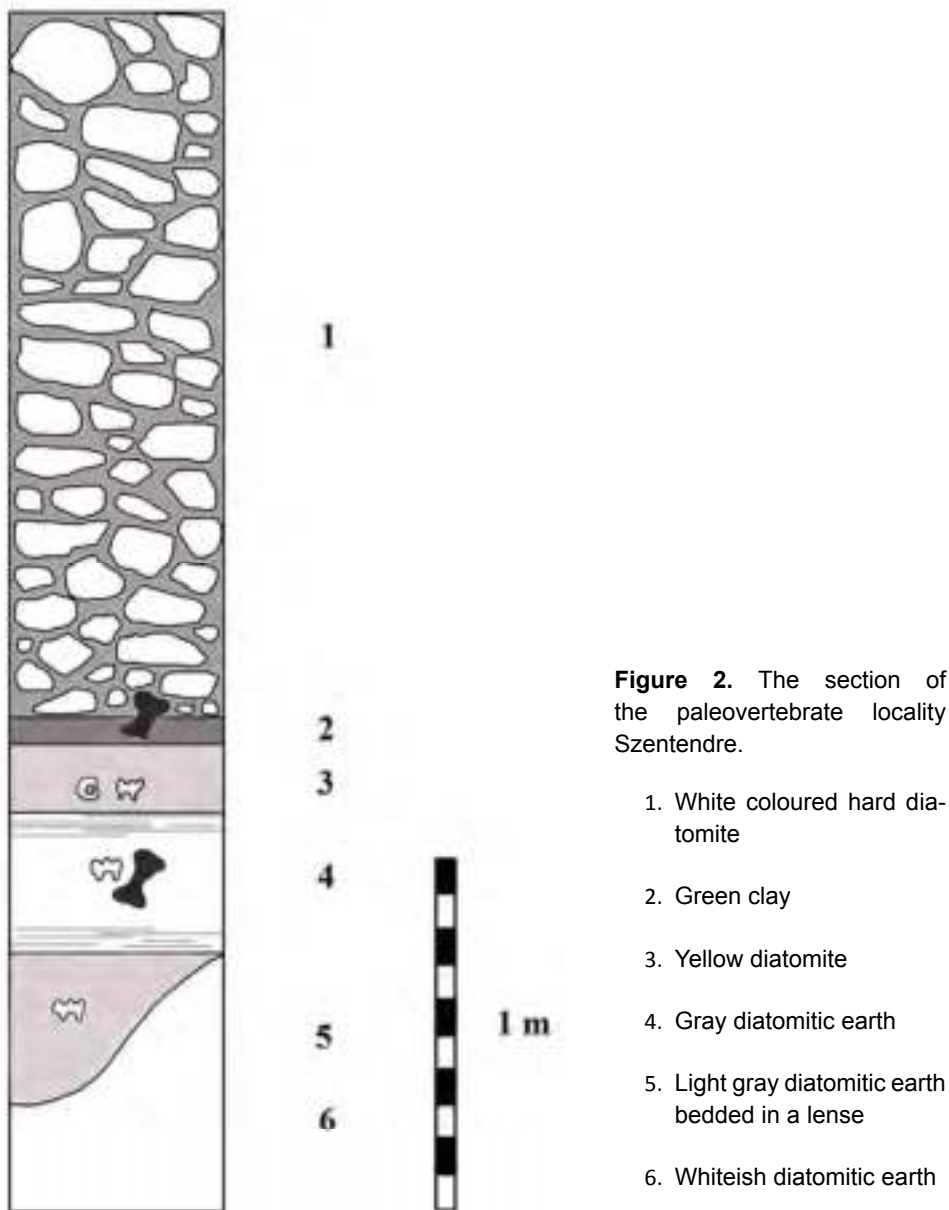


Figure 1. Geographical position of the paleovertebrate locality Szentendre (After Kordos1982: fig. 1.).



In 2018 we cleaned the section of the locality and we could distinguish the following layers (Fig. 2):

1. White coloured hard diatomite: this level were visible on the top of the section without cleaning of the overburden. During the field activity in 1980 it

was sampled by László Kordos and Peter Solt. It contains bones but those are very difficult to extract from the cemented matrix. During the field campaign in 2018 this level was not sampled.

2. Green clay: it is a 5 cm thick compact level in the lower border of the first layer. It contains bone fragments of large vertebrates. In 2018 it was not sampled.
3. Yellow diatomite: it consists of 30 cm thick soft ochre diatomitic earth, which is easy to wash. A test sample was taken from this level in 2017. In 2018 400 kg of sediment was collected and washed. It contains pieces of silicified trunks, microvertebrate bones and teeth, shells of freshwater and land snails and fragments of bird eggs.
4. Gray diatomitic earth: It consists of 40 cm thick soft diatomitic earth with some thin coal bands. 400 kg sample was taken. It contains pieces of silicified trunks, microvertebrate bones and teeth, bones of large sized mammals, shells of freshwater and land snails and fragments of bird eggs.
5. Light gray diatomitic earth bedded in a lense: It is not a continuous layer, but a lense below the darker gray fourth layer. It is bordered by coal bands. 200 kg sample was taken, but during the washing and sorting we realized that this part of the studied section is the richest in vertebrate fossils. Beyond the bones it produced shells of land molluscs, fragments of bird eggs and *Celtis* stones.
6. Whiteish diatomitic earth: 50 cm thick layer at the lower part of the section. It is very rich in small pieces of silicified trees and *Celtis* stones. The vertebrate material is relatively poor.

Material and methods

The washing of the sampled material took place in Pásztó. The sediment samples were air dried. After drying, the material was soaked in water and H_2O_2 . We used a sieve with 0.5 mm mesh for washing. The collected finds belong to the Natural-history Collection of the Municipal Museum of Pásztó.

Dental morphological nomenclatures followed in the text: for Sciuridae: Cuenca-Bescos (1988), for Gliridae: Daams (1981, 1999), Wu (1993), Daxner-Höck & Höck (2009), for Cricetodontini: Mein & Freudenthal (1971b), Rummel (1998), Lopez-Guerrero et al (2013) and for Cricetini: Mein & Freudenthal (1971b), Daams & Freudenthal (1988).

Abbreviations used in the text:

D4:	deciduous (milk) upper premolar
P4:	upper permanent premolar
M1-M2-M3:	upper permanent molars
d4:	deciduous (milk) lower premolar
p4:	lower permanent premolar
m1-m2-m3:	lower permanent molars
fr:	fragment
L:	maximal antero-posterior length on the occlusal surface of a tooth
W:	maximal linguo-labial width on the occlusal surface of a tooth
Hyps:	hypsodonty of the <i>Cricetodon</i> molars, measured after Weerd (1976)
Min.	minimal value in a sample
Max.	maximal value of a sample
X:	arythmetic average of a sample

All the numeric data are given in mm. The digital images of lissamphibians and squamates were taken by a Canon Eos 400 D digital camera with a Canon Macro Lens EF-S 60mm, and images were processed using a Combine ZP Image Stacking Software by Alan Hadley, whereas the micrographs with the Rodent teeth in the plates were taken by a Canon Eos 400 D digital camera with a Canon MP-E65 mm macro objective. Retouching of the micrographs with the rodent teeth was made by HJ using Photoshop.

Systematic part

Order: Caudata Scopoli, 1777

Family: Salamandridae Goldfuss, 1820

Genus: *Salamandra Laurenti*, 1768

Salamandra sp.

Referred material: 2 humeri (MMP. 2019.1.1-2); 4 fragmentary vertebrae (MMP. 2019.2.1-4).

Description. All the vertebrae are fragmentary. The largest specimens represents the anterior part of a precaudal vertebra (Fig. 3B). The specimen is opistocoelous provided with a large condyle, clearly separated from the vertebral centrum. The neural arch is strongly flattened and in ventral view the centrum preserves part of



Figure 3. Remains of Salamandridae from Szentendre. A– *Salamandra* sp. (MMP.2019.1.1) distal humeral fragment in ventral view; B – *Salamandra* sp. (MMP.2019.2.1) fragmentary precaudal vertebra in ventral view; C – *Lissotriton* sp. (MMP.2019.3.1) fragmentary precaudal vertebra in lateral view. Scale = 2 mm.

a subcentral keel. A small caudal vertebra preserves the remnants of the haemal arch. The other specimens preserve part of the neural arch showing a low neural crest. Two humeral fragments of relatively large size (Fig. 3A) represent the distal part of these bones. The ventral cubital fossa is deep and of triangle shape.

Comments. The relatively large sized opistocoelous vertebrae with strongly flattened neural arch and low neural crista is typical for the genus *Salamandra*. The material in hand is too fragmentary for a more closer assignment.

Genus: *Lissotriton* Bell, 1839

Lissotriton sp.

Referred material: 1 precaudal vertebra (MMP. 2019.3.1).

Description. The only vertebra is of small size (Fig. 3C). The centrum is opistocoelous, however the condyle and the transverse processes are damaged. The centrum is gently concave dorsally and provided with relatively small subcentral

foramina; the neural arch is flattened, whereas the neural spine is high and long extending from the anterior part of the neural lamina to the posterior border of the postzygapophyses; the only prezygapophysis preserved has a nearly horizontal articular surface.

Comments. The small-sized opistocoelous precaudal vertebrae, provided with a high and long neural spine occur typically in the members of *Lissotriton*. *Carpathotriton* is another salamandrid taxon provided with an extremely high neural spine, known from the middle Miocene of Mátraszőlős 1 and 2 (N-Hungary) and Tauț (W-Romania) (Venczel 2008, Venczel & Știucă 2008). However, the neural spine of *Carpathotriton* has a gradual posterior enlargement bearing pit and ridge sculpture (Venczel 2008).

Order: Anura Fischer von Waldheim, 1813

Family: Alytidae Fitzinger, 1843

Genus: *Latonia*

Latonia gigantea (Lartet, 1851)

Referred material: 18 fragmentary frontoparietals (MMP.2019.4.1-3, 2019.10.1-12, 2019.26.1-3); 23 fragmentary maxillae (MMP.2019.5.1-3, 2019.11.1-13, 2019.27.1-9); one fragmentary pterygoid (MMP.2019.6.1); one fragmentary premaxilla (MMP.2019.12.1); four angulosplenials (MMP.2019.13.1-3, 2019.28.1); two presacral vertebral centra (MMP.2019.15.1, 2019.29.1); one fragmentary urostyle (MMP.2019.14.1); one fragmentary scapula (MMP.2019.7.1); one fragmentary distal humerus (MMP.2019.30.1); three left posterior ilial fragments (MMP.2019.16.1-3).

Description and comments. The material has belonged to various sized individuals. Typical features of *L. gigantea* include: the azygous frontoparietal is covered by a strong secondary sculpture (see e.g. Venczel 2004: text.fig.1A) that is visible even in the relatively small (i.e. young) individuals (Fig. 4B, C); the labial surface of the posterior part of maxillae is covered by a secondary sculpture; the angulosplenial bears two coronoid processes (Fig. 4A); the ventral process of the pterygoid is wide (Fig. 4D). The remaining material include two presacral vertebrae of relatively small size having opistocoelous centra; the centrum of the single sacral vertebra is bicondylar (Fig.E). A fragmentary scapula is provided with an extremely short and wide scapular blade. The ilial fragments are strongly damaged preserving only the acetabular region.



Figure 4. Remains of *Latonia gigantea* from Szentendre. A – fragmentary angulosplenial (MMP.2019.28.1) in dorsal view; B, C – fragmentary frontoparietal in ventral (B) and dorsal (C) views; D – fragmentary pterygoid in dorsal view; E – fragmentary sacral vertebral centrum in ventral view. Scale = 2 mm.

Family: Pelobatidae Bonaparte, 1850

Genus: *Pelobates* Wagler, 1830

Pelobates sanchizi Venczel, 2004

Referred material: three fragmentary frontoparietals (MMP.2019.17.1-3); four fragmentary maxillae (MMP.2019.18.1-3, 2019.31.1).

Description. Only small fragments are available. One of the best preserved specimen (MMP.2019.31.1) preserves the middle part of a maxilla (Fig. 5A, B). The sculpture on the labial surface consists of various sized pits enclosed completely by bony ridges that is typical for *Pelobates sanchizi*. The lamina horizontalis is flattened labio-lingually and terminated posteriorly in a small pterygoid process, as it is preserved in the specimen MMP. 2019.18.1. Three foramina (one larger and two smaller ones) are present posterior to the pterygoid process of the latter specimen. Comments. *P. sanchizi* Venczel, 2004 is known from the late early (MN 4) to the late Miocene of Central Europe (Ivanov 2008, Roček 2013) and previously it has been listed from Szentendre (Venczel 2004).

Family: Bufonidae Gray, 1825

Genus: *Bufotes* Rafinesque, 1815

Bufotes sp.

Referred material: one fragmentary squamosal (MMP.2019.25.1).

Description. The single specimen preserves a short and pointed zygomatic process and a similarly short but widened posterodorsal process (Fig. 5C, D). The distal part of the posterolateral process is broken off. The above morphology is reminiscent of recent *B. viridis* (e.g. see Bailon 1999: Plate 6D).

Comment. Another taxon with a comparable morphology to *Bufotes viridis* is *Bufo priscus*, described from the middle Miocene (MN 6) of Devinska Nova Ves (= Neudorf, Dévényújfalú), near Bratislava, Slovakia. The status of that species (i.e. synonymy to *B. viridis* is possible) has been commented by Rage & Roček (2003) and Venczel (2004).

Family: Scincidae Gray, 1825

Scincidae indet.

Referred material: one fragmentary maxilla (MMP.2019.20.1); one fragmentary dentary (MMP.2019.21.1).

Description. The referred material is extremely fragmentary. The maxillary



Figure 5. Remains of Anura from Szentendre. A, B – fragmentary maxilla of *Pelobates sanchizi* (MMP.2019.31.1) in labial (A) and lingual (B) views; C, D – fragmentary squamosal of *Bufotes* sp. (MMP.2019.25.1) in medial (C) and lateral (D) views. Abbreviations: pdp - posterodorsal process, plp - posterolateral process, zp - zygomatic process. Scale = 2 mm.

fragment represent the anterior part of the bone; the labial surface is smooth and displays several nutritive foramina; there is no intact tooth is preserved. The dentary fragment represents the anterior part of a right dentary with six tooth positions (two tooth crowns are preserved only). The tooth crown apparently is monocuspid bearing striations only lingually. The meckelian groove is open up to the symphyseal region and oriented ventrally being roofed by a moderately wide subdental shelf. Unfortunately the material is too fragmentary for a more closer assignment.

Comments. Scincid remains have been reported from the Sarmatian (MN 7/8) localities of Felsőtárkány Basin, Hungary by Venczel & Hír (2013) and from the early Pannonian (MN 9) of Crețești, Romania by Codrea et al. (2017).

Family Lacertidae Bonaparte, 1831

Lacertidae indet.

Referred material: three fragmentary dentaries (MMP.2019.22.1-3).

Description. The specimens are fragmentary preserving parts of the dentaries (two

specimens are larger and one is rather small) of small lacertid lizards. The meckelian groove is open extending up to the symphysis and oriented ventromedially; the lamina horizontalis is thin with convex lingual margin; the subdental shelf is shallow and moderately wide. The teeth are pleurodont with their crown bicuspid without any trace of labial or lingual striations; the main cusp is situated distally; the labial surface is smooth and convex and a single row of nutritive foramina is present.

Comments. The lacertids are quite common in the middle Miocene localities of the Central and Eastern Paratethys area (Codrea et al. 2017).

Family Anguidae Gray, 1825
Anguidae indet.

Referred material: 12 osteoderms (MMP.2019.8.1, 2019.19.1-6, 2019.32.1-5).

Description. The specimens are of rectangular shape or with rounded margins (Fig. 6A). The outer surface displays a prominent medial ridge delimited by several anastomosed lateral ridges, irregular pits and grooves. The outer surface has an ornamentation free gliding surface positioned anteriorly.

Comments. The shape and morphology of the osteoderms is reminiscent of the genus *Ophisaurus*, but the material is too limited for such an assignment.

Suborder Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
"Colubrinae"
Colubrinae indet.

Referred material: five fragmentary vertebrae (MMP.2019.9.1-5, 2019.23.1).

Description. The material consist of three trunk vertebrae and two caudal vertebrae. Two of the trunk vertebrae are of larger size (the centrum length of the largest specimen = 5,65 mm). The neural arch is moderately vaulted and provided with relatively high neural spines. The haemal keel is slightly sinuous with a more prominent part at mid-length of the centrum (Fig. 6C). Another specimen has a more flattened haemal keel with rounded subcentral surface (Fig. 6B).

Comment. The material probably represent two different colubrine taxa. However, the material is too limited for a more closer assignment.

"Natricinae"
Natricinae indet.



Figure 6. Remains of squamates from Szentendre. A – fragmentary osteoderm of *Anguillidae* indet. in dorsal (outer) view; B – fragmentary trunk vertebral centrum in ventral view; C – fragmentary trunk vertebra in ventral view. Scale = 2 mm.

Referred material: one fragmentary vertebra (MMP.2019.24.1).

Description. The only specimen is a fragment of a vertebral centrum. The vertebral centrum is elongated, whereas the hypapophysis is prominent with a sinuous and deep ventral margin, however, the distal part is missing.

Comment. The morphology of the specimen approaches those of natricine snakes. In colubrine snakes the anterior trunk vertebrae also possess hypapophyses resembling superficially that of the specimen, but the hypapophyses in that group are long and with more or less straight ventral margins. It is not surprising the presence of natricine snakes in the sediments of this locality, a group of snakes rather common in the middle Miocene of the Pannonian basin.

Family: Sciuridae Fischer von Waldheim, 1817
Sub-family: Sciurinae Fischer von Waldheim, 1817
Genus: *Spermophilinus* De Bruijn & Mein, 1968
Spermophilinus bredai De Bruijn & Mein, 1968

Material and measurements: 1 P4: 1.55x1.82, 1M1-2: 1.82x2.25, 1d4: 1.2x1.09, 1m1: 1.76x1.95, 1m2: 1.86x2.10.

Description. The description of the rather general morphology of the species was given in the previous publications of Hír (2006) and Hír & Kókay (2010). The Szentendre material has no special characters and a repeated description is not necessary. The species is a constant element of the Central European Middle Miocene vertebrate faunas (Hír et al. 2017).

Genus: *Palaeosciurus* Pomel, 1853
Palaeosciurus sp.

Material: 2 M1-2: 2.17x2.44, 2.2x2.52, 1 m1: 2.28x2.27

Description. The teeth are rather worn. The morphological description is difficult, but the general sciurid structure is visible and the dimensions are similar to the *Palaeosciurus* genus. After giving a review of the last occurrences of the genus in the different regions in Europe we can see that *Palaeosciurus* disappeared from Spain, Greece and Turkey during the early Miocene. In Central Europe it existed up to the late middle Miocene. In the Carpathian Basin the genus was found in Hasznos (Hír & Pászti, 2012) and Subpiatră 2/2.

