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Late Middle Miocene amphibians and reptiles from Subpiatră (Bihor district, Romania)

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Abstract. The Middle Miocene (MN 6) Subpiatră 2/1 locality yielded at least five different lissamphibians (*Lissotriton* sp., *Latonia gigantea*, *Pelobates* sp., *Bufo* cf. *viridis*, *Rana* (*Pelophylax*) sp.) and ten reptile taxa (*Diplocynodon* sp., Lacertidae indet. sp. 1 and sp. 2, *Ophisaurus* sp., Varanidae indet., Scolecophidia indet., *Natrix* sp., Colubrinae indet. sp. 1. and 2, *Vipera* sp.), while that of the late Middle Miocene (MN 7/8) of Subpiatră 2/2 produced four lissamphibians (Salamandridae indet., *Latonia gigantea*, *Palaeobatrachus* sp., *Hyla* sp.) and seven reptile taxa (*Diplocynodon* sp., Gekkonidae indet., Lacertidae indet. sp. 1 and sp. 2, *Ophisaurus* sp., Colubrinae indet. sp. 1). The composition of the assemblages from the above localities indicates different palaeoenvironments: the fauna of Subpiatră 2/1 accumulated in a lacustrine deposit probably lived in partially forested habitats, while that of Subpiatră 2/2 coming from a channel deposit contained remains of taxa which lived in habitats dominated by forests. The unexpected presence of *Diplocynodon* sp. in both localities suggests the persistence of relatively higher mean annual temperature (MAT) up to the Early Sarmatian then considered before.

Keywords. Caudates, Anurans, Reptiles, Miocene, Romania, paleoecology

Introduction

The occurrence of Middle Miocene freshwater sediments ("deltaic facies") in the post tectonic basin of Vad (Borod) have been mentioned by a number of authors (e.g. Vadász 1957: p. 602; Istocescu *et al.* 1971; Istocescu & Istocescu 1974). These strata, overlain discontinuously on Badenian sediments, were referred by these contributors to the Volhynian, which, based on the terminology used for the Central Paratethys (Harzhauser & Piller 2004, Grigorescu & Kazár 2006), may correspond to the lowermost part of the Sarmatian (late Middle Miocene).

In the summer of 2004 during a geological survey in the Rece Valley near Subpiatră, I discovered two new vertebrate fossil-bearing layers, named as Subpiatră 2/1 and Subpiatră 2/2. Hir & Venczel (2005) and Venczel *et al.* (2005) had been done the preliminary description of these fossil vertebrates. The preliminary description of these vertebrate remains was provided by Hir & Venczel (2005) and Venczel *et al.* (2005). Based on the micromammalian assemblages, they concluded that the Subpiatră 2/1 fauna might be older than that of Subpiatră 2/2 and may belong to the MN 6 unit, while the Subpiatră 2/2 fauna may be correlated with the MN 7/8 unit.

During 2005-2006 from both of the Subpiatră 2/1R and Subpiatră 2/2 localities about two tons of sediments have been processed for study. The samples were repetitively dried and washed using screens with meshes of 0.8 and 0.6 mm. The microvertebrate remains had been identified using taxonomic criteria. The resulted herpetological material is rather fragmentary but includes a series of bones bearing important morphological details.

In this paper I provide a detailed morphological description of the amphibians and reptiles discovered in the above localities, and discuss the palaeoenvironmental and palaeobiogeographic implications of the described fossils. Common English terms and the standard anatomical orientation system are used throughout this paper. All the fossil remains described in the present study are curate in the Natural History Department of Țării Crișurilor Museum, Oradea, Romania.

Abbreviations: **MTC** – Țării Crișurilor Museum, **SP** – Subpiatră, **CL** – centrum length, **CW** – centrum width.

Systematic palaeontology

Class AMPHIBIA Linnaeus, 1758

Order CAUDATA Scopoli, 1777

Family SALAMANDRIDAE Goldfuss, 1820

Genus *Lissotriton* Bell, 1839

Montori & Herrero (2004) resurrected the genus name *Lissotriton*, comprising at present *L. boscai*, *L. helveticus*, *L. italicus*, *L. montandoni* and *L. vulgaris*. *L. (=Triturus) roehrsi*, an extinct member of the genus, was described by Herre (1955) from the Middle Miocene (MN 6-8) of Děvínska Nová Ves (= Neudorf, Dévényújfalu) (Bratislava district), Slovakia.