Tribus: Pteromyini Brandt, 1855
Genus: *Albanensia* Daxner-Höck & Mein, 1975
Albanensia sansaniensis (Lartet, 1851)

Material and measurements (see Table 1.).

Description. **M 1-2.** Subrectangular outline with rounded lingual side because the concave lingual wall of the protocone. Width of the crown is larger than the length. Anteroloph developed as a continuous ridge on the mesial margin of the crown between the protocone and the anterior basis of the paracone. This ridge is without cuspulas. Protoloph and metaloph converge to the labial side of the protocone in V shape. Protoconule is incipient. Protoloph is a continuous ridge between the pro-

Table 1. Material and measurements of *Albanensia sansaniensis* (Lartet, 1851)

NO. inv.	Position:	L:	W:	Figure:
MMP. 18. 431.	M1-2	2.65	3.30	Pl. I.-1
MMP. 18. 432.	M3	2.50	2.55	
MMP. 18. 433.	d4	2.07	1.77	
MMP. 18. 434.	p4	2.70	2.50	
MMP. 18. 435.	m1	2.65	2.77	Pl. I.-2
MMP. 18. 436.	m1	2.62	2.75	
MMP. 18. 440.	m1	2.67	2.90	
MMP. 18. 437.	m2	2.95	3.0	Pl. I.-3
MMP. 18. 438.	m2	2.87	2.90	
MMP. 18. 439.	m2	2.95	3.12	
MMP. 18. 441.	m3	3.37	3.21	

tocone and the paracone. It does not form a “zigzag line” which is characteristic in *A. grimmi* (Daxner-Höck 2004a). The mesostyle christa on the posterior side of the paracone is underdeveloped and the mesostyle is a tiny but distinct cuspula. The metaloph connects the protocone, metaconule and metacone. A secondary ridge starts from the metacone to the posteroloph. The metaconule has a large posterior ledge, but it does not reach the posteroloph. Hypocone is incipient. Posteroloph is thinner and lower developed than the other main ridges. In all the secondary ridges are much less developed than those in the molars of *A. albanensis* and *A. grimmi*.

M3. Subtriangular outline with rounded angles. Anteroloph and protoloph are nearly parallel. Protoconule, mesostyle and mesostyle christa are absent. Metaloph is a short curved ridge between the posterior side of the protocone and the posterolingual part of the posteroloph. Secondary ridges are absent.

d4. Trapezoidal outline with rounded angles. Anterior width is narrower than the posterior one. The greatest part of the occlusal surface is occupied by a large talonid basin. The cusps are definitely smaller than the cusps of the permanent molars. Protoconid and the metaconid are situated in the mesial surface. Those are close to each other. In the postero-labial angle the hypoconid is developed. The entoconid is incorporated into the posterolophid. Mesoconid is a low-developed cuspula between the protoconid and the hypoconid. There is an incision between the hypoconid and the metaconid in the lingual margin.

p4. Trapezoidal outline with rounded angles. Anterior margin is narrower than the posterior one. Three cusps are developed on the mesial part of the crown: the

well developed protoconid and metaconid and a lower developed anteroconulid. A narrow trigonid basin is closed by these three cusps. Anteroconulid and metaconid are connected by a narrow anterolophid. The V shaped metalophid is developed on the posterior slope of the protoconid and metaconid. An enamel ridge is developed on the posterior slope of the metaconid reaching to the mesolophid. It is less expressed than the same structure in *A. grimmi*. The mesoconid is a low developed cuspula. The trench between the mesoconid and the labial margin (which is found in *A. grimmi*) is not developed. Mesoconid is connected to the base of the protoconid and hypoconid by enamel ridges. The posterolophid is a continuous ridge between the hypoconid and the entoconid. It is not dissected by minor cusps which is visible in *A. albanensis* and *A. grimmi*. No incision between the posterolophid and the entoconid. A deep and wide incision is found between the entoconid and mesolophid. The surface of the talonid basin is not complicated by secondary ridges and crenulation. Two roots are present.

m1-2. Rhomboidal outline. Related to the p4 the anterior margin is wider. A strong anterolophid is extending on the mesial margin between the protoconid and the metaconid.

These two ridges are connected by the lower developed metalophid too. This metalophid is straight, transversal and not V-shaped (the V-shaped configuration is visible in *A. grimmi*). A trigonid basin is rounded by the protoconid-metaconid-antrolophid- metalophid system. An enamel ridge is developed on the posterior slope of the metaconid reaching to the mesolophid.

There is a closed C-shaped basin between the labial cingulum and the mesoconid. The posterolophid is a continuous ridge between the hypoconid and the entoconid. It is not dissected by minor cusps which is visible in *A. albanensis* and *A. grimmi*. No incision between the posterolophid and the entoconid. There is a deep and narrow incision between the mesolophid and the entoconid. The surface of the central basin is complicated by secondary ridges and crenulation, but these ridges are less developed than those in *A. albanensis* and *A. grimmi*. Four roots are present.

m3. The basic structure is similar to the crown of m1-2. The differences are the followings: more elongated rhomboid outline; no closed basin on the labial side of the mesoconid, because the labial cingulum is not so strong; four roots are present; the hypoconulid is not developed.

Discussion. The classification of the finds is based on the small dimensions and the morphology. Up to the present *A. sansaniensis* has not been reported from Hungary. *Albanensia grimmi* (Black, 1966) populations are known from the late

Sarmatian (MN 7+8) fauna of Felsőtárkány 3/2 (Hír, 2003) and the early Pannonian (MN9) material of Rudabánya (Kretzoi & Fejfar 2004). An only *A. albanensis* m3 was found in the Early Sarmatian (MN 7+8) assemblage of Kozárd (N-Hungary, Nógrád County) (Hír, 2015).

Albanensia sansaniensis differs from *A. albanensis* in the following morphological characters (Ginsburg & Mein (2012): in the smaller dimensions; in the more simple parastyle in the upper molars; in the absence of hypoconulid in the lower molars. In the Szentendre material there are some additional morphological specialities: the two impressions on the lingual surface of the M1-2 are absent; the mesostyle christa is underdeveloped, mesostyle is a distinct small cusp in M1-2; posteroloph is continuous, it is not a “string of pearls”; the crenulation of the enamel surface is less developed, during the wearing process it can be disappeared.

The earliest occurrence of *A. sansaniensis* is reported from the Early Miocene fauna of Montalvos 2 in the Calatayud-Teruel Basin, Spain (Hordijk et al. 2015). Among the *Albanensia* species, *A. sansaniensis* is unambiguously the smallest one. But consequent time transgressiv magnification of the dimensions is not found when we compare the *Albanensia albanensis* and *Albanensia grimmi* finds collected from the faunas of the MN 7/8 and MN 9 zones. Moreover the *A. grimmi* molars from Felsőtárkány 3/2 (late MN7/8) are definitely larger than the *A. grimmi* teeth from Rudabánya (MN9). The dimensions of the later population is closer to *A. albanensis* materials from La Grive and Gratkorn. (Remarkabler that the finds from Rudabánya were first described as *A. albanensis* by Kretzoi et al, 1974 and finally revised and determined as *A. grimmi* by Kretzoi & Fejfar (2004).

Family: Gliridae Thomas, 1897

Genus: *Muscardinus* Kaup, 1829

Muscardinus sansaniensis (Lartet, 1851)

Material and measurements.

No. inv.	Position:	L:	W:	Figures
MMP. 18. 453.	P4	0,63	0,77	
MMP. 18. 451.	M1	1,04	1,13	Pl. III.-21.
MMP. 18. 452.	m1	1,06	1,01	Pl. III.-22.
MMP. 18. 495.	m2	1,13	1,05	

Description. **P4**. Oval outline. 3 main ridges (protoloph, metaloph and posteroloph), 2 shorter centrally positioned ridges: anteroloph, anterior centroloph (?).

M1. Rectangular outline. Width is larger than the length. Posterior width is slightly larger than the anterior one. The 1th ridge (anteroloph) is free in both sides. The 2nd, 8th, 9th ridges are always complete and connected to the endoloph. 3rd, 4th, 5th, 6th, 7th ridges are incomplete and labially positioned.

m1. Trapezoidal outline, posterior width is slightly larger than the anterior one. 8 ridges. 1th, 5th, 7th, 8th, 9th ridges are complete. 2nd, 4th ridges are short lingually positioned ridges. 6th ridge is ended just before the labial margin.

m2. Trapezoidal outline, anterior width is slightly larger than the posterior one. 7ridges. 1th, 3th, 5th, 7th ridges are complete. 2nd and 4th ridges are shorter and lingually positioned. 6th ridge is labially positioned. This is the only ridge which is not conncted to the endolophid. Endolophid is interrupted between the 4th and 5th ridges.

Discussion. These *Muscardinus* M1, m1 molars show the most plesiomorph characters in the Carpathian Basin (nearly isodiametric M1 with numerous additional ridges, m1 with 3 additional ridges). The morphology of the molars from Szentendre are similar to the pattern of the "*Eomuscardinus* aff. *sansaniensis*" specimen described from Puttenhausen (Wu 1990).

Genus: *Miodyromys* Kretzoi, 1943

Miodyromys sp.

Material and measurements.

No. inv.	Position:	L:	W:	Figures:
MMP. 2018. 479.	M1	1.06	1.26	
MMP. 2018. 483.	M1	1.02	1.19	
MMP. 2018. 484.	M1	1.05	1.18	
MMP. 2018. 486.	M1	1.12	1.19	
MMP. 2018. 487.	M1	1.06	1.23	
MMP. 2018. 478.	M2	0.99	1.33	Pl. III.-16.
MMP. 2018. 482.	M2	1.05	1.29	
MMP. 2018. 484.	M2	1.04	1.32	Pl. III.-17.
MMP. 2018. 488.	m1	1.12	1.11	Pl. III.-18.
MMP. 2018. 494.	m1	1.15	1.11	
MMP. 2018. 491.	m2	1.22	1.12	
MMP. 2018. 492.	m2	1.13	1.12	
MMP. 2018. 496.	m3	1.06	0.99	

Description. **M1-2.** Rectangular outline, concave occlusal surface. Four main ridges (anteroloph, protoloph, metaloph, posteroloph). Lingual and labial ends of the anteroloph are free. The lingual ends of the other three main ridges are lingually merged. Anterior centroloph is long and connected to the protoloph in the paracone. Posterior centroloph is shorter than the anterior one and connected to the metaloph in the metacone. There is a short anterior extra ridge in (3/8) cases. Anterior and posterior extra ridges are found together in (1/8). Extra ridges are absent in (4/8).

m1. Trapezoidal outline, anterior with narrower than the posterior one. Four main ridges (anterolophid, centrolophid, mesolophid, posterolophid). The labial ends of the ridges are free. In the lingual side anterolophid and centrolophid are connected in the metaconid. Mesolophid and posterolophid are connected in the entoconid. Metalophid is developed in diagonal position in the anterior sinusid and connected to the anterolophid and the metalophid. Beyond this "irregular ridge" there are 1 or 2 small pearl-like extra ridges in the anterosinusid.

m2. Trapezoidal outline, anterior width is slightly larger than the posterior one. The four main ridges are: anterolophid, metalophid, mesolophid, posterolophid. Beyond the main ridges there are the shorter centrolophid and posterior extra ridge. The connections of the ridges is like in m1, but the lingual end of the metalophid is ended just before the metaconid.

m3. Subtriangular outline, posterior part is narrower. The structure of the ridges is similar to the m2, but there is an anterior extra ridge between the anterolophid and metalophid.

Discussion. The taxonomy and evolution of the *Miodyromys* genus is best documented and studied in the Northern Alpine Foreland Basin (Mayr 1979, Heissig 2006, Wu 1990, 1993, (Kälin & Engesser 2001). In this region a time transgressive increase of the mean measurements of the *M. aff. aegercii* and *M. aegercii* populations was found (Kälin & Engesser 2001: Abb. 27.) from MN5 to MN9. Later Heissig (2006) verified that two sympatric *Miodyromys* species left in Southern Germany from the Early MN5 to the MN6 faunas.

The evolution of the *Miodyromys* finds from Hungary are not possible to explain on the score of the scheme of the OSM. During the elaboration of the late MN5 "*Cricetodon meini* faunas" of Litke (Hír 2013) we found that the *Miodyromys* teeth are definitely smaller than the *Miodyromys* finds from the "*C. meini* faunas" of the OSM (eg. Edelbeuren-Maurerkopf, Sach (1999); Wannenwaldtobel 2, Sach (1999); Hohenraunau, Seehuber (2008); Unterneul 1a, Heissig (1989); Ebershausen, Heissig (2006). Larger difference is found when we compare the dimensi-

ons of the *Miodyromys* teeth of the “*Cricetodon aueus* faunas” of Szentendre and Rümikon (Kálin & Engesser 2001). The founded explanation of this phenomenon needs more material.

Genus: *Microdyromys* De Bruijn, 1966
Microdyromys koenigswaldi De Bruijn, 1966

Material and measurements.

No. inv.	Position:	L:	W:	Figures:
MMP. 2018.480.	M1	0,97	1,05	Pl. III.-15
MMP. 2018.481.	M1	1,05	1,13	
MMP. 2018.489.	m1	1,12	1,01	Pl. III.-19.

Description. **M1**. Trapezoidal outline, posterior width is a bit larger than the anterior one. 6 main ridges: anteroloph, protoloph, anterior centroloph, posterior centroloph, metaloph, posteroloph. One extra ridge between the protoloph and anterior centroloph. A tiny lingually positioned extra ridge is found between anteroloph and protoloph. Endoloph is continuous in the specimen no. 481. It is interrupted between the anteroloph and the protoloph in no. 2018. 480.

m1. Trapezoidal outline, posterior width is a bit larger than the anterior one. 5 main ridges: anterolophid, metalophid, centrolophid, mesolophid, posterolophid. The position and development of the extra ridges are referable to the original diagnosis. Labial end of the mesolophid is strongly curved anteriorly. Endolophid is interrupted between the centrolophid and mesolophid.

Discussion. *Microdyromys koenigswaldi* is a rare species in the Miocene of the Carpathian region. Beyond Szentendre it was reported only from Sámsonháza (Hír & Mészáros 2002).

Genus: *Glirulus* Thomas, 1897
Glirulus lissiensis (Hugueney & Mein 1965)

Material and measurements.

No. inv.	Position:	L:	W:	Figure:
MMP. 2018. 497	m2	0,92	0,85	Pl. III.-20.

Description. Rectangular outline. Anterior width is slightly larger than the posterior one. Four main ridges: anterolophid, metalophid, mesolophid, posterolophid. All of them and the centrolophid are connected to the endolophid. Anterolophid and metalophid have a labial connection. The labial ends of the metalophid and the mesolophid are anteriorly curved. Centrolophid reaches the center of the toothcrown. The endolophid is interrupted between the centrolophid and the mesolophid. There are two extra ridges: one between the centrolophid and the metalophid, one between the mesolophid and the posterolophid. There is a short longitudinal ridge on the anterior side of the mesolophid.

Discussion. The *Glirulus lissiensis* occurrences in Eastern Central Europe are as follows: Rudabánya (MN9): Daxner-Höck (2005); Richardhof –Golfplatz (MN9): Daxner-Höck (2005); Richardhof-Wald (MN9): Daxner-Höck (2005); Borsky Svätý Jur (MN9): Sabol et al (2004), Joniak (2005); Belchatow A (MN9): Kowalski (1997), Garapich (2002); Schernham (MN10): Daxner-Höck (2004b); Kohfidisch (MN 11) Daxner-Höck & Höck (2009); Eichkogel (MN 11) Daxner-Höck & Höck (2009); Egerszólát (MN 7+8) Hír (2011); Subpiatră 2/2 (MN 6) Hír & Venczel (2005); Felsőtárkány 3/8 (MN 9) Hír & Kókay (2010).

Genus: *Myoglis* Baudelot, 1965

Myoglis meini (De Bruijn, 1966)

Material and measurements.

No. inv.	Position:	L:	W:	Figures:
MMP. 2018. 464	P4	1,62	1,81	Pl. III.-11.
MMP. 2018. 466	P4	1,47	1,58	
MMP. 2018. 465	M2	1,65	2,06	Pl. III.-12.
MMP. 2018. 467	M2	1,61	1,96	
MMP. 2018. 468	M3	1,64	1,85	
MMP. 2018. 469	M3	1,51	1,82	
MMP. 2018. 470	M3	1,65	1,88	
MMP. 2018. 471	p4	1,29	1,29	
MMP. 2018. 472	p4	1,26	1,22	
MMP. 2018. 473	p4	1,26	1,19	
MMP. 2018. 474	m1	1,83	1,75	Pl. III.-13.
MMP. 2018. 475	m2	1,82	1,90	
MMP. 2018. 476	m3	1,79	1,74	Pl. III.-14.

Description. General characters: flat occlusal surface, the cross section of the valleys between the main ridges are V-shaped.

P4. The outline of the occlusal surface is oval. Four main ridges: anteroloph, protoloph, metaloph, posteroloph. The lingual end of the protoloph, metaloph and posteroloph are merged into the protocone. A slender extra ridge (anterior centroloph?) occurs between the protoloph and the metaloph. Three roots.

M2. The outline of the occlusal surface is rectangular, broader than its own length. 5 main ridges: anteroloph, protoloph, anterior centroloph, metaloph, posteroloph. Anteroloph is independent, protoloph, metaloph and posteroloph are merged in the protocone. Anteroloph, protoloph and anterior centroloph are diagonally positioned, metaloph and posteroloph are transversal. There are two labially positioned extra ridges: one between the protoloph and anterior centroloph, another one between the anterior centroloph and the metaloph. The earlier one has a labial connection to the protoloph. There is an incipient extra ridge between the anteroloph and the protoloph. Three roots.

M3. The outline of the occlusal surface is subtriangular, posteriorly narrowed. A continuous endoloph is developed. 5 main ridges are connected to the endoloph. The nomenclatural homology of them is uncertain. 2-3 extra ridges are found in the posterior segment of the occlusal surface. Three roots.

p4. The outline is subtriangular. There are four ridges with free lingual and labial ending. In one juvenile molar the two anterior ridges are connected. One root.

m1. The outline of the occlusal surface is rectangular: the posterior margin is wider than the anterior one. Four main ridges: anterolophid, metalophid, mesolophid, posterolophid. The anterior extra ridge is developed as a lingually positioned curved ridge between the anterolophid and the metalophid. The anterior end of the anterior extra ridge has a nearly central connection to the anterolophid. Among the Middle Miocene *Myoglis* populations of the Carpathian region this connection is developed only in the Subpiatră material (Hír & Venczel, 2005) beyond the Szentendre finds.

m2. The outline of the occlusal surface is rectangular. Broader than its own length. The four main ridges are regular like in m1. Three secondary ridges are developed, one lingually positioned between the anterolophid and the metalophid, a second one between the metalophid and the mesolophid and a third one between the mesolophid and the posterolophid. Tiny secondary ridges by the side of the anterior extra ridge are not developed.

Discussion. In the Carpathian Basin *Myoglis* was first mentioned in Neudorf Spalte (Fejfar 1990, Sabol et al. 2004). The absence of the genus in the faunas of Litke

1-2 (MN5), Hasznos, Sámsonháza (MN6), Mátraszőlős 1-2-3, Tasád (MN7/8) can be casual, but not impossible that during the time interval of the MN6-MN7/8 zones there were periods when the climate of the Carpathian Basin was not suitable for *Myoglis*. The flourishing of the genus is found in the late Astaracian–early Vallesian faunas (e.g. in the Felsőtárkány Basin: Hír 2003, 2006, Hír & Kókay 2010) and Rudabánya (Daxner-Höck 2005).

Family: Cricetidae, Fischer, 1817

Subfamily: Cricetodontinae, Simpson, 1945

Tribe: Cricetodontini, Simpson, 1945

Genus: *Cricetodon* Lartet, 1851

Cricetodon aureus Mein & Freudenthal, 1971

1982 *Cricetodon (Cricetodon) albanensis* (Mein & Freudenthal), *Cricetodon* sp. (s.l.), Kordos, p. 381 (Hung.), 383 (Eng.).

1986 *Deperetomys hagni hungaricus* n. ssp., Kordos, p. 524 -529 (Hung.), 539-542 (Eng.), Pl. III, figs 1-6.

1993 *Cricetodon hungaricus*, De Bruijn et al, p.208., pl., figs 1-9, pl. 19, figs 1-9.

Measurements.

		No.	Min.	X	Max.		No.	Min.	X	Max.
M1	L	23	3.07	3.26	3.50	W	23	1.87	2.06	2.20
M2	L	29	2.25	2.51	2.77	W	29	1.72	1.97	2.17
M3	L	29	1.82	2.08	2.32	W	29	1.69	1.88	2.10
m1	L	20	2.50	2.70	2.87	W	20	1.62	1.75	1.92
m2	L	23	2.35	2.57	2.82	W	23	1.80	1.95	2.12
m3	L	24	2.37	2.64	2.92	W	24	1.75	1.93	2.15

Description. **M1**. Anterocone is mainly split and consists of two equally developed conelets, which are divided by a shallow groove on the mesial surface. In the subsenile-senile specimen the anterocone is undivided. The posterior ectoloph of the labial unit of the anterocone is mainly absent, or it can be middle developed but does not reaches the anterior surface of the paracone. A short protolophule II is regular, protolophule I is absent. Paracone posterior spur is mainly short, never reaches the anterior surface of the metacone, or absent. The mesoloph is variable: it can be absent (8/23), or short (6/23) or it is only a small enamel knob on the entoloph (9/23). A short entomesoloph is rare 3/23. The lingual margin is straight, (not

undulated after the sense of Carro-Rodriguez et al 2018). A shallow vertical groove on the anterior surface of the paracone and the metacone is developed mainly in the juvenile unworn molars (18/23). This character is described by Maridet & Sen (2012), and Lopez –Guerrero et al (2014 a) in *C. sansaniensis*.

M2. Rectangular outline. The lingual anteroloph is a ridge, the labial anteroloph is a cusp. The anterosinus is deep and labially curved, the protosinus is shallow and transversally directed. The connection between the lingual anteroloph and the paracone anterior surface is rare 4/26. Protolophule I is absent, protolophule II is regular. Paracone posterior spur is short (2/26) or middle developed (24/26), but never reaches the anterior surface of the metacone. Metacone anterior spur is found only in 2/26. Those are not connected with the paracone posterior spur. A short mesoloph is rare. Short entomesoloph is similarly rare (3/26).

M3. Trapezoidal outline. Anterior width is larger than the posterior one. Labial anteroloph is well developed (mainly ridge like, sometimes cusp like) and the anterosinus is deep. Lingual anteroloph is less developed and the protosinus is shallow, sometimes disappeared. Labial anteroloph–paracone anterior surface connection is rare: 2/28. Paracone posterior spur is long and in most cases reaches the apex of the long mesoloph or the anterior spur of the metacone. Tendency for the development of neo-entoloph is absent.

m1. Anteroconid is simple, unicuspid. Labial anterolophid and the protosinuisid are well developed and regular. Lingual anterolophid is absent, or it is developed only as a short remnant ridge on the lingual side of the anteroconid. Posterior metalophulid is regular, specimen having both posterior and weaker (but continuous) anterior metalophulid are rare (2/20). Mesolophid is mainly absent (13/20), or short (5/20) or long (2/20) but low developed. Ectomesolophid is similarly rare (6/20). It is long and reaches the labial cingulum (3/20 15%) or short (3/20 15%). The sinusid is regularly closed by a cingulum, the lingual sinusid is open.

m2. Rectangular outline. Labial anterolophid and closed protosinuisid are well developed and regular. Lingual anterolophid is absent. The mesolophid is short. Its terminal part is free (14/23), or in subsenil and senil worned specimen it reaches the posterior basis of the metaconid (9/23). A short ectomesolophid is rarely found (5/23). Sinusid is closed by a cingulum, lingual sinusid is open. Posterosinuisid is mainly open 13/23, or closed 10/23. The narrow neck between the hypoconid and the posterolophid and the impression in the posterior margin is similarly developed to the same structures on m1.

m3. Subtriangular outline with rounded angles. Labial anterolophid and closed protosinuisid are well developed and regular. Lingual anterolophid is absent. The mesolophid is short 4/24, or middle developed 17/24, or long 3/24. In 11/24 ca-

ses the middle developed mesolophid is connected to the posterior basis of the metaconid. Ectomesolophid is absent. Sinusid is closed, but the cingulum is less developed than those on m2s. Lingual sinusid is open. Posterosinusid is closed in 19/24, or open in 5/24.

Table 2. Comparison of the typical characters of *Cricetodon aureus* in the type material and in the fauna of Szentendre

	<i>C. aureus</i> LÓPEZ-GUERRERO et al. 2013	<i>C. aureus</i> MEIN & FREUDENTHAL 1971b	<i>C. aureus</i> Szentendre
M1 anterocone posterior ectoloph		short or absent	43%, but never reaches the paracone
M1 entomesoloph	absent	rare	13%
M1 Lingual quersporn II		33%	65%
M2 paracone posterior ectoloph	“some M2s with styls and complete posterior ectolophs”	“paracone always has a posterior ectoloph, which is mainly well developed and reaches the basis of the paracone”	short: 25% middle developed: 75% never reaches the paracone.
M2 mesoloph		short or rarely middle developed	absent: 61% short: 39% middle developed: 0
m1 metalophid	“some m1 displaying exclusively type I or type II metalophid”	metaconid posterior connection 77% anterior connection 3% double connection 18% no connection 2%	posterior connection 90% anterior connection 0 double connection 10% no connection 0
m1 mesolophid	“mesolophids are longer than the ones from <i>C. soriae</i> ”	short 53% middle 32% long 2% absent: 13%	short : 25% middle: 0 long: 10% absent: 65%
m1 ectomesolophid		more than 50%	43%
m2 ectomesolophid		10%	9%

In some respects the morphology of the Szentendre population seems to be more archaic, than that of the type population of Vieux-Collognes because the less developed ectolophs in M1, M2; the better developed and more frequent lingual quersporn II in M1 and the more frequent metalophulid II (posterior metalophulid) in m1.

The origin and evolutionary position of *Cricetodon aureus* and *Cricetodon* aff. *aureus* is discussed in the literature. According to Prieto & Rummel (2016) *C. aureus* and *C. aff. aureus* are the members of the same evolutionary line. The two species *C. meini* and *C. aureus* are characterized by Lopez-Guerrero et al (2015) which are widely distributed through Europe from the earliest Middle Miocene having basal morphology with low intraspecific variability and little diversification.

Mein & Freudenthal (1971 b) found that *C. albanensis* is the descendant of *C. aureus*, because the better developed ectolophs and more frequent metalophulid I in m1. Maridet & Sen (2012) postulated that the presume of an anagenetic evolutionary line of *C. aureus*, *C. sansaniensis* and *C. albanensis* is the most probable hypothesis, but these species arrived to Europe independently.

Remarkable, that up to the present *C. aureus* has been reported nor from Anatolia and neither from the Balkan. For this reason we think, that a local European evolution of the species is not impossible.

Tribe: Copemyini Jacobs & Lindsay 1984

Genus: *Democricetodon* Fahlbusch, 1964

Democricetodon hasznosensis Kordos, 1986

1982 *Democricetodon minor* (Lartet), Kordos, p. 381, 383 (Hung.), p. 384 (Eng.).

1986 *Democricetodon hasznosensis* n. sp., Kordos, p. 529- 533 (Hung.), 542- 544 (Eng.), Pl. IV, figs. 6, 13, 18.

Measurements.

Description. **M1**. Anterocone is undivided, narrow, blade-like. The lingual part of the

	L	no.	min	X	max	W	no.	min	X	max
M1	L	41	1.74	1.87	2.02	W	41	1.16	1.26	1.34
M2	L	46	1.36	1.46	1.61	W	46	1.19	1.27	1.36
M3	L	16	1.05	1.13	1.26	W	16	1.08	1.16	1.26
m1	L	34	1.47	1.60	1.76	W	34	0.99	1.11	1.26
m2	L	31	1.34	1.47	1.58	W	30	1.12	1.21	1.32
m3	L	22	1.29	1.36	1.47	W	21	1.02	1.11	1.19

anterocone is continued in the lingual anteroloph. This ridge reaches the anterior basis of the protocone and closes the protosinus. The labial anteroloph developed between the labial basis of the anterocone and the anterior basis of the paracone and closes the anterosinus. In some cases (6/39) a comma shaped cingulum developed on the mesio-lingual surface of the anterocone. Normal paracone posterior spur is not found. Mesoloph is variable. It can be short (9/39), middle developed (25/39), or long, but doesn't reach the labial margin (2/39), or long and reaches the labial margin (3/39). Metaloph is short and posteriorly directed.

M2. Rectangular outline. The lingual and the labial anteroloph are equally well developed. Protosinus and anterosinus are closed. Anterosinus is deeper than the protosinus. Protolophule I and II are equally developed. Mesoloph is regular but variable. It can be short (14/45), middle developed (26/45), long, but doesn't reach the labial margin (4/45), long and reaches the labial margin (1/45). Normal paracone posterior spur is rare (2/45), it is continued in the labial cingulum between the paracone and the metacone. The metalophule can be anterior (3/45), posterior (31/45), doubled (9/45), or completely absent (2/45).

M3. Subtriangular outline, the width is larger than the length. The lingual and the labial anteroloph are well developed, but the lingual one is longer. Anterior protolophule is regular. Axioloph and centrocone forms a continuous longitudinal ridge. Paracone posterior spur is found in 7/16 and continued in the labial cingulum. Short mesoloph is rare (3/16). Metacone can be ridge-like or cusp-like.

m1. The tooth is relatively short. The anteroconid is cusp like (7/32), mainly in the juvenile unworn specimen, or triangular. Labial anterolophid is always well developed between the anteroconid and the antero-labial basis of the protoconid. The protosinusid is bordered by this ridge. Lingual anterolophid is weakly developed or substituted by metastylid, but it is mainly absent. In the latter cases the narrow anterosinusid is open. Anterolophulid is a short ridge between the anteroconid and the anterior angle of the protoconid. Metalophulid is short, antero-labially directed. Mesolophid can be middle developed (2/32), short (25/32), or absent (5/32). Ectomesolophid is developed only in 1 m1, but it is well developed and complete (reaches the labial border).

m2. Rectangular outline. Labial anterolophid is well developed and reaches the antero-labial basis of the protoconid. In 5/31 cases it is continued in the labial side of the protoconid and in the labial cingulum, which is closing the sinusid and reaches the antero-labial basis of the hypoconid. Mesolophid is short (14/31) (never reaches the posterior basis of the metaconid) or absent (17/31). Metalophulid is short, in 2/31 cases it doesn't reach the anterolophulid.

m3. Triangular outline, the posterior part of the toothcrown is narrowed, because

the strong reduction of the entoconid. Lingual anterolophid is absent (10/20), short (9/20) or middle developed (1/20). Labial anterolophid is regular and reaches the antero-labial basis of the protoconid. In 2/20 cases it is continued on the labial side and reaches the anterior basis of the hypoconid. Mesolophid is absent, because the posterior arm of the protoconid and the anterior arm of the hypoconid are connected at the lingual margin.

Discussion. The *Democricetodon* from Szentendre was first reported by Kordos (1982) as *D. minor*. Later he modified the classification as *Democricetodon hasznosensis* n. sp. Kordos (1986) after 1m1, 1m2 and 1 m3 fragm. However at the end of the description he emphasized that *Democricetodon hasznosensis* is a member of the “minor s. l.” group (Kordos 1986, p. 533 only in the Hungarian text).

After a long nomenclatural discussion cleared that *Democricetodon minor* is not a valid name. The details of this labyrinthine history is given by Maridet & Sen (2012). *D. sp. aff. D. gracilis* is accepted for the small sized *Democricetodon* from Sansan and *D. gracilis* is accepted for the material of Sandelzhausen and the later one is the type species of the *Democricetodon* genus (Maridet & Sen 2012).

Up to the present *Democricetodon hasznosensis* is known only from the Hungarian localities of Hasznos, Szentendre and Sámsonháza. In the OSM two *Democricetodon* species are characteristic from the early MN5 to the MN6 faunas: *D. gracilis* and *D. mutilus*. The origin of *D. hasznosensis* is unclear. However the comma shaped cingulum in the antero-lingual surface of the M1 is described in the Early Miocene *Democricetodon suensis* from Shunggou, Sihong, Jiangsu Province, China (Qiu 2010). This only common character is interesting, but without detailed comparison is inadequate for any founded conclusion.

Genus: *Megacricetodon* Fahlbusch, 1964

Megacricetodon minor (Lartet, 1851)

Measurements.

Description. **M1**. Anterocone is always divided. The anterior apex of the anterolo-

	L	no.	Min.	X.	Max.	W	no.	Min.	X.	Max.
M1	L	17	1.40	1.50	1.58	W	17	0.91	0.95	0.99
M2	L	16	1.12	1.17	1.26	W	15	0.91	0.96	1.02
M3	L	2	0.80	0.82	0.85	W	2	0.83	0.84	0.85
m1	L	23	1.26	1.39	1.51	W	23	0.78	0.86	0.98
m2	L	27	1.08	1.13	1.20	W	27	0.87	0.94	1.04
m3	L	3	0.95	0.98	1.02	W	3	0.74	0.80	0.84

phule is connected to the lingual unit of the anterocone or terminated between the two units of the anterocone. In 3/16 cases it forms an "Y" and the two branches are connected to the two units of the anterocone. Mesial cingulum is developed in 3/16. Protolophule I is long, reaches the anterior basis of the paracone in 7/16. It is short, doesn't reach the anterior basis of the paracone in 4/16. It is absent in 5/16. Protolophule II is mainly started from the centroloph (12/16), or started from the posterior angle of the protocone. Mesoloph is variable: short (4/16), middle developed (6/16), long, but doesn't reach the labial margin (4/16) or reaches the labial margin (2/16). Paracone posterior spur is mainly short (8/16), reaches the mesoloph (2/16) or absent (6/16). Metalophule connected to the posteroloph (6/16) or connected to the posterior angle of the hypocone.

M2. Labial anteroloph is regularly well developed and the anterosinus is deep. Lingual anteroloph is mainly weak and the protosinus is shallow or disappeared. Only protolophule I. is found in 9/15. Protolophule I and II are equally developed in 5/15. In one tooth protolophule II is stronger and protolophule I is remnant. Mesoloph is variable. It can be long, reaches the labial margin (2/15), or long, but doesn't reach the labial margin (7/15), middle developed (4/15), or short (2/15). Paracone posterior spur is frequent. In 9/15 it is continued in the cingulum between the paracone and the metacone. It reaches the apex of the mesoloph in 3/15, it is short in 2/15. In one case it is absent. Metalophule started from the hypocone (11/15), or started above the hypocone (4/15).

M3. Subrectangular outline. Labial anteroloph, protocone, protolophule, metacone, centrocone are developed. There is an incision from the protocone and the hypocone. Axioloph and neo-entoloph are absent.

m1. Anteroconid is always unicuspid and undivided. The anterolophulid is connected to the center of the anteroconid (21/25) or connected to the labial angle of the anteroconid (4/25). Anterolophulid bears a labial spur (19/25) in two cases it reaches the antero-labial margin. In 6/25 the spur is absent. The labial anterolophid between the anteroconid and the basis of the protoconid is regular. The lingual anterolophid is mainly developed (21/25), or substituted by a metastylid (1/25), or absent (3/25). In 8/25 cases the metaconid is anteriorly pushed and the anterolophulid is connected only to the metalophulid (Pl. III.-6.). Mesolophid is mainly short (24/25) or middle developed (1/25).

m2. Rectangular outline. Lingual anterolophid is absent (5/27), short (6/27), middle developed (13/27) or long (3/27). Mesolophid can be absent (8/27), short (13/27) or middle developed (6/27). In two cases a postero-labial branch of the posterolophid is developed.

m3. Subtriangular outline. Labial anterolophid is constant, it closes the protosinu-

sid. Lingual anterolophid is absent (1/3) or middle developed (2/3). Mesolophid is absent, entoconid is strongly reduced. *Democracetodon* and *Megacricetodon* m3s are possible to distinguish only after the dimensions (*Democracetodon* teeth are larger).

Discussion. *Megacricetodon* was not reported from Szentendre in the publications of Kordos (1982, 1986). The rich material of the new sampling is not surprising, because *Megacricetodon* is a regular element of the Badenian and Sarmatian (MN5 –MN7+8) faunas in the Pannonian Basin (Hír et al. 2017). Furthermore in the Vienna Basin the genus was reported from the early MN9 assemblages (e.g. Richardhof-Golfplatz, Vösendorf, Inzersdorf Daxner-Höck & Höck 2015, Borsky Svätý Jur (Joniak 2005).