Lissotriton cf. *vulgaris*

Material examined: **SP 2/1R**: 3 trunk vertebrae (MTC 23524/1-3), 1 femur (MTC 23525), 1 humerus (MTC 23526).

Description and comments. The vertebrae are opistocoelous and of minute size. The centrum is short with the neural spine relatively high and forking backward without any dorsal enlargement of the dorsal margin. The transverse processes are widely spaced and connected into their distal end by a bony lamina; the rib articulating surfaces have oval shape. The subcentral lamina is connected to the parapophysis; the subcentral foramina are relatively large.

MTC 23526 represents a proximal humeral fragment, which belonged to a small sized individual. The proximal articular surface, partially broken off, is connected to the ventral humeral crest. The dorsal humeral crest is relatively short and of triangular shape, its height diminishing below the level of the ventral humeral crest.

MTC 23525 is a right distal femoral fragment. The shaft of the bone is dorsoventrally flattened with a distinct ventrolateral crest and with well developed distal embayment.

Both the size and morphology of the above described remains approach the condition seen in *Lissotriton vulgaris*. The vertebrae from Subpiatră 2/1R differ from those of *L. roehrsi* by their relatively smaller size (e. g. see Sanchiz 1998a)

and by lack of enlargement and sculpture of the neural spine's dorsal margin. In fact, according to Sanchiz, *L. roehrsi* shows a number of morphological features shared with *Ommatotriton* (= *Triturus*) *vittatus* and most probably might be removed from the genus *Lissotriton*.

The fossil record of *L. vulgaris* (or forms morphologically close to this taxon) includes a number of Lower and Middle Miocene European localities, of which the geologically oldest one might be the Lower Miocene (Orleanian, MN 4) Agramon locality, Spain (Böhme & Ilg 2003). Further evidence for the genus *Lissotriton* is from the Early Miocene (MN 4) of Béon 1 locality, France, which might represent the earliest fossil record of a form closely related to *L. helveticus* (Rage & Bailon 2005). Thus, it may be concluded that the differentiation of the genus *Lissotriton* took place very probably during or previous to the Early Miocene.

Lissotriton sp.

Material examined: **SP 2/2**: 1 angular-prearticular (MTC 23580), 9 humeri (MTC 23581/1-9), 18 femurs (MTC 23582/1-18), 1 ilium (MTC 23583).

Description and comments. All the available specimens are rather fragmentary. The angular-prearticular is fused completely; the anterior (i.e. distal) portion is broken off.

From the nine humeral specimens only three represent proximal fragments (MTC 23581/1-3). MTC 23581/1 and 23581/2 are reminiscent of MTC 23526 from Subpiatra 2/1R (assigned to *Lissotriton* cf. *vulgaris*) in having a rather prominent ventral humeral crest, but their dorsal humeral crest is broken off. In MTC 23581/3 the ventral humeral crest is less elevated than in MTC 23581/1 and 2, while the dorsal humeral crest is extremely short. The remaining specimens represent distal humeral shafts (MTC 23581/4-9) which belonged to various sized individuals. Their distal section is slightly widened and provided with a rather shallow ventral cubital fossa.

The distal section of the iliac shaft in MTC 23583 is broken off; there is no waisting between the acetabulum and the iliac shaft. The acetabulum is elongated and provided with a well-developed posteroventral expansion outlining a deep fossa.

The femur head is slightly thickened and provided with a rather shallow

ventral depression. The *crista trochanterica* is faintly developed, while the distal femoral shaft is only moderately widened and provided with a rather shallow distal embayment.

The morphology of the humeri and the femoral fragments are rather different than those assigned to *Lissotriton cf. vulgaris*. Based on the above morphology I can assume the presence of a second *Lissotriton* species in Subpiatră 2/2.