Up to the present the *Megacricetodon minor* and the slightly smaller *Megacricetodon minutus* the most frequent representatives of the genus in the Carpathian region. The earlier one is characteristic in the Badenian faunas: Litke 1-2, Hasznos, Szentendre. The later one occurred first in the early Sarmatian faunas Kozárd and Varciorog, but those samples have not statistic amount. Rich material was collected from the Felsőtárkány Basin (e.g. Felsőtárkány 3/2). A well elaborated population was described from Borsky Svätý Jur, Slovakia by (Joniak, 2005). *Megacricetodon minor* and *Megacricetodon minutus* are distinguishable only in rich materials.

Beyond the “*minor-minutus* group” only *Megacricetodon similis* is known from the localities Subpiatră 2/1, 2/2, 2/3 (Hír & Venczel 2005). Up to the present the representatives of the “large sized” west European *Megacricetodon* species are unknown from the Carpathian Basin.

Subfamily: Paracricetodontinae Mein & Freudenthal, 1971

Tribe: Eucricetodontini Mein & Freudenthal, 1971

Genus: *Eumyarion* Thaler, 1966

Eumyarion sp.

Description. **M1.** Anterocone is wide, it consists of two units, which are not divided. Mesial surface is without any groove. A short lingual anteroloph and a small proto-sinus is developed. Anteromesoloph is diagonally positioned and connected to the labial unit of the anterocone. Sinus is anteriorly curved. Paracone posterior spur is found in specimen 18. 455. The mesoloph is medium developed and free ended. **M2.** Rectangular outline. Lingual anteroloph is absent, the labial one is well developed and transversally directed. Protoloph and metaloph are also transversal. Mesoloph is medium sized, paracone posterior spur is long.

Table 3. Material and measurements of teeth in *Eumiarion* sp.

No. inv.	Position:	L:	W:	Figures:
MMP. 18. 454.	M1	2.03	1.45	Pl. II.-4.
MMP. 18. 455.	M1	2.10	1.50	
MMP. 18. 461.	M2	1.48	1.50	
MMP. 18. 456.	M3	1.22	1.15	
MMP. 18. 457.	m1	2.0	1.25	Pl. II.-8
MMP. 18. 458.	m2	1.61	1.39	Pl. II.-18.
MMP. 18. 459.	m2	1.44	1.19	
MMP. 18. 460.	m3	1.64	1.26	

M3. Subtriangular outline. The anterior portion is similar to the same part of M2. Protocone and hypocone are connected by a short labial ridge (neo-entoloph ?). Axioleph is not developed. Centrocone and a medium developed mesoloph is found.

m1. Anteroconid is unicuspid. Labial anterolophid is strong and closes the protosinusid, lingual anterolophid is incipient. Anterolophulid is relative long. Metalophulid I and II are incipient. Mesolophid and ectomesolophid are equally middle developed. Hypocone posterior arm is short.

m2. Rectangular outline. Labial anterolophid is longer than the lingual one. Protoconid posterior arm is middle developed, the mesolophid is short. Hypoconid posterior arm is found in the specimen 18. 458.

m3. Subtriangular outline. Lingual anterolophid is short, the labial one is long. Protoconid posterior arm is long, mesolophid is not found. A short hypoconid posterior arm is developed.

Discussion. The dentition of the medium-sized *Eumyarion* species do not show a consistent change through time, the reconstruction of phylogenetic lineages on the basis of the available record is hypothetical. (De Bruijn 2009). The Szentendre material is limited and an "exact" species determination would not be founded.

Genus: *Anomalomys* Gaillard, 1900

Anomalomys gaudryi Gaillard, 1900

1989 *Anomalomys (Myospalax) kowalskii* n. sp., Kordos, p. 293 (Hun.), p. 301, 302 (Eng.), Fig. 2:5.

Material and measurements.

Description. General characters: hypsodont molars with flat occlusal surface and

No. inv.	Position:	L:	W:	Figures:
MMP. 2018. 462.	m1	1.50	0.81	Pl. II.-11.
MMP. 2018. 463.	m2	1.54	0.91	Pl. II.-12.

thick enamel.

m1. Elongated subrectangular outline. The posterior width is larger than the anterior width. The occlusal surface consists of three main enamel folds: anterior fold: involves the anteroconid and the metaconid; central fold: involves the protoconid, mesoconid, entoconid; posterior fold: involves the hypoconid and the posterolophid. The anterior- and central folds are completely divided by the confluent protosinusid–anterior mesosinusid. The central- and posterior folds are connected by a narrow posterolabial isthmus. These folds are divided by the posterosinusid. Two enamel islets are found in the anterior fold. Two enamel bays are found in the anterior side of the central fold. One enamel islet is found in the lingual part of the posterior fold.

m2. The anterior- and the central folds are divided by the confluent protosinusid and anterosinusid. The central- and the posterior folds are divided by the mesosinusid and the posterosinusid. The development and position of enamel islets and enamel bays are similar to m1.

Discussion. Kordos (1989) described an M2 from Szentendre as *Anomalomys kowalskii* n. sp., but the validity of this taxon was strongly criticised by Kowalski (1994). The newly collected two teeth are the smallest representatives of *A. gaudryi* in the Carpathian Basin. Remarkable plesiomorph character is the long m2 (it is longer than m1!).

In Southern Germany *A. gaudryi* appeared at the base of the OSM F, in company with *C. aff. aureus* Abdul-Aziz et al (2008), Prieto & Rummel 2016 (early MN6 zone). In Switzerland *A. gaudryi* appeared slightly earlier in the *Megacricetodon lappi* taxon range zone (in the localities Chatzloch, Uzwil-Nutzenbuech). Chatzloch is magnetostratigraphically dated of about 14.7 Ma.

Conclusions

The new sampling of the locality Szentendre, Cseresznyés-árok produced a rich microvertebrate fauna. Having new material the taxonomic revision of the *Cricetodon* finds is possible. *C. hungaricus* is deleted, *C. aureus* is verified.

The biostratigraphic and biochronologic importance of *C. aureus* is possible to understand in the Northern Alpine Foreland Basin. Abdul-Aziz et al (2008) found that the localities belonging to OSMF are found between the Brock horizon and the main bentonite layer, both in the Landshut (e.g. Sallmannsberg) and the Augsburg area (e.g., Laimering 3) (Heissig 1997). The characteristic element of these faunas is *C. aureus*. In the faunas collected under the Brock horizon *C. meini* and *Megacricetodon lappi* were found (Heissig 2006).

The radiometric age of the Ries impact has been intensively studied. Referring to the latest results of Rocholl et al (2017) the Ries impact occurred between 14.94 and 15.00 Ma. The age of the Laimering bentonite is classified as 14.925 ± 0,01 MY by Rocholl et al (2017). Taking into consideration the above data, it is clear that *C. aureus* is possible to correlate with a time period of about 14.90-15.00 Ma.

The presence of *Democricetodon hasznosensis* is confirmed, but some special morphologic characters were found, which are absent in the type material of Hasznos.

From faunistic point of view the occurrence of *Albanensia sansaniensis* and *Muscardinus sansaniensis* are remarkable, but these species have biochronological importance as well. These are referable to the early period of the MN6 zone.

The actual faunal list of the rodent material from Szentendre is:

Albanensia sansaniensis
Spermophilinus bredai
Palaeosciurus sp.
Myoglis meini
Microdyromys koenigswaldi
Miodyromys sp.
Glirulus lissiensis
Cricetodon aureus
Democricetodon hasznosensis
Megacricetodon minor
Eumyarion sp.
Anomalomys gaudryi

An unsolved question is the lithostratigraphical relation of the fossiliferous diatomaceous sediment to the volcanites of the surroundings. Referring to Wein (1939), Majzon (1953), Kordos (1982) the diatomite is bedded on the top of the andesite complex. However the diatomitic claymarl was put into the Fót Formation

and the tuff on the top of the diatomit was classified as the member of the Tar Dacite Tuff by Halmai (1982). His opinion is based on the study of the well-logs from the cores Fót 1, Mogyoród 1, Budapest 4.

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Plate I.

- | | | | | |
|-----|---------------|--------------------------------|------|----------|
| 1. | MMP. 18. 431. | <i>Albanensia sansaniensis</i> | M1-2 | reversed |
| 2. | MMP. 18. 435. | <i>Albanensia sansaniensis</i> | m1 | |
| 3. | MMP. 18. 437. | <i>Albanensia sansaniensis</i> | m2 | |
| 4. | MMP. 18. 5. | <i>Cricetodon aureus</i> | M1 | |
| 5. | MMP. 18. 14. | <i>Cricetodon aureus</i> | M1 | reversed |
| 6. | MMP. 18. 17. | <i>Cricetodon aureus</i> | M1 | reversed |
| 7. | MMP. 18. 31. | <i>Cricetodon aureus</i> | M2 | |
| 8. | MMP. 18. 32. | <i>Cricetodon aureus</i> | M2 | |
| 9. | MMP. 18. 39. | <i>Cricetodon aureus</i> | M2 | reversed |
| 10. | MMP. 18. 74. | <i>Cricetodon aureus</i> | M3 | reversed |
| 11. | MMP. 18. 75. | <i>Cricetodon aureus</i> | M3 | reversed |
| 12. | MMP. 18. 102. | <i>Cricetodon aureus</i> | M3 | reversed |
| 13. | MMP. 18. 106. | <i>Cricetodon aureus</i> | m1 | |
| 14. | MMP. 18. 112. | <i>Cricetodon aureus</i> | m1 | reversed |
| 15. | MMP. 18. 124. | <i>Cricetodon aureus</i> | m1 | reversed |
| 16. | MMP. 18. 131. | <i>Cricetodon aureus</i> | m2 | |
| 17. | MMP. 18. 142. | <i>Cricetodon aureus</i> | m2 | reversed |
| 18. | MMP. 18. 79. | <i>Cricetodon aureus</i> | m3 | |
| 19. | MMP. 18. 89. | <i>Cricetodon aureus</i> | m3 | |

Bare: 1 mm

Plate I.



Plate II.

1.	MMP. 18. 175.	<i>Democricetodon hasznosensis</i>	M1	reversed
2.	MMP. 18. 187.	<i>Democricetodon hasznosensis</i>	M1	
3.	MMP. 18. 167.	<i>Democricetodon hasznosensis</i>	M1	
4.	MMP. 18. 454.	<i>Eumyarion</i> sp.		M1
5.	MMP. 18. 197.	<i>Democricetodon hasznosensis</i>	M2	
6.	MMP. 18. 202.	<i>Democricetodon hasznosensis</i>	M2	
7.	MMP. 18. 205.	<i>Democricetodon hasznosensis</i>	M2	
8.	MMP. 18. 457.	<i>Eumyarion</i> sp.	m1	
9.	MMP. 18. 238.	<i>Democricetodon hasznosensis</i>	M3	
10.	MMP. 18. 242.	<i>Democricetodon hasznosensis</i>	M3	
11.	MMP. 18. 462.	<i>Anomalomys gaudryi</i>	m1	reversed
12.	MMP. 18. 463.	<i>Anomalomys gaudryi</i>	m2	reversed
13.	MMP. 18. 288.	<i>Democricetodon hasznosensis</i>	m1	
14.	MMP. 18. 301.	<i>Democricetodon hasznosensis</i>	m1	reversed
15.	MMP. 18. 302.	<i>Democricetodon hasznosensis</i>	m1	reversed
16.	MMP. 18. 382.	<i>Democricetodon hasznosensis</i>	m2	
17.	MMP. 18. 294.	<i>Democricetodon hasznosensis</i>	m2	reversed
18.	MMP. 18. 458.	<i>Eumyarion</i> sp.	m2	reversed
19.	MMP. 18. 256.	<i>Democricetodon hasznosensis</i>	m3	
20.	MMP. 18. 262.	<i>Democricetodon hasznosensis</i>	m3	reversed

Bare: 1 mm

Plate II.

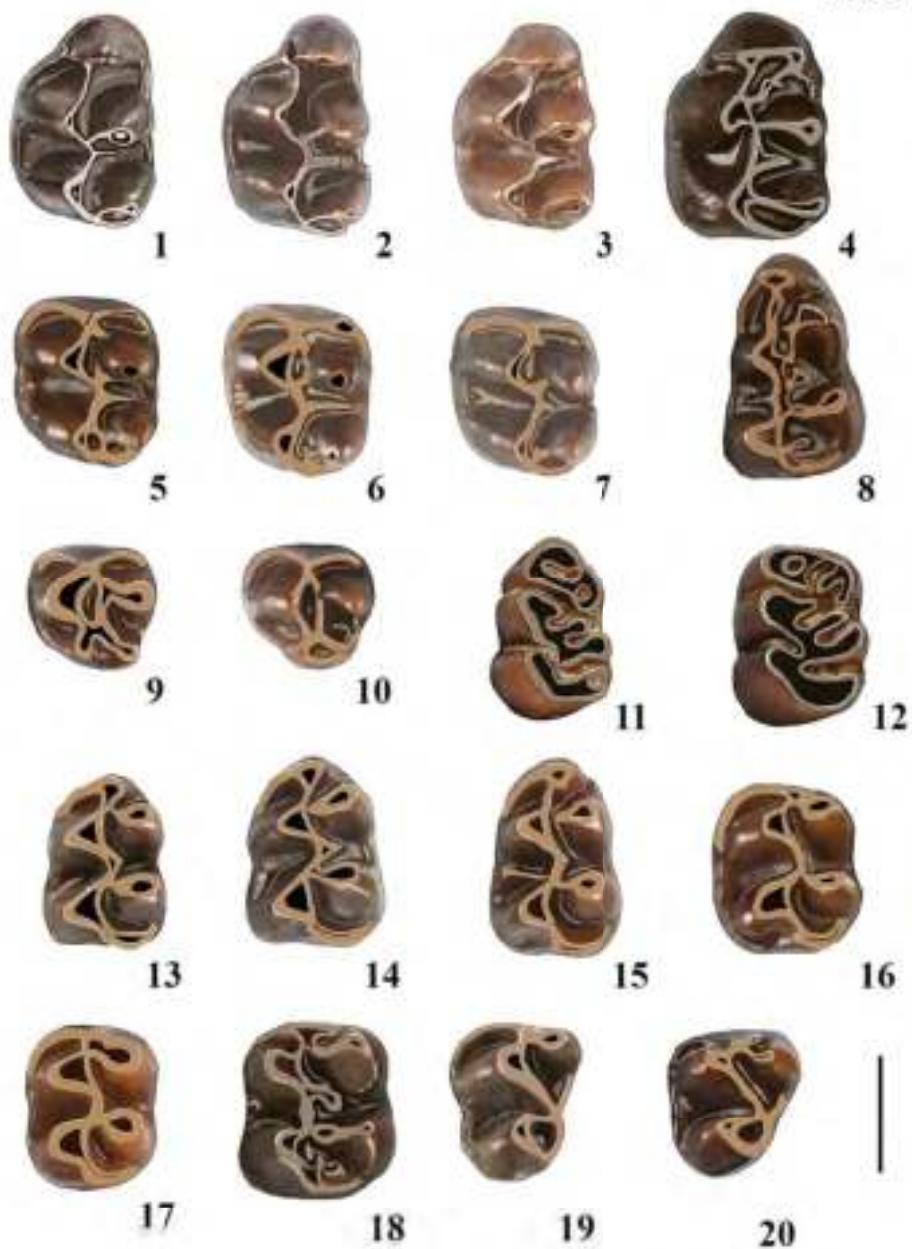


Plate III.

1.	MMP. 18. 339.	<i>Megacricetodon minor</i>	M1	
2.	MMP. 18. 340.	<i>Megacricetodon minor</i>	M1	
3.	MMP. 18. 415.	<i>Megacricetodon minor</i>	M2	
4.	MMP. 18. 416.	<i>Megacricetodon minor</i>	M2	
5.	MMP. 18. 252.	<i>Megacricetodon minor</i>	M3	
6.	MMP. 18. 314.	<i>Megacricetodon minor</i>	m1	
7.	MMP. 18. 321.	<i>Megacricetodon minor</i>	m1	
8.	MMP. 18. 362.	<i>Megacricetodon minor</i>	m2	
9.	MMP. 18. 357.	<i>Megacricetodon minor</i>	m2	reversed
10.	MMP. 18. 275.	<i>Megacricetodon minor</i>	m3	
11.	MMP. 18. 466.	<i>Myoglis meini</i>	P4	
12.	MMP. 18. 465.	<i>Myoglis meini</i>	M2	reversed
13.	MMP. 18. 474.	<i>Myoglis meini</i>	m1	
14.	MMP. 18. 476.	<i>Myoglis meini</i>	m3	reversed
15.	MMP. 18. 480.	<i>Microdyromys koenigswaldi</i>	M1	reversed
16.	MMP. 18. 478.	<i>Miodyromys</i> sp.	M2	
17.	MMP. 18. 484.	<i>Miodyromys</i> sp.	M2	reversed
18.	MMP. 18. 488.	<i>Miodyromys</i> sp.	m1	
19.	MMP. 18. 489.	<i>Microdyromys koenigswaldi</i>	m1	reversed
20.	MMP. 18. 497.	<i>Glirulus lissiensis</i>	m2	
21.	MMP. 18. 451.	<i>Muscardinus sansaniensis</i>	M1	reversed
22.	MMP. 18. 452.	<i>Muscardinus sansaniensis</i>	m1	

Bare: 1 mm

Plate III



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Bioerosion and encrustation on a middle Miocene *Gigantopecten nodosiformis* shell from Tășad, Bihor, Romania

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Abstract. The studied specimen of *Gigantopecten nodosiformis* manifests bioerosion and bioencrustation traces, caused by sponges, bivalves, worms and bryozoans. The high frequency of well developed bioerosional and encrustation structures on a single specimen of *Gigantopecten nodosiformis* suggests a slow burial of the shell with a significant amount of time being exposed on the sea bottom. The analyses of these traces revealed four ichnospecies. These include *Entobia cateniformis* borings, produced by clionaid sponges, *Gastrochaenolites lapidicus* produced by lithophagian bivalves and channel-like traces identified as *Maeandropolydora sulcans* and *Caulostrepsis* isp, produced by polychaete annelids. Bivalve and bryozoan overgrowth, as well as polychaete dwelling tubes can be observed among encrustation structures. The spatial distribution and relationship between the bioerosion structures allow the reconstruction of the succession of the bioerosion stages. First a sponge-dominated community colonized the shell, followed by the polychaete annelid-dominated community, which produced traces cross-cutting those produced by sponges. The last bioeroder was probably the bivalve-dominated community, which made their dominichia first in the sediment which already has been deposited on the surface of the shell, penetrating only partially the shell surface. The bioerosion trace fossil assemblage can be regarded as the *Entobia* ichnofacies, which indicates a near-shore, shallow marine environment with low sedimentation rate.

Introduction

Although bioerosion traces reveal so many data regarding the depositional environment, the sea-level changes in shallow marine deposits, as well as the determination of palaeoenvironmental aspects (Uchman et al. 2001, Dávid et al. 2006, El-Hedeny 2007, Santos et al. 2010, Dermican 2012, Brlek et al. 2016, Brlek et al. 2018), there are few publications in Romania dealing with bioerosion.

Brustur (1997a, 1997b) synthesized the contributions made on Romanian ichnological studies, including the identification of worms' tubes in the Badenian of Şimleu Basin or the borings produced by *Cliona* and *Polydora* on *Ostrea* shell in the Sălătruc Formation.

In the last decades more and more attention has been paid to the study of bioerosion structures worldwide, thus the number of papers dealing with Neogene bioerosion traces and epibiont fauna from Romania is increasing as well (Hladilova 2004, Munteanu & Munteanu 2001, Anistoroae & Miclăuş 2015).

Experimental studies of bioerosion allowed more precise determinations of the tracemakers and observations on the temporal patterns of macro and micro-bioerosions (Bromley & D'Alessandro, 1989, Bromley et al. 1990).

Temporal pattern of bioerosion can be assessed by analyzing the spatial distribution of bioerosion and encrustation structures. Thus, Santos et al. (2008) defined three colonization stages: stage I – structures produced when the host bivalve was still alive; stage II – structures produced immediately after the death of the bivalve, and stage III – structures produced post-mortem, when the bivalve was already disarticulated.

Long-term experimental studies revealed more information related to the temporal sequence of bioerosion, the relationship between traces and bioeroders, respectively their impact made in different rocky shorelines throughout different geographic regions (Färber et al. 2016).

Location

The specimen described in this paper came from the Badenian deposits of Cuţii Valley (Fig. 1), from Tăşad, Bihor County, Romania, which is located 22 km away from Oradea.

The Middle Miocene marine deposits are cropping out along the Morii Valley and Cuţii Valley with a rich invertebrate fauna, consisting of bivalves, corals, gastropods and echinids. The analysed *Gigantopecten* shell was embedded in a bio-lithoclastic limestone in Cuţii Valley, located in the close vicinity of corraligeno-



Figure 1. Location of the Middle Miocene site. The collecting site of *Gigantopecten* \square \square is marked with X

us deposits. The sediment also contains clasts of different rocks, which may have been incorporated in the sediment due to wave-action during storm events.

Palaeogeographically this area belongs to the Pannonian Basin, to the Eastern compartment of the Central Paratethys.

Material and methods

A total number of six specimens of *Gigantopecten nodosiformis* were collected: three articulated specimens from the Cuşilor Valley, one disarticulated specimen and two specimens preserving both valves were found in the Morii Valley. Four of the articulated specimens are hosted by the Association for Conservation and Promotion of the Local Natural and Cultural Heritage "Tasadia".

The present paper is based on a single specimen of *Gigantopecten nodosiformis* (MTCO 25700), hosted in the collection of the Department of Natural Sciences - Ţării Crişurilor Museum Oradea. The shell preserved both valves in connection, which are filled with coarse-grained sediment.

The shell was prepared mechanically, using a vibrating cutter connected to an air compressor, which permitted the elimination of the bio-lithoclastic matrix without damaging the shell surface. Microscopic analyses of the shell surface and of the bioerosion structures were made using a NIKON SMZ 800 stereoscopic microscope.

On the surface of the right valve there are 7 sections presenting intense bioerosion and encrustation, marked by squares (Fig. 2). The left valve is poor in bioerosion, but encrustation structures are present in two sections (Fig.3). The bioerosion traces and encrustations are described for each section separately.

Abbreviations used: MTCO – Ţării Crişurilor Museum, Oradea; LV – left valve; RV – right valve.

Gigantopecten nodosiformis

The taxonomy of this Neogene extinct genus is controversial, there are different opinions whether *Gigantopecten* (Bongrain 1988, Micuţ 2009) or *Macrochlamis* (Mandic 2004) should be used as the name of the genus.

Thomas Waller and Madeleine Bongrain (2006) asked the International Commission on Zoological Nomenclature to preserve the name *Gigantopecten* Rovereto, 1899. The above mentioned authors counted the usage of the different names designating this genus for the last 20 years and mentioned 12 articles which used the name *Macrochlamis*, eight that used *Macrochlamys* and 48 articles using

the name *Gigantopecten* (Waller & Bongrain 2006). The majority of the authors recently agreed that the usage of the name *Macrochlamys* Sacco, 1897 is incorrect, being a junior homonym of the gastropod name *Macrochlamys* Benson, 1832.

The authors of the present paper will use the name *Gigantopecten* in order to designate the studied specimen.

Genus *Gigantopecten* Rovereto, 1899
Gigantopecten nodosiformis Pusch, 1837

Material: completely articulated shell MTCO 25700 (Fig. 2-3)

Dimensions: Right valve – disc height = 194 mm, disc length=208 mm, anterior auricle length = 52 mm, anterior auricle height = 44 mm.

Description. The large, thick, articulated shell is lacking the posterior auricle. The shell is biconvex, possessing radial ribs with wide interspaces. The dorso-ventral diameter of the shell is smaller than the antero-posterior one.

The outer surface of the right valve presents eight radial ribs, which widen towards the ventral margin. The central ribs are wider than the rest of the ribs and are also slightly wider than the interspaces. The ribs are flattened towards the ventral margin, having shallow grooves on their lower part. The left valve has a lesser number of radial ribs (seven), with more rectangular borders, the three central ribs being wider than the lateral ones. The ribs of the left valve are ornamented with nodular structures which are more prominent in the dorsal region of the shell.

The stratigraphic range of the genus *Gigantopecten* is documented from Miocene to Pliocene. *Gigantopecten nodosiformis* is common in the Middle and Late Miocene, when it is replaced by *Gigantopecten latissima*.

Trace fossil description

The studied specimen of *Gigantopecten nodosiformis* (MTCO 25700) preserved exceptionally structures of bioerosion and encrustation. The bioerosion traces are frequent on the right valve and consist of borings and galleries made by sponges, bivalves and polychaete worms. Encrustation is indicated by the presence of bivalve and bryozoan overgrowth on both valves, as well as dwelling tubes of polychaete worms, which occurs only on the right valve.

Bioerosion - Borings of clionaid sponges

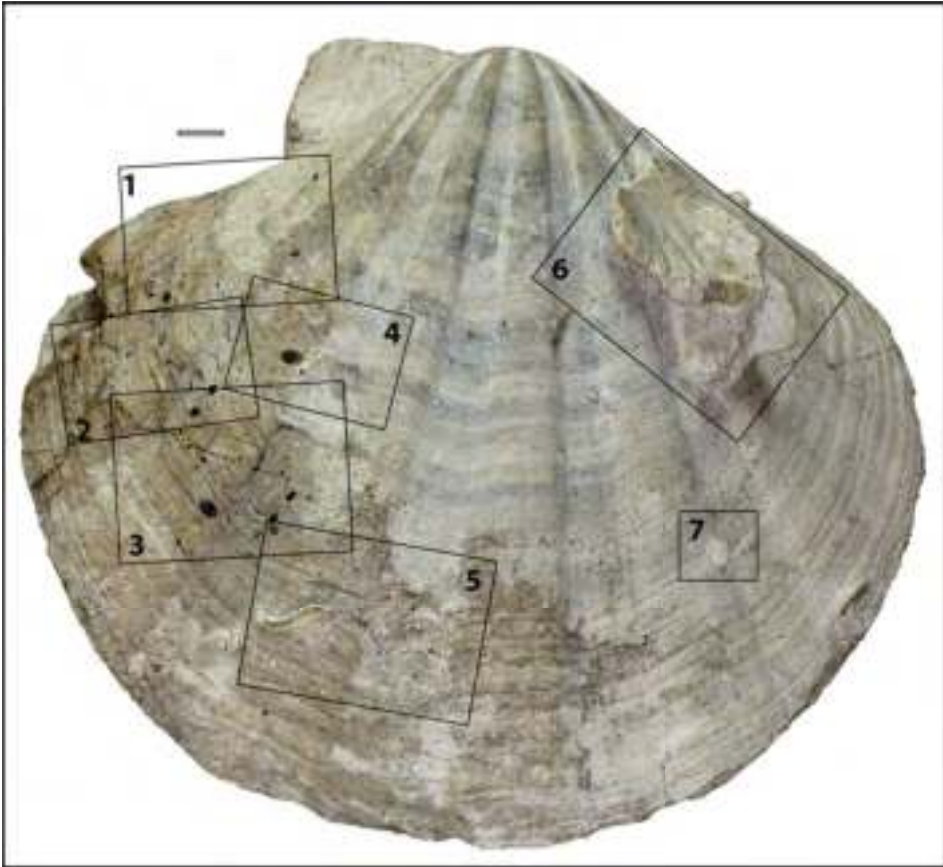


Figure 2. Right Valve of *Gigantopecten nodosiformis* (MTCO 25700), with bioerosion and encrustation structures. 7 sections manifest intense bioerosion and encrustation, marked with squares. Line indicates 1 cm.

Ichnogenus *Entobia* Bronn, 1837

The RV of the shell is covered with chamber openings bored by clionid sponges. The borings occur on the anterior part of the shell, especially in the dorsal half. The borings are disposed more or less parallel to the ribs, occupying the interspace as well as the ribs.

In order to conserve the shell, we did not perform analyses using “cast-embedding technique” which would permit 3D visualization of the borings and the structure of the chambers’ network.

The borings are small, rounded and relatively close to each other in order to connect the chambers (Figs. 4-7). There are several interconnected chambers with



Figure 3. Left Valve of *Gigantopecten nodosiformis* (MTCO 25700), with encrustation structures. Two sections with bivalve and bryozoans encrustation are marked with squares. Line indicates 1 cm.

aperture diameter ranging between 0.2 and 1 mm, with a maximum depth of 3 mm.

The morphology of the borings corresponds to the B - C growth phase (Figs. 4-7), described by Bromley and D'Alessandro, 1989. In the lower part of Section 1 of the RV (Fig. 3) there is a portion where the borings were subject of subsequent erosion, partly exposing the internal chamber network. The chambers are fused together, lacking inter-cameral canals. This part corresponds to the D growth phase. Phase A is not distinguishable.

The openings are disposed sublinear chains (Figs. 4-5, Fig. 7) and show a changing of direction of growth at an almost right angle or are disposed in a T-shaped arrangement (Figs. 6-7). The morphology of the exposed chambers and the appearance of the rectilinear network, forming right angles to each other indicate the *Entobia cateniformis* ichnospecies.

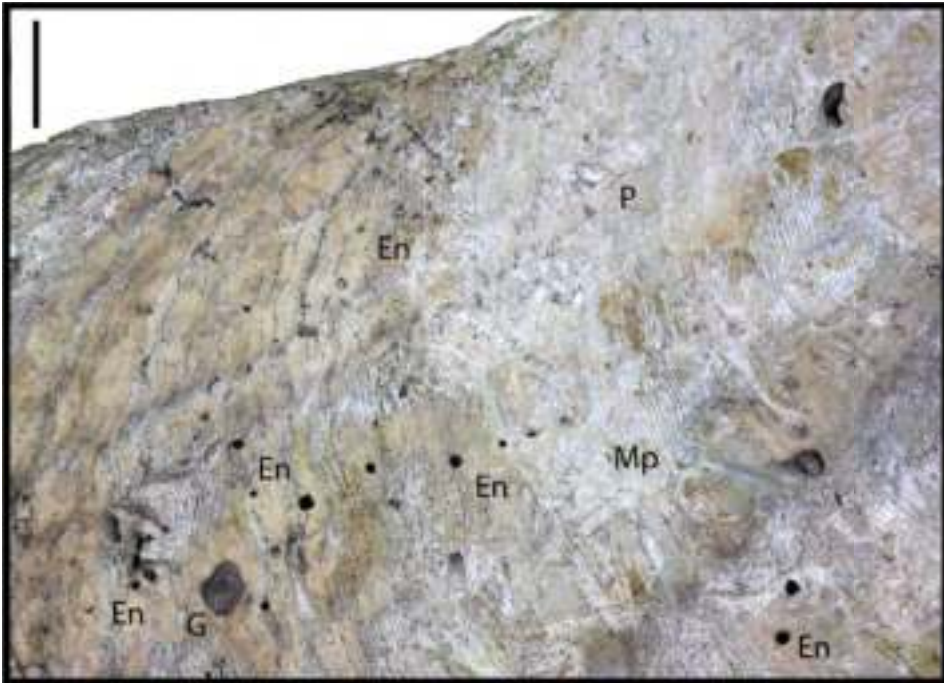


Figure 4. Close-up of Section 1 of the RV. Bioerosion traces of *Entobia cateniformis* (En), *Gastrochaenolithes* (G) and *Maeandropolydora* isp. (Mp), and Polychaete encrustation (P). Line indicates 5 mm.

Entobian borings are produced by endolithic sponges. According to Bromley and D'Alessandro (1989), *Entobia cateniformis* is produced by several species of *Cliona*, such as *Cliona vastifica*, which inhabit the lowest part of the shore (Radwanski et al. 2011).

Experimental studies have shown that borings of sponges are invisible in the first year of exposure (Bromley et al. 1990, Färber et al. 2016). Färber et al. (2016) observed the first distinct sponge borings on the experimentally exposed blocks after two years. Färber et al. (2016), using micro-computed tomographic visualisation of bioerosion traces in experimental blocks deployed for two years, identified cylindrical chambers of sponge boring that were arranged in long, sub-linear chains that coalesced in cross-, T-, or L-shape, which is characteristic for *Entobia cateniformis* Bromley and D'Alessandro, 1984 in the late ontogenetic growth phase C.

The preferential arrangements of the *Entobian* borings, corroborated with previous experimental studies, show that the clionaid sponges were the first bio-eroders, which affected the *Gigantopecten* shell.

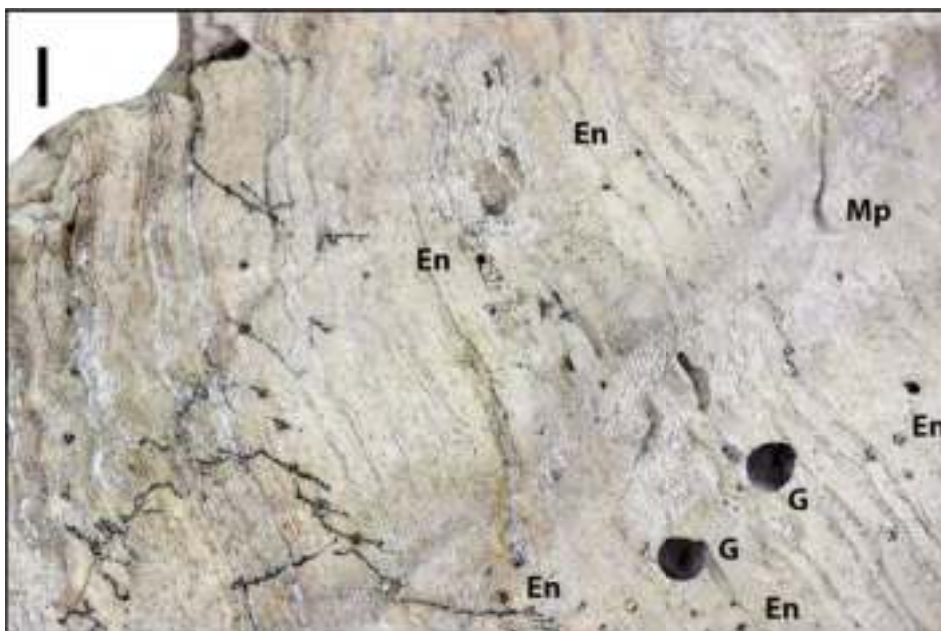


Figure 5. Close-up of Section 2 of the RV. Bioerosion traces of *Entobia cateniformis* (En), *Gastrochaenolithes* (G) and *Maeandropolydora* isp. (Mp). Line indicates 3 m

Entobia cateniformis was reported in several European Miocene sediments, e. g. in Hungary, Ukraine and Turkey (David et al. 2006, Radwanski et al. 2011, Dermican 2012).

The presence of *Entobia* indicates shallow marine environment (Bromley & D'Alessandro 1989, Santo & Mayoral 2008, Santos et al. 2010, El-Hedeny & El-Sabagh 2018), the producers of *Entobia cateniformis* preferring habitats with little wave action and low energy environments (El-Hedeny 2007).

Borings of mytilid bivalves

Ichnogenus *Gastrochaenolithes* Leymerie, 1842

The analysed *Gigantopecten nodosiformis* specimen includes *Gastrochaenolithes* trace fossils on the right valve of the shell. The distribution of the bivalve made borings is the same as that of *Entobia*, respectively the anterior half of the right valve, appearing in the region below the anterior auricle down to the dorsal half (Fig. 2). The borings are perpendicular (Fig. 5) or oblique (Figs. 4, 6, 7) in relation to the surface of the shell. The neck region is eroded completely, thus the dimensions of the entire chamber cannot be determined. The bioeroder bivalve must have bored

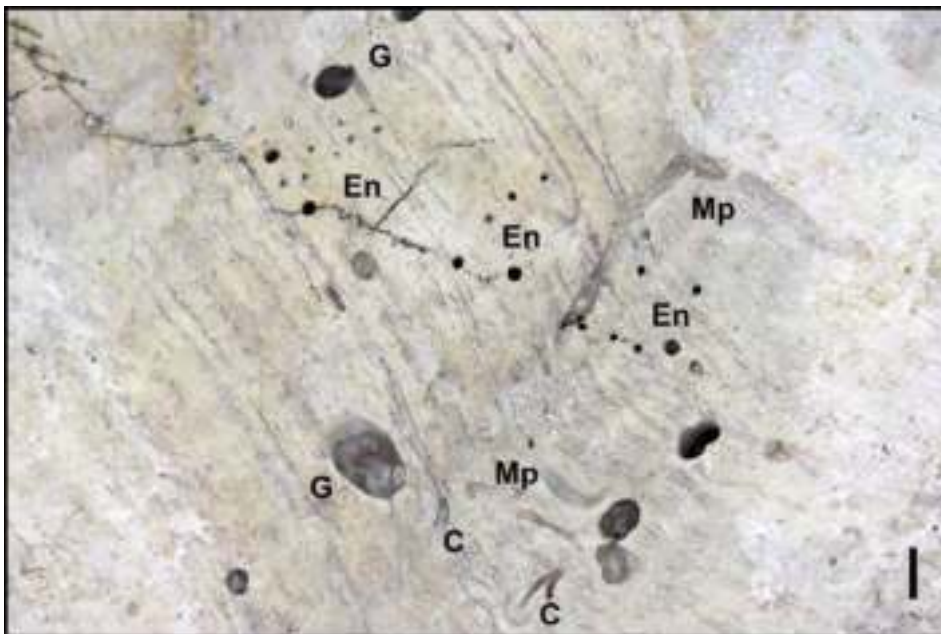


Figure 6. Close-up of Section 3 of the RV. Bioerosion traces of *Entobia cateniformis* (En), *Gastrochaenolithes lapidicus* (G) and *Maeandropolydora* isp. (Mp) and *Caulostrepsis* (C). Line indicates 3 mm.

its perforation by penetrating the sediment first, already deposited on the surface of the shell. Subsequent erosion cleared the sediment, exposing only the remains of the bivalve borings, which have reached and penetrated the shell.