Order ANURA Rafinesque, 1815
Family DISCOGLOSSIDAE Günther, 1858
Genus *Latonia* Meyer, 1843

Latonia gigantea

Material examined: **SP 2/1R**: 21 maxillae (MTC 23527/1-11, 23528/1-5, 23605/1-5), 5 frontoparietals (MTC 23529/1-2, 23530/1-2, 23604), 2 nasals (MTC 23531/1-2), 10 prearticulars (MTC 23535/1-7, 23606/1-3), 5 atlases (MTC 23532/1-4, 23533), 2 trunk vertebra (MTC 23534, 23536/1), 1 sacral vertebra (MTC 23536/2), 2 scapulae (MTC 23537, 23538), 4 ilia (MTC 23539/1-4, 23540/1-5, 23607/1-5); **SP 2/2**: 3 frontoparietals (MTC 23544/3-5), 10 prearticulars (MTC 23542/1-10), 15 maxillae (MTC 23543/1-15), 3 atlases (MTC 23545/1-3), 4 vertebrae (MTC 23545/4-7), 2 sacra (MTC 23545/8-9), 2 humeri (MTC 23544/1-2), 15 ilia (MTC 23541/1-15).

Description and comments. The nasals are very fragmentary and belonged to two specimens of different size. The bones are slightly convex dorsally and both are covered by a dense secondary sculpture.

Fragmentary specimens covered by a secondary sculpture consisting of bony ridges and tubercles represent the frontoparietals (Fig. 1: A, B). The specimens from SP 2/2 (MTC 23544/3-5) also preserve on their ventral side the *incrassatio frontoparietalis* (Roček 1994).

The maxillary remains are originating from various sized individuals. Most specimens from SP 2/1 R belonged to small individuals and there is no sign of secondary sculpture on the labial surface of maxilla. On the contrary, several specimens from SP 2/2 bear a secondary sculpture on the *processus*

zygomaticomaxillaris maxillae (Fig. 1: D). MTC 23543/1, on the lingual side has a rather prominent pterygoid process (its tip is broken off), but the posterior depression is not clearly delimited (Fig. 1: C). The horizontal lamina is relatively wide with a strongly convex labial margin. The tooth row extends backward to the base of pterygoid process.