The main chambers of the borings are ovate, slightly elongate. The outline of the borings is semicircular (Fig. 5) to oval (Figs. 4, 6, 7) in cross section. The size of the borings varies from 2 mm to 7 mm in length and 2-3 mm in width, with a maximum depth of 3.5 mm. The internal wall of the chamber is smooth, without any sign of ornamentation. Kelly and Bromley (1984) described two *Gastrochaenolithes* species based of the shape of the distal parts of the borings, *G. lapidicus* displaying a bluntly paraboloid, rounded base, which distinguished it from *G. torpedo*, where the base is more acutely paraboloid or pointed.

Based on the subcircular to oval cross-section and rounded shape of the bottom part, these borings can be assigned to *Gastrochaenolithes lapidicus* Kelly and Bromley 1984 ichnospecies. According to Kelly and Bromley (1984), borings of this type are produced by several bivalve species, including *Lithophaga* and *Hiatella*.

The analyzed borings of *Gastrochaenolithes* did not preserve its producer, probably due to the fact that it had thin valves which were rapidly destroyed after

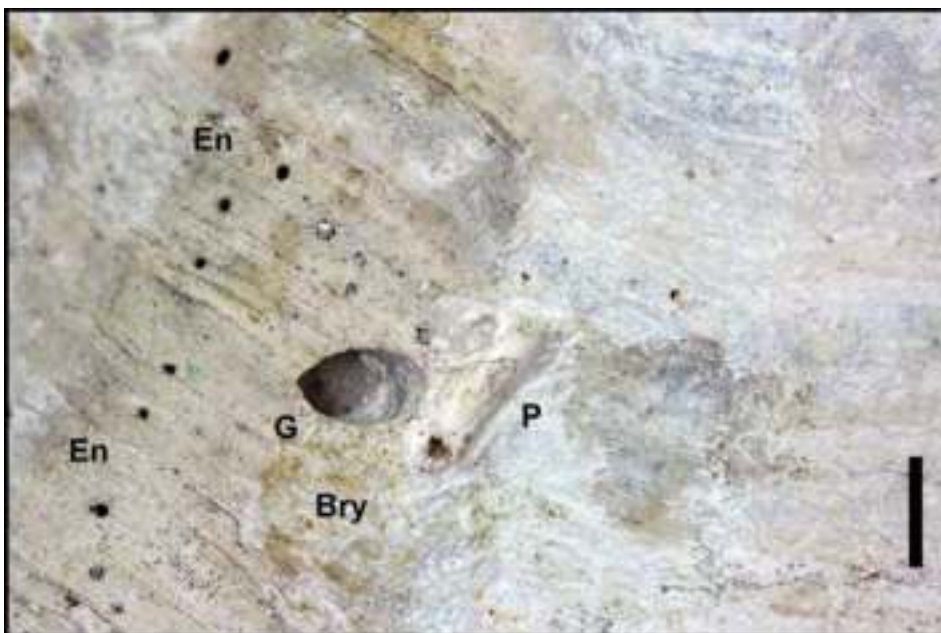


Figure 7. Close-up of Section 4 of the RV. Bioerosion traces of *Entobia cateniformis* (En) and *Gastrochaenolithes lapidicus* (G). Encrustation of polychaete annelid (P) and bryozoans colony (Bry). Line indicates 3 mm.

its death.

Gastrochaenolithes occurs in near shore, shallow marine environments with a low sedimentation rate (Kelly & Bromley 1984, Farinati & Zavala 2002), being a common ichnotaxon in Miocene deposits (Uchman et al. 2001, David et al. 2006, El-Hedeny 2007, Santos et al. 2010, Dermican 2012).

Bioerosion - Borings of polychaete worms

Ichnogenus *Maeandropolydora* Voigt, 1965

The RV of the *Gigantopecten nodosiformis* shows several traces of polychaete worms. The traces are straight (Fig. 6) or sinuous galleries (Figs. 4-5, Fig. 8), for which the authors measured the length and the maximum width, as well as observed their relation with other boring traces on the surface of the shell.

In the Section 1 of the RV there is a sinuous gallery, which describes a loop (Fig. 4), with a constant width measuring 0.5 mm. The length of the trace is 8.5 mm. Based on constant diameter and shape of the trace, this boring is identified as *Maeandropolydora* isp.

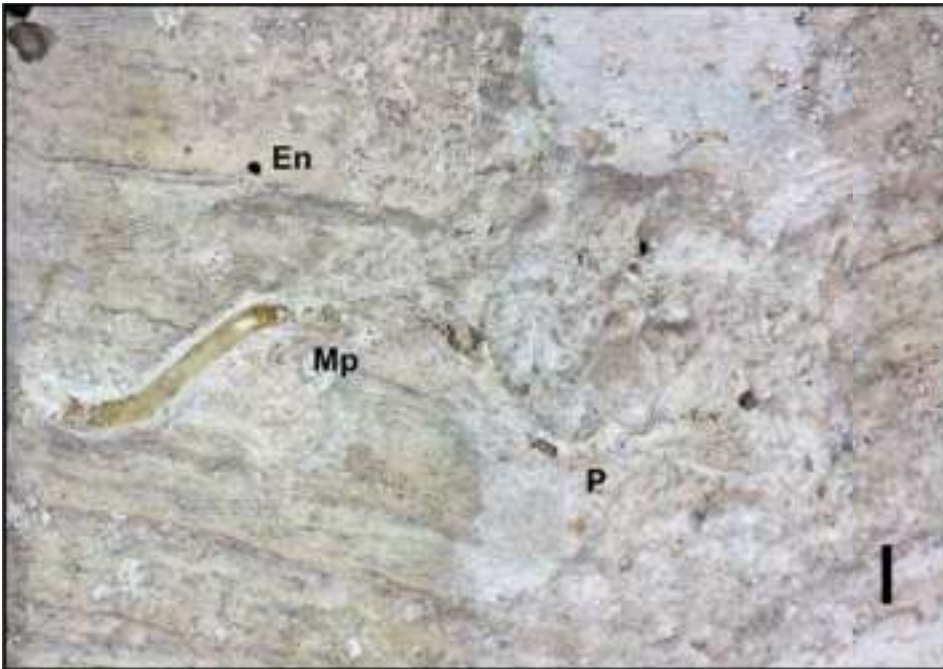


Figure 8. Close-up of Section 5 of the RV. Bioerosion trace of *Maeandropolydora sulcans* (Mp) and polychaete encrustation (P).

In Section 2 of the RV there is a boring referable to *Maeandropolydora* isp. (Fig. 5), it is 7.8 mm in length and 0.3 mm in width.

The straight, tube-like trace in the Section 3 of the RV is positioned parallel with the ribs, along the border between the rib / inter-rib space (Fig. 6). The trace has a constant width of 1 mm and shows two openings in the proximal end, penetrating the shell. The length of the tube-like gallery is 13 mm. There is a cross-cutting relationship between this *Maeandropolydora* trace and former *Entobian* borings. This section of the shell manifests a second trace identified as *Maeandropolydora* boring, measuring 6 mm in length and 0.8 mm in width.

More ventrally on the shell (Section 5 of the RV – Fig. 8), a sinuous, cylindrical boring is found, partly preserving the dwelling tube of its producer, a polychaete annelid. Its diameter is 2 mm and is constant through its entire length, which measures 26 mm. This trace is preserved in semi-relief on the shell surface as a result of the erosion of the polychaete tube, exposing its remained internal structure. On the base of its morphology, this trace is attributed to *Maeandropolydora sulcans* Voigt, 1965.

Maeandropolydora is regarded as a domicion of suspension-feeding polychaete worms and is a frequent ichnotaxon in Miocene deposits (Dávid 2006,



Figure 9. Close-up of Section 6 of the RV, with bivalve encrustation. Line indicates 5 mm. Dávid et al. 2006, El-Hedeny 2007, Dermircan 2012, El-Hedeny & El-Sabagh 2018). According to Herman et al. 2012, *Maeandropolydora* has palaeoecological significance, its producer attacking the shells of dead mollusks, never those of living species.

Ichnogenus *Caulostrepsis* Voigt, 1965

Smaller polychaete galleries can be observed on Section 3 of the right valve (Fig. 6). The galleries are cylindrical, showing a clear U-shape in the first trace, the second preserving only the united branches of the U-shaped boring, lacking its base due to subsequent erosion. The limbs of the U-shaped borings are connected by a vane, a characteristic morphology for *Caulostrepsis* isp.

This trace fossil was mainly produced by polychaete annelids of the genus *Polydora* (Radwanski 1969) and is recorded in Miocene sediments (David 2006, David et al. 2006, Dermican 2012, El-Hedeny & El-Sabagh 2018).

Encrustation structures



Figure 10. Close-up of Section 7 of the RV, with bryozoan encrustation. Line indicates 3 mm.

Encrustation structures are present on both valves of the studied *Gigantopecten nodosiformis* shell. On the right valve polychaete annelids, bivalves and bryozoans encrusted the shell (Fig. 2 Sections 4, 5, 6, 7). The left valve shows bivalve and bryozoans encrustation (Fig. 3, Sections 1 and 2).

Polychaete annelid encrustation occurs only on the RV. There is a short dwelling tube of a polychaete worm in Section 4, near the *Gastrochaenolithes* boring (Fig. 7). It has a constant diameter of 1.8 mm and a length measuring 8 mm.

Near the *Maeandropolydora* isp. of Section 5 of the RV there is a sinuous tube of spionid polychaete, which is slightly in touch with the trace identified as *Maeandropolydora sulcans* (Fig. 8). This spionid tube has a circular cross section with 2 mm diameter and a total length 16 mm.

Bivalve encrustation occurs on both valves. The right valve preserved an ostreid encrusting the *Gigantopecten nodosiformis* shell in its postero-dorsal region, just under the auricle, which is missing (Fig. 2 – Section 6; Fig. 9). Bivalve encrustation is preserved on the left valve as well, in the antero-dorsal region of the *Gigantopecten nodosiformis* shell (Fig. 3 – Section 1; Fig. 11).

Bryozoans encrusted the *Gigantopecten* shell on both sides, colonies can



Figure 11. Close-up of Section 1 of the LV, with bivalve encrustation. Line indicates 5 mm



Figure 12. Close-up of Section 2 of the LV, with bryozoan encrustation. Line indicates 3 mm.

be observed in Section 4 (Fig. 7) and Section 7 of the right valve (Fig. 7). The left valve preserved a bryozoan encrustation, represented by a fan-shaped colony (Fig. 3, Section 2; Fig. 12).

Conclusions

The high frequency of well developed bioerosion and encrustation structures on a single specimen of *Gigantopecten nodosiformis* suggests a slow burial of the shell with a significant amount of time being exposed on the sea bottom.

The bioerosion consists of the following ichnotaxa: *Entobia cateniformis*, *Gastrochaenolithes lapidicus*, *Meandropolydora sulcans*, *Maeandropolydora* isp. and *Caulostrepsis* isp. The bioerosion trace fossil assemblage can be regarded as the *Entobia* ichnofacies, which is frequent worldwide on the Miocene rocky shorelines. The producers of the bioerosion are suspension feeders, indicating clear waters and high plankton productivity, which is their main food source.

The spatial distribution and relationship between the bioerosion structures allow the reconstruction of the succession of these ichnocoenoses. First a sponge-dominated community colonized the shell, followed the polychaete annelid-dominated community, which produced traces which cross-cut those produced by sponges. The last bioeroder was probably the bivalve-dominated community, which made their dominichia in the thin sediment which has already been deposited on the surface of the shell, producing shallow borings while penetrating the shell. Thus the borings represent truncated chambers of *Gastrochaenolithes lapidicus* after the sediment was eroded.

The shell surface is encrusted by worms, bivalves and bryozoans, but it is impossible to establish if the shell was encrusted during the bivalve's life or after its death.

Acknowledgements

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The type material of *Parahynobius betfianus*

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Abstract. *Parahynobius betfianus* Venczel, 1999 is the only hynobiid salamander known up to present from the Quaternary of Central and Western Europe. The type and referred material is briefly redescribed and reevaluated taken into consideration the new results in the molecular phylogeny of Hynobiidae. The lack of premaxillary fontanelle, due to extensive ossification of the alary process of premaxilla, may represent a synapomorphy shared with *Salamandrella* and *Hynobius*. Beside *Parahynobius*, the bicapitate transverse processes in the trunk vertebrae are also present in *Hynobius leechi*, *Onychodactylus* and *Salamandrella keyserlingii* and this condition may be considered as an intracolumnar variation. However, the presence of osseous knobs on the distal part of the transverse processes in *Parahynobius* are never present in *Salamandrella* and *Hynobius*. The fossil record of hynobiids from the Carpathian region and the palaeoenvironmental conditions from the type locality are also discussed.

Keywords. Central Europe, Extinction, Hynobiidae, Morphology, Quaternary.

Introduction

The Hynobiidae are a small group of primitive salamanders consisting of about 69 extant species assigned to nine genera (AmphibiaWeb 2018) with a mostly Asiatic distribution and in the northeastern part of European Russia (Zhang et al. 2006, Frost 2016).

The hynobiids have been regarded by many authors as the most primitive living tetrapods in retaining a suit of ancestral features: external fertilization, presence of a lacrimal bone in the skull and a separate angular in the mandible, a large number of microchromosomes (Estes 1981), and the spinal nerves, excepting the atlas, exit intervertebrally (Edwards 1976). They are grouped with the Cryptobranchidae in the suborder Cryptobranchoidea, from which differ in having a more complete metamorphosis (Estes 1981). The monophyly of Hynobiidae is supported by molecular data (Zhang et al. 2006, Pyron & Wiens 2011, Weisrock et al. 2013), or by combined molecular and morphological data (Larson & Dimmich 1993, Wiens et al. 2005). The earliest fossils related to Cryptobranchoidea are known from the Middle Jurassic - Lower Cretaceous of China consisting of well-preserved skeletons, like that of *Chunerpeton tianyiensis* from the Middle Jurassic Jiulongshan Formation (about 161 Ma) of Inner Mongolia (Gao & Shubin 2003), *Liaoxitriton zhongjiani* from the Lower Cretaceous Yixian Formation of western Liaoning (Dong & Wang 1998) and *Nuominerpeton aquilonaris* from the Lower Cretaceous Guanghua Formation of Inner Mongolia (Jia & Gao 2016). The hypothetical place of origin of this group, as indicated by the above fossils, may be in the present-day northern China (Zhang et al. 2006). In contrast to the extant fully aquatic Cryptobranchidae (giant salamanders), *Aviturus exsecratus*, known from the late Paleocene of Mongolia (Gubin 1991), exhibits adaptation to a terrestrial life-style (Vasilyan & Böhme 2012).

Contrary to giant salamanders, the fossil remains of Hynobiidae are extremely rare being unknown from the Palaeogene. The geologically oldest fossil record from Asia is an isolated vertebra, identified as *Salamandrella* sp., recorded from the early Miocene Khalagay Formation (Syromyatnikova 2014); *Salamandrella* sp. has been also reported from Malyi Kalkaman 1 (middle Miocene, western Siberia, Russia) by Vasilyan et al. (2017); *Salamandrella* sp. was reported also from the Upper Miocene of China (Vasilyan et al. 2012) and from several localities of Middle Pleistocene of European Russia (Ratnikov 2002). *Ranodon* cf. *sibiricus* (eight incomplete vertebrae, two partial humeri and a femur), is known from the late Pliocene (MN16) of Kiikbai, southern Kazakhstan Averianov & Tjutkova 1995).

The first occurrence date (FOD) of hynobiid salamanders from the European continent may be considered the record from the latest Sarmatian/ earliest Pannonian (MN 7/8 - MN 9) of Felsőtárkány 3/10, from northern Hungary (Venczel & Hír 2013; Hír et al. 2017), consisting of eight precaudal and two caudal vertebrae that have been assigned to *Parahynobius* sp. (Venczel & Hír 2013). The remaining fossil record is much younger, as follows: late Miocene (MN 12) of Tardosbánya, Hungary (six incomplete trunk vertebrae of cf. *Parahynobius* sp.); late Miocene

(MN 13) of Polgárdi 4 “Lower”, Hungary (four trunk vertebrae and one caudal vertebra of *Parahynobius kordosi* Venczel, 1999), early Pliocene (MN 14) of Osztramos 1C, Hungary (two trunk vertebrae and one sacral vertebra of cf. *Parahynobius* sp.) and early Pleistocene of Betfia 9/C, Romania, described as *Parahynobius betfianus* Venczel, 1999 (Venczel 1999, 2000a)(see below). The record from Betfia 9/C represents the only record of Hynobiidae from the Quaternary of Central Europe (from western Europe this group has never been recorded) and therefore the last occurrence date (LOD) from this area.

The purpose of the present paper to amend the descriptions of the type material of *Parahynobius betfianus* given by Venczel (1999, 2000a) and comment on the morphological variations observed in the vertebrae and appendicular skeletal parts.

The fossil locality and taphonomy

The Betfia fossil locality is situated about nine kilometres southwest to Oradea. The fossil site Betfia 9/C is situated approximately 20 m north to Betfia pothole, at 314 m altitude, presumably close or more probably parts of the classical locality Betfia 2 (Fig. 1). It consists of sediments of a partly eroded endokarst system, grooved in early Cretaceous limestone of Barremian-Aptian age.

The micromammals coming from this locality were first published by Terzea (1988). The brecciated sediments of type ‘terra rosa’ have yielded among others: *Talpa* cf. *fossilis*, *Crocidura kornfeldi*, *Sorex* gr. *minutus*, *Petenya hungarica*, *Beremendia fissidens*, *Cricetus cricetus*, *Mimomys pusillus*, *Mimomys tornensis*, *Pliomys episcopalis*, *Allophaiomys pliocaenicus*, *Lagurus praepannonicus*, *Hypolagus brachygnathus*, *Mustella praeivalis*, *M. palerminea*, *Canis lupus mosbachensis*. In 1994 Venczel re-excavated the locality and found a rich microvertebrate fauna (named as Betfia 9/B to differentiate from that excavated by E. Terzea and T. Jurcsák) with an abundant series of *Allophaiomys* molars. However, the list of micromammals from Betfia 9/B (Hír & Venczel 1997), with few exceptions, is closely like that of Terzea (1988). In 1995 M. Venczel has found a ‘terra rossa’ layer (named as Betfia 9/C) under the brecciform sediment of 9/B. This lower layer produced a special fauna dominated by *Apodemus*, *Pliomys* and *Muscardinus* indicating a forested palaeoenvironment.

Rzebik-Kowalska (2000a, 2000b) gave the following list of insectivores (based on the material coming from all these localities: Betfia 9 A+B+C): *Sorex* cf. *subaraneus*, *S. minutus*, *S. runtonensis*, *Sorex* (*D.*) *margaritodon*, *Asoriculus gibberodon*, *Petenya hungarica*, *Beremendia fissidens*, *Crocidura kornfeldi*,



Figure 1. Location of the type locality of *Betfia 9/C* (marked with arrow) near the *Betfia* cave, Bihor County, Romania.

Crocidura cf. obtusa, *Sorex* sp., *Erinaceus* sp. 2, *Talpa minor*, *T. fossilis*, *T. cf. episcopalis*, *T. cf. semseyi* and *Desmana thermalis*.

Kessler (1975) listed the birds identified from this locality (noted as coming from “*Betfia 3*” and respectively from “breccia with microfauna”): *Anas clypeata*, *Falco subbuteo*, *Perdix perdix*, ?*Otis tarda*, ?*O. lambrechtii*, *Asio* cf. *otus*, *Corvus* cf. *monedula*, *Garrulus glandarius*, *Turdus merula*, *Anthus* aff. *trivialis*.

The fossil herpetofauna of this locality complex consisted of *Parahynobius betfianus*, *Triturus* cf. *crystallus*, *Lissotriton* cf. *vulgaris*, *Bombina* cf. *bombina*, *Palaeobatrachus* (= *Pliobatrachus*) *langhae*, *Pelobates fuscus*, *Bufo bufo*, *Bufo viridis*, *Hyla* cf. *arborea*, *Rana* cf. *dalmatina*, *R. temporaria*, *Scolecophidia* indet., *Hierophis viridiflavus*, *Coronella austriaca*, *Zamenis paralongissimus*, *Elaphe quatuorlineata*, *Telescopus* cf. *fallax*, *Natrix natrix*, *N. tessellata*, *Vipera ammodytes* and *V. berus* (Venczel 2000b, 2000c). The fauna may be correlated with the *Miomys pusillus* - *M. savini* biozone with an approximate age of 1.5-1.2 Ma.

Material and Methods

The hynobiid specimens described here originate from about 500 kg of sediment collected between 2004–2008 from the locality *Betfia 9/C*. The samples were dried

and screen-washed using a sieve set with the mesh size ranging between 1.2–0.8 mm. The resulting isolated skeletal remains were sorted under a binocular microscope and identified by applying standard taxonomic criteria. The digital photographs were taken at the Țării Crișurilor Museum, Oradea, using a Canon EOS digital camera equipped with a 60-mm f/2.8 macro lens. The standard anatomical orientation system is used throughout this paper; osteological terms come from Estes (1981) and Venczel (1999).

Descriptions and comments

Premaxilla (holotype). The specimen MTC. No. 19913, represents a right premaxilla that may have belonged to an adult individual. The dorsal process (alary process) is moderately high, flattened and projecting faintly dorsolaterally; the base of the process is broadened and produced into a sinuous lateral crest connected to the pars dentalis. The labial surface is faintly ornamented by rarely distributed small pits. The dorsal process displays a constriction above the lateral crest owing to a lateral sinuosity and by an incompletely closed medial foramen; the lingual surface is thickened by a bony ridge extending dorsoventrally that might have been connected to a spur like process extending to the nasal, as observed in recent hynobiids (Venczel 1999: fig. 1b, c). The pars palatina is moderately wide with its posterior margin thickened; the lateral portion is damaged. The pars dentalis is well developed; medially the ventral part is damaged, whereas laterally the distal portion is missing; the remaining part preserves the basal parts of about nine pedicellate teeth; in the intact premaxilla the inferred number of teeth could have been about 13-15.

Comments. The holotype specimen shares with some hynobiids (*Hynobius*, *Pachyhynobius* and *Salamandrella*) a moderately high premaxillary dorsal process with ossification medially and therefore the premaxillary fontanelle is closed. The studies of Zhao & Hu (1983, 1984) have shown that the presence of a premaxillary fontanelle may represent a plesiomorphic feature, reason of which they placed the hynobiids into two 'natural groups': the *Hynobius*-group (*Hynobius*, *Pachyhynobius* and *Salamandrella*) lacking a premaxillary fontanelle and the *Ranodon*-group (*Batrachuperus*, *Liua*, *Onychodactylus* and *Ranodon*) possessing a fontanelle. However, the reconstruction of the ancestral states proposed by Zhang et al. (2006), based on molecular phylogeny and Bayesian inference, suggests that the ancestral state for hynobiids is the presence of a premaxillary fontanelle. This proposal is also reinforced by the fossil record of presumed early hynobiid-like

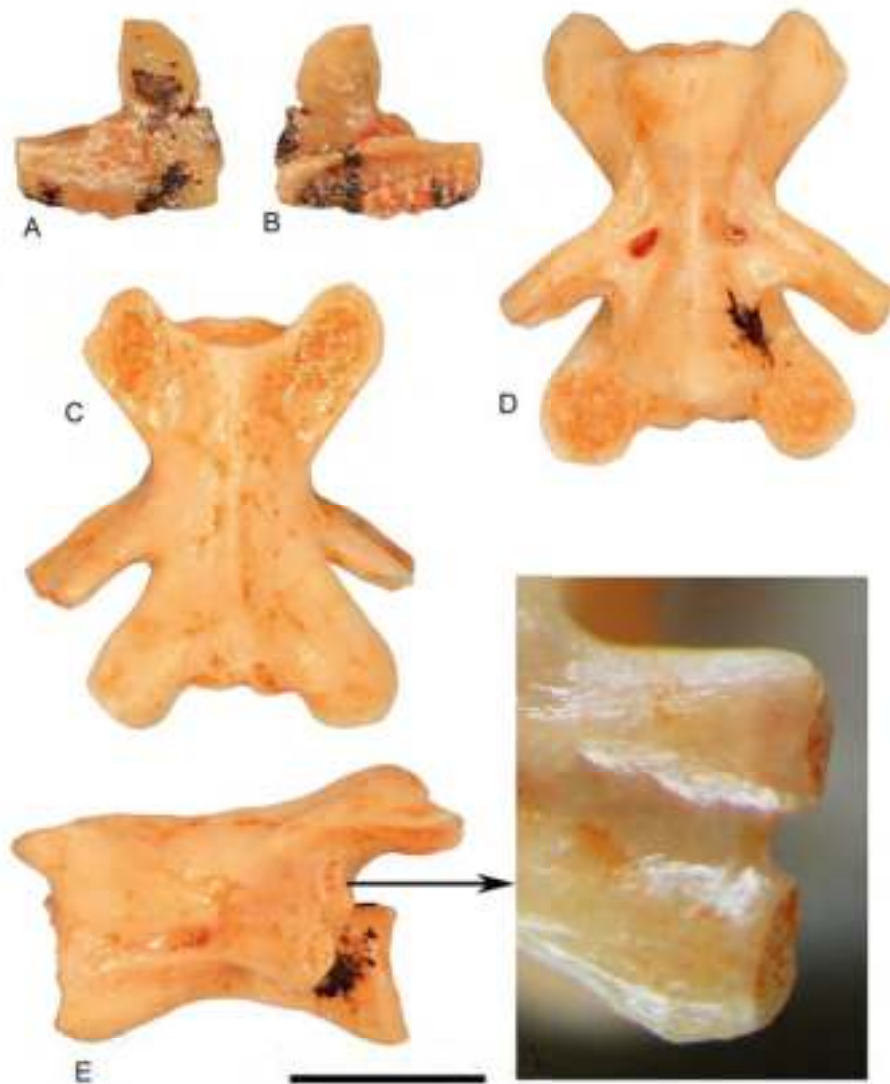


Figure 2. Type material of *Parahynobius betfianus* Venczel, 1999. A, B, holotype right premaxilla (MTC No. 19913) in anterior (A) and posteroventral (B) views. C–E, paratype middle trunk vertebra (MTC No. 19910) in ventral (C), dorsal (D) and left lateral (E) views; the arrow points to detail of the transverse process possessing a bicapitate condition. Scale = 2 mm. fossils, like *Liaoxitriton* (Wang 2004) and *Jeholotriton* (Wang & Rose 2005), both possessing a premaxillary fontanelle.

Trunk vertebrae. The best-preserved specimen is a completely preserved middle trunk vertebra (except the distal part of the right prezygapophysis and of the right diapophysis that are missing) designated as the paratype (MTC No. 19910). The centrum is amphicoelous and moderately elongated; small and flattened anterior basapophyses are inserted near the ventrolateral side of the cotylar rim. The transverse processes, inserted near the midpoint of the centrum, are relatively long and distally widening with their distal margin distinctly bicapitate; a bony prominence is present on the dorsal margin of the diapophysis and on the ventral margin of the parapophysis near their distal end; the ventral prominence is distinctly larger. Posterior to the transverse processes there is no trace of a spinal nerve foramen. The neural arch is flattened, whereas the neural spine is reduced to a low neural ridge; the interzygapophyseal ridges are faintly developed. In dorsal view, the anterior border of the neural lamina is moderately wide and concave, whereas the prezygapophyses are oval in shape trending anterolaterally and slightly obliquely; the posterior border of the neural lamina bears the imprints of the paired hyperapophyses. In ventral view, the subcentral keel is reduced, whereas a pair of subcentral foramina are present near the base of the transverse processes. The postzygapophyses are ovaloid in shape, and their lateral sides are slightly bent ventrally and therefore the postzygapophyseal surface is concave. The centrum length of the paratype is 3.42 mm.

The remaining trunk vertebrae closely resemble the shape of the paratype specimen (Figs. 4-8). However, the sizes of most specimens are usually smaller depending on their individual age and a few damages are observed (e.g. in most specimens the transverse processes are broken off). In most specimens the insertion point of the transverse processes is near the mid-length of the centrum, but in some examples the insertion point is more posterior (Figs. 5G, H, K; 6A, C, H; 8H); the bicapitate condition of the distal part of the transverse processes is present in several better-preserved examples; in some vertebrae the transverse process is distinctly curved posteriorly (Figs. 4C, 5B, 6A, K, L). The neural ridge of few examples is nearly imperceptible (Figs. 4A, C; 5G, 6A), but in some others it is more prominent (Figs. 4E, H; 5I, J); the subcentral ridge is variably present, whereas the paired subcentral foramina of variable sizes are present in most specimens. The imprints of the hyperapophyses are well discernible, but sometimes seem confluent.

The morphology of the anterior trunk vertebrae may be differentiated from those of the middle trunk vertebrae in having a considerably shorter centrum, a relatively higher neural arch and a more prominent neural ridge (Fig. 3). In some examples the dorsal margin of the neural ridge widens posteriorly (Figs. 3C, E, K, O, P). The transverse processes are usually short, flattened anteroposteriorly

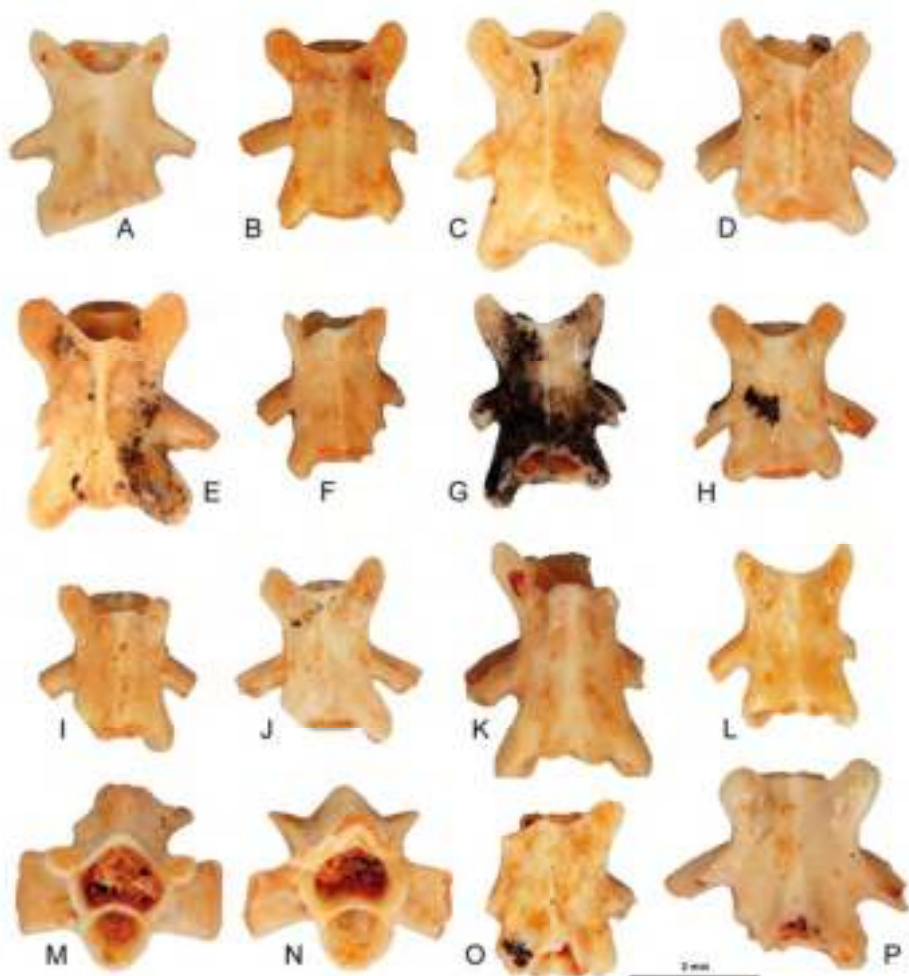


Figure 3. Anterior trunk vertebrae of *Parahynobius betfianus* (MTC No. 19911/1-15). A-L, O, P, anterior trunk vertebrae in dorsal views. M, anterior trunk vertebra in anterior view. N, anterior trunk vertebra in posterior view. Scale = 2 mm.

and high dorsoventrally and with unicapitate distal margins (in few specimens the transverse processes are distinctly bicapitate). The subcentral keel is usually reduced, whereas the subcentral foramina are extremely small or lacking. No spinal nerve foramina are observed.

Anterior caudal vertebrae. The neural arch of the anterior caudal vertebrae is flattened and provided with unicapitate transverse processes; the rib articulating sur-

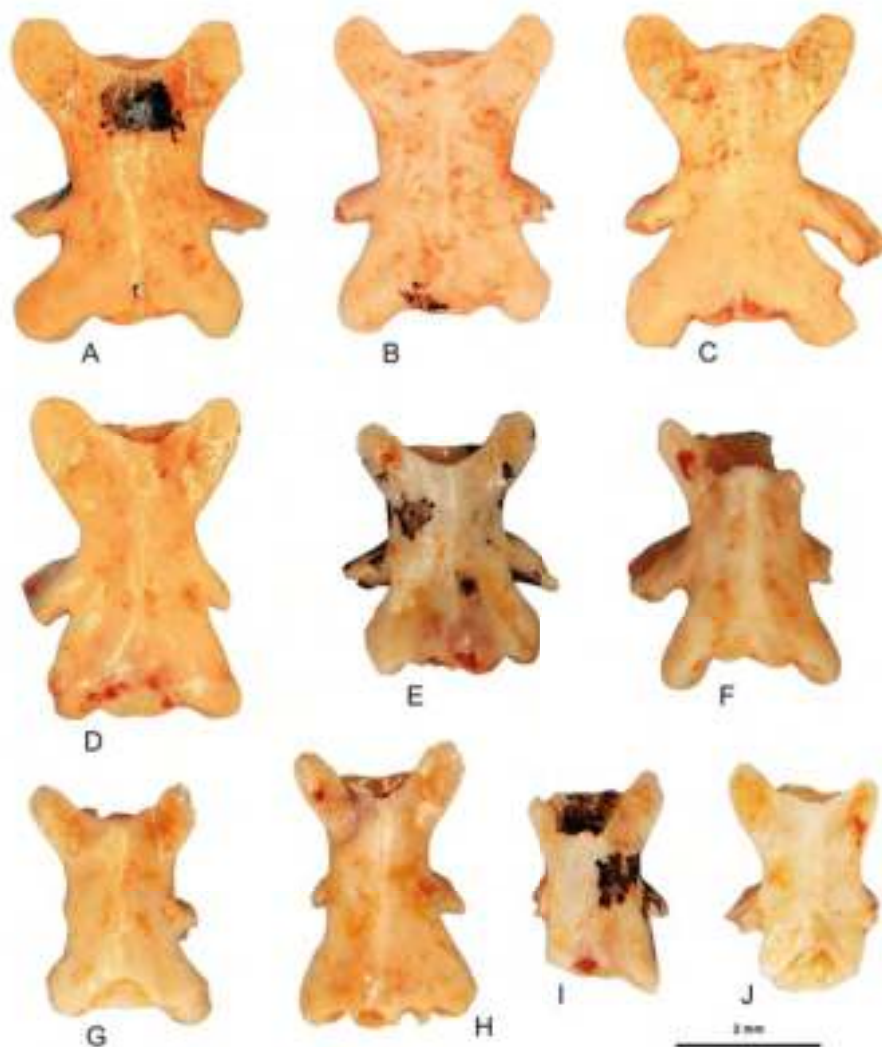


Figure 4. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19911/16-25). A-J, various sized specimens in dorsal views. Scale = 2 mm.

face is present and therefore the postsacral ribs were present (Figs 9, 10). The haemal arch is closed completely ventrally (Fig. 10D), and the haemal canal is oval in shape. The neural spine is reduced to a median neural ridge. In some specimens, the insertion surface of the hyperapophyses is prominent and distantly spaced from each other (Figs. 9A; 10I, G). There are no spinal nerve foramina are present.

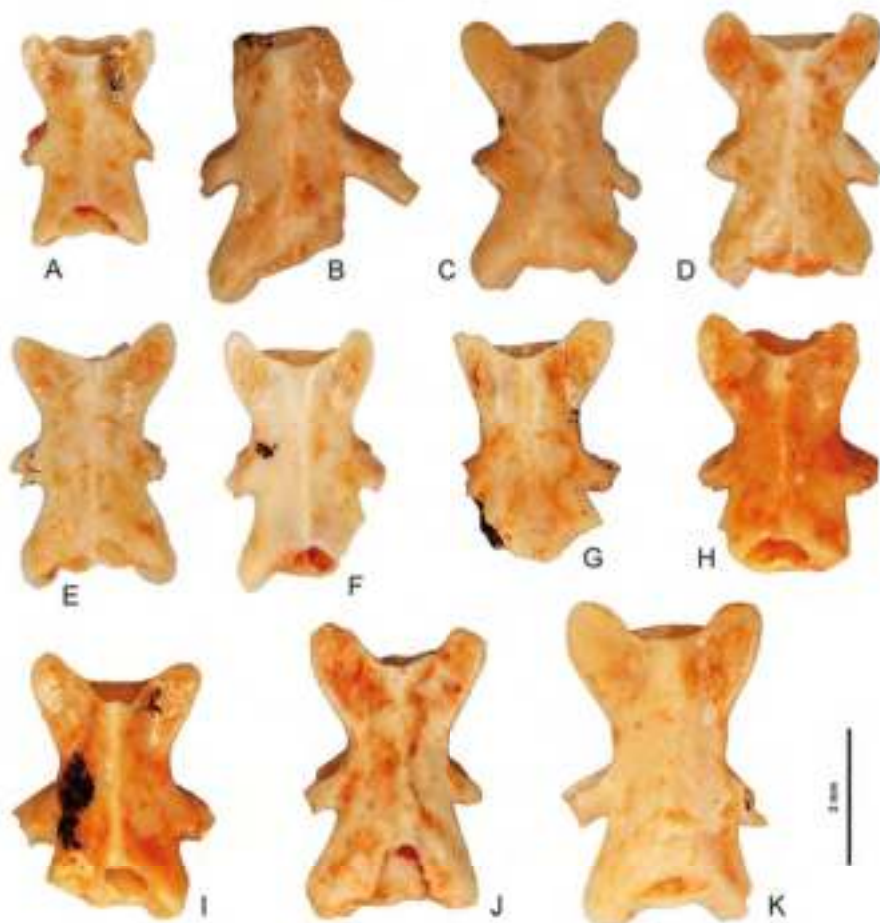


Figure 5. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19908/1-11). A-K, various sized specimens in dorsal views. Scale = 2 mm.

Posterior caudal vertebrae. The posterior caudal vertebrae are much smaller in size than the anterior caudal vertebrae and lack any transverse processes; the haemal arch is closed ventrally (Fig. 9I), and the spinal nerve foramen is lacking (Figs. 9H, I; 10K-M).

Comments. The centrum length of the trunk vertebrae is variable in length being shorter in the anterior ones (Duellman & Trueb 1986), however Jiang et al. (2018) reported that in *Batrachuperus londongensis* there is no significant change in length of the centrum along the trunk series. In most hynobiids the parapophyses



Figure 6. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19909/1-12). A, D-L, various sized specimens in dorsal views. B, C, specimens in ventral views. Scale = 2 mm.

(situated ventrally) and diapophyses (situated dorsally) in the trunk vertebrae are closely connected by a bony lamella to form unicapitate (= unicipital) transverse processes (Estes 1981). However, this condition was never explored in detail in most hynobiids (but see below). In the transverse processes of *Parahynobius betfianus* and *P. kordosi* the bicapitate condition is rather frequent (considering that in the most available specimens the transverse processes are strongly damaged) and both conditions occur at least in *P. betfianus* (Venczel 1999, 2000a). The unicapitate condition is present in *Onychodactylus*, *Ranodon* (pers. obs.) and *Batrachuperus londongensis* (Jia et Gao 2016, Jiang et al. 2018), whereas



Figure 7. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19914/1-14). A-F, H, J-L various sized specimens in dorsal views. G, I, specimens in ventrolateral views. Scale = 2 mm.

in *Salamandrella keyserlingii* and some *Hynobius* (e.g. *H. leechi*) there are some trunk vertebrae with bicapitate transverse processes; the bicapitate condition is also present in *Onychodactylus* and *Ranodon* cf. *sibiricus* (Vasilyan et al. 2013 and references therein). Osseous prominences on the distal parts of transverse processes, reported in *P. betfianus*, are also present in *R. sibiricus*, but on the parapophyses only (pers. obs.), whereas these are lacking in *Onychodactylus*, *Salamandrella* (Ratnikov & Litvinchuk 2007) and *H. leechi* (pers. obs.).

Scapulocoracoid. Both specimens are fragmentary lacking most part of the scapular blade (Figs. 11A, B). The procoracoid foramen is present, whereas on the lat-



Figure 8. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19916/1-8). A-H, various sized specimens in dorsal views. Scale = 2 mm.

eral surface of the scapular blade, starting from the margin of the glenoid cavity, a prominent ridge is present.

Comments. In *Ranodon sibiricus* and *Onychodactylus japonicus* the scapular blade is without a sharp crest, whereas in *Salamandrella keyserlingii* there is a prominent ridge as it has been also reported in *Batrachuperus londongensis* (Jian et al. 2018).

Humerus. The bone is almost straight, when viewed laterally or medially. The humeral head is rounded and well ossified in the larger (i.e. older) specimens (Fig. 11 F-H), whereas it remains flat (i.e. unossified) in the smaller examples (Fig. 11D, E). The ventral crest is extremely prominent and short, connected to the humeral head. The dorsal crest is triangular and of low height in the smaller specimens (Fig. 11D, H), whereas it is more strongly developed in the largest specimen (Fig. 11F, G) with a more prominent proximal projection, continued with a sinuous distal part extending approximately one third of the humeral length. The distal end of the humerus is well ossified in one of the specimens (Fig. 11C), whereas it remains unossified in a smaller example (Fig. 11D, E) with discernible facets for the radial and ulnar condyles; the fossa cubitalis ventralis is well defined. In one of the speci-

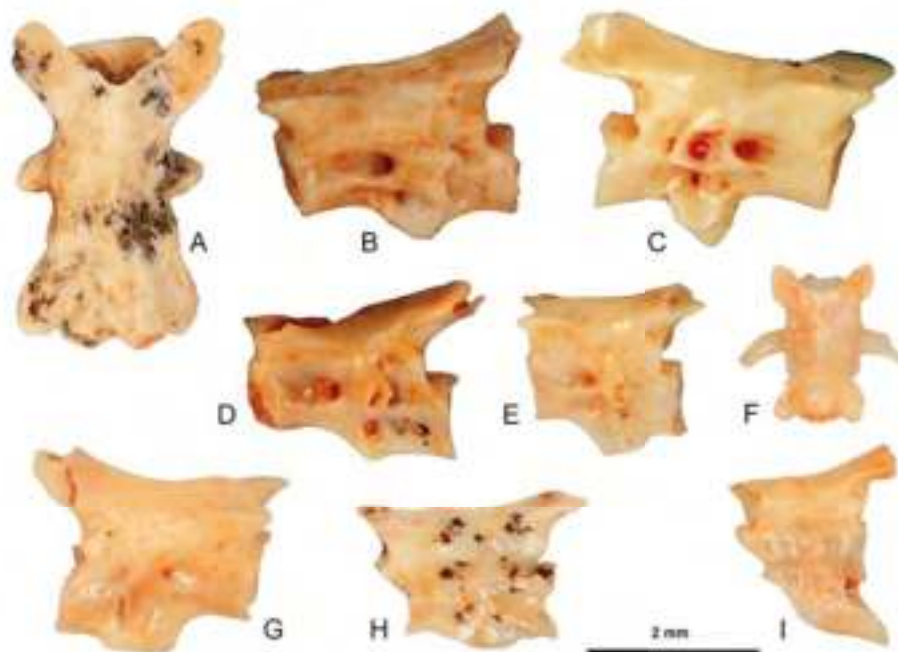


Figure 9. Caudal vertebrae of *Parahynobius betfianus* (MTC No. 19917/1-9). A, F, various sized anterior caudal vertebrae in dorsal (A, F) and lateral (B-E, G) views. H, I, posterior caudal vertebrae in lateral views. Scale = 2 mm.

mens (Fig. 11H), a fracture line is observed on the humeral stem that was healed up likely during the life of that individual.

Comments. The dorsal humeral crest has a triangular or even knob-like projection in *Batrachuperus londongensis* (Jiang et al. 2018) and *B. persicus* (AmphibiaTree. 2004), comparable to *Parahynobius betfianus*. The dorsal humeral crest is relatively short in *Ranodon shihi*, *R. tsinpaensis* (Zhao & Zhiang 1985) and in the fossil *R. cf. sibiricus* (Averianov & Tjutkova 1995: fig.4: 1b-d). In *Salamandrella keyserlingii* and *S. tridactyla* the dorsal humeral crest appears as a faint triangular projection (Ratnikov 2015), whereas in *Onychodactylus japonicus* it is undeveloped (Ratnikov 2015, AmphibiaTree. 2004).

Femur. The bone is slightly sigmoidal, with well ossified epiphyses in the larger specimens (Fig. 12A, B, E), whereas it remains cartilaginous in the smaller examples (Fig. 12C, D). The head of the bone is thickened and rounded, provided with a deep ventral depression. The femoral trochanter possesses a relatively thin and



Figure 10. Caudal vertebrae of *Parahynobius betfianus* (MTC No. 19911/26-38). A-G, various sized anterior caudal vertebrae in anterior (A), lateral (B-F) and dorsal (H-G) views.

J-M, various sized posterior caudal vertebrae in lateral views. Scale = 2 mm.

rounded spur-like process connected to a short and sharp crista trochanterica; the latter is lacking in the smaller specimens (Fig. 12C, D). The distal part of the bone is widened and flattened dorsoventrally.

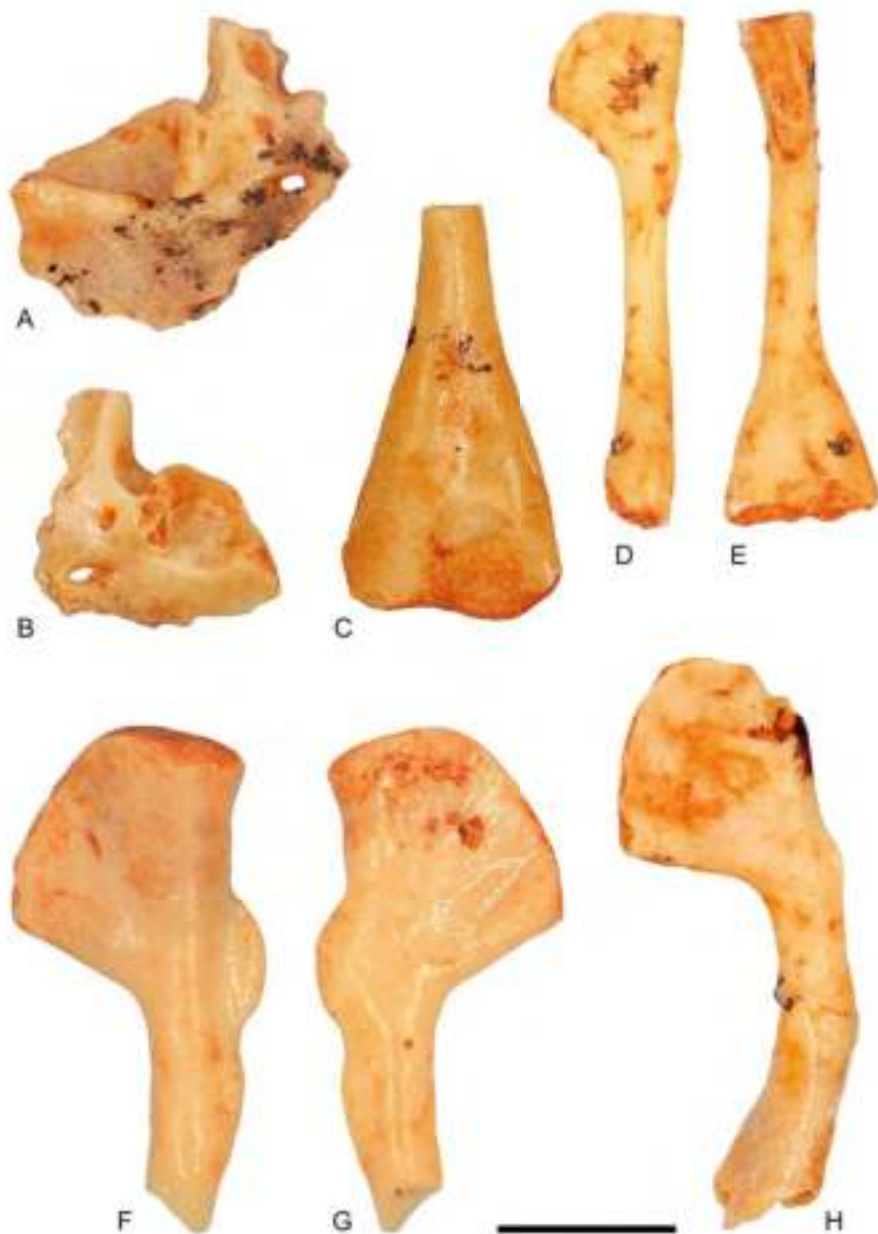


Figure 11. Scapulocoracoid and humerus of *Parahynobius betfianus*. A, fragmentary scapulocoracoid (MTC No. 19912/1) in lateral view. B, fragmentary scapulocoracoid (MTC No. 19915/1) in lateral view. C, distal humeral fragment (MTC No. 19915/2) in ventral view. D, E, humerus (MTC No. 19912/3) in lateral (D) and ventral (E) view. F, G, proximal humeral fragment (MTC No. 19912/2) in lateral views. H, proximal humeral fragment (MTC No. 20391) with healed up marks. Scale = 2 mm.

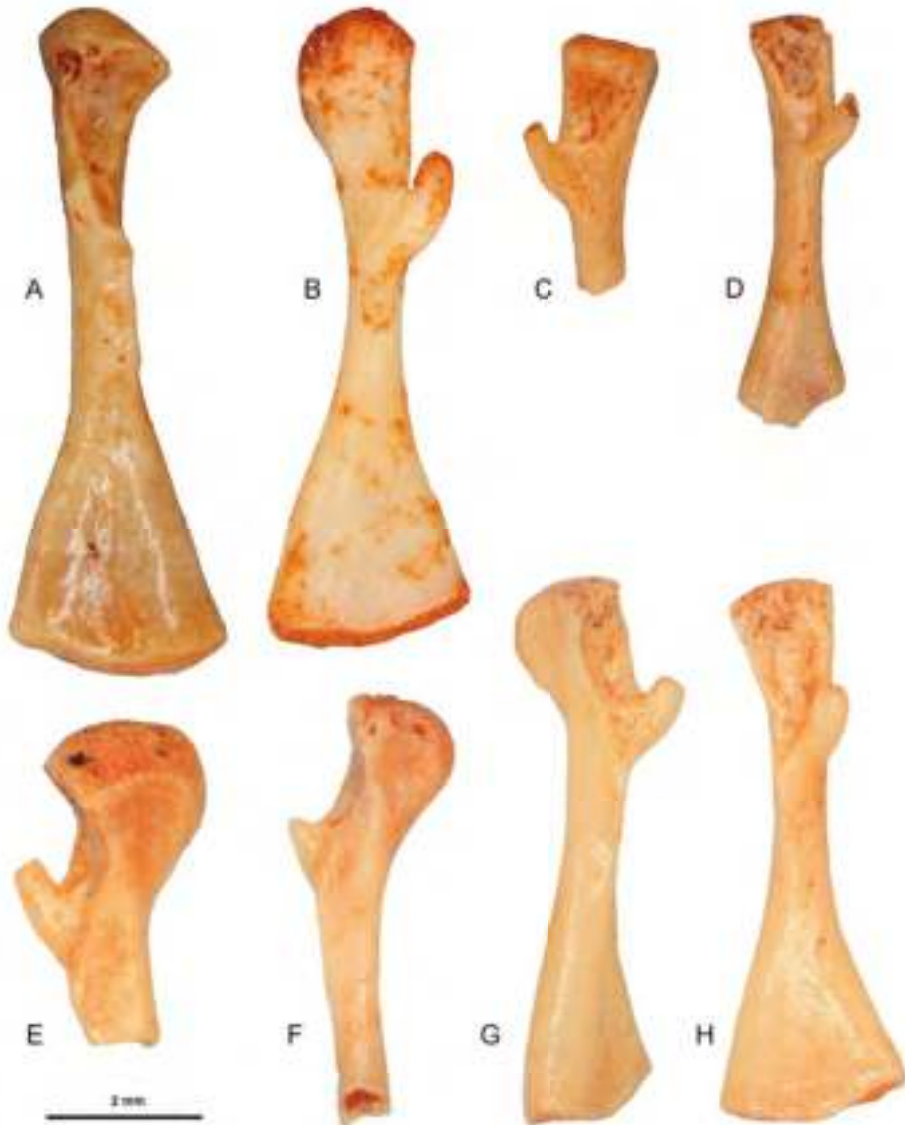


Figure 12. Femur of *Parahynobius betfianus*. A, B, G, H, various sized specimens (MTC No. 19907/1, 19907/2 and 19915/3) in ventral (A, B, H) and lateral (G) views. C-F, proximal femoral fragments (MTC No. 19912/4, 19912/5, 19915/4, 19915/5) in ventral (C, D) and lateral (E, F) views. Scale = 2 mm).

Comments. In *Salamandrella keyserlingii* and *Ranodon sibiricus* the crista trochanterica is faintly developed as a small triangular projection below and medial

to the femoral trochanter (pers. obs.), whereas in *Batrachuperus londongensis* it is relatively long extending from the femoral trochanter distally into the tibial condyle (Jiang et al. 2018).

Concluding remarks

The hynobiid material from Betfia 9/C is unique because it represents the single fossil record from the Quaternary of Europe. The isolated skeletal parts (premaxilla, vertebrae, scapulocoracoids, humeri and femora) most likely have belonged to a single species, and the variations observed, especially those on the trunk vertebrae (e.g. presence of unicapitate or bicapitate transverse processes, subcentral foramina, subcentral keels, height of neural crest, a.o.) may be considered intra-specific variations. In fact, the combined presence of unicapitate and bicapitate transverse processes is not unique (i.e. autapomorphic) to *Parahynobius betfianus*, since it has been observed in other hynobiid genera (e.g. *Hynobius*, *Onychodactylus* and *Salamandrella*).

The fossil material from Betfia 9/C may represent an attritional assemblage that may have belonged to at least seven or even more individuals (estimation based on the number of femoral examples) of various size. In spite of the fact that the material is fragmentary rarely were documented deformed bones (except the fracture observed on a single partial humerus).

If the assumption of Zhang et al. (2006) on the character evolution of the hynobiids is correct, then *Parahynobius* may have belonged to the pond-type hynobiids sharing the breeding places with newts (*Triturus* and *Lissotriton*) and with the palaeobatrachid frog *Palaeobatrachus langhae*, a permanent water dweller. Both the climatic and ecologic changes may have contributed to the extinction of *Parahynobius betfianus* and *Palaeobatrachus langhae*.

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