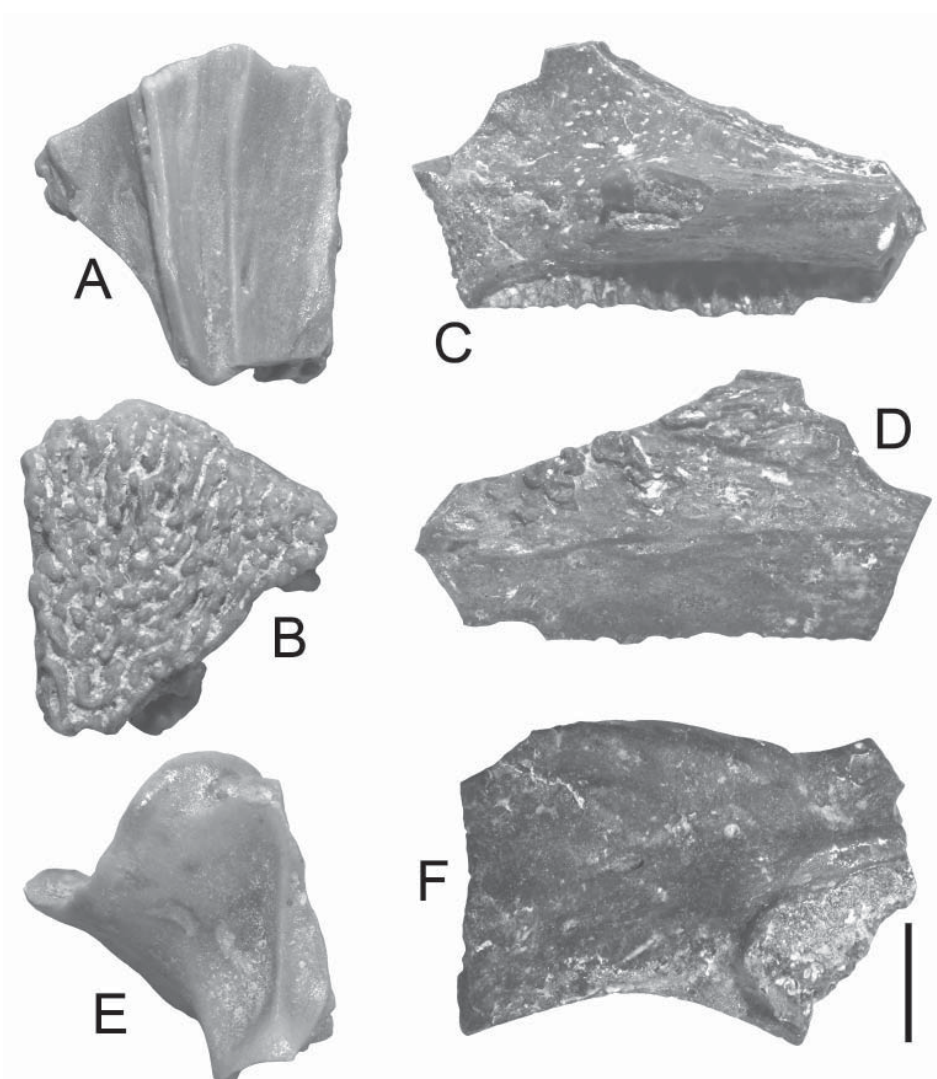


Figure 1. *Latonia gigantea* from Subpiatra 2/1R (A, B, E) and 2/2 (C, D, F). A, B: MTC 23604 fragmentary frontoparietal in ventral (A) and dorsal (B) views; C, D: MTC 23543 fragmentary maxilla in medial (C) and lateral (D) views; MTC 23532/1 fragmentary atlas in ventral view; MTC 23541/1 fragmentary ilium in lateral view. Scale equals 2 mm.

The prearticulars are strongly compressed labiolingually and bear two coronoid processes of which the posterior one (= paracoronoid process) has a vertical trend.

In all the vertebrae the neural laminae are broken off. The atlas is provided with two condyloid fossae and on the ventral surface of the centrum a prominent ventral crest is developed (Fig. 1: E). The presacral vertebrae are opistocoelous, while the sacral ones are provided with biconvex centra.

The scapula is cleft and provided with an extremely short and wide suprascapular part.

The humeral ball in the two available humeri is preserved in the smaller specimen only (MTC 23544/2). However, even in the larger specimen is clearly seen that the humeral ball was shifted laterally with a distinctly smaller *epicondylus lateralis*; there is a small ventral cubital fossa.

MTC 23541/1 represents a fragmentary ilium of which the posterior acetabular margin, part of the supraacetabular region and the distal iliac shaft is broken off. Nevertheless the morphology of the remaining fragment is indicative for a rather large supraacetabular region combined with a faintly defined preacetabular region (Fig. 1: F). The acetabular rim strongly projects anterolaterally and in consequence the first half of the acetabulum faces posterolaterally. However, the dorsal margin of the acetabulum is incompletely separate from the supraacetabular region. The supraacetabular fossa is well expressed. The dorsal protuberance is indistinctly separated from the extremely high iliac crest. In MTC 23541/1 the dorsal margin of the dorsal protuberance is flattened and thickened.

The morphological features of the above-described specimens (e.g. presence of secondary sculpture on frontoparietal and maxilla, presence of two coronoid processes) are diagnostic for *L. gigantea*. *L. ragei*, another large discoglossid frog, known from the Early Miocene of Europe (Hossini 1993, Böhme 2002, Rage & Roček 2003), lacks a secondary sculpture on the outer surface of maxilla (the frontoparietal is unknown). The same is true for the distinctly smaller sized *Discoglossus*, known in Europe since the Oligocene (Rage & Roček 2003).

Palaeobatrachus sp.

Material examined: **SP 2/2**: 1 frontoparietal (MTC 23195), 1 vomer (MTC 23588/1), 1 sphenethmoid (MTC 23588/2), 2 premaxillae (MTC 23584/1-2), 2 maxillae (MTC

23587/1-2), 1 dentary (MTC 23587/3), 7 prearticulars (MTC 23590/1-7), 1 scapula (MTC 23625), 2 humeri (MTC 23585/1-2), 2 ilia (MTC 23585/3, 23589), 3 atlantal centra (MTC 23586/1-3).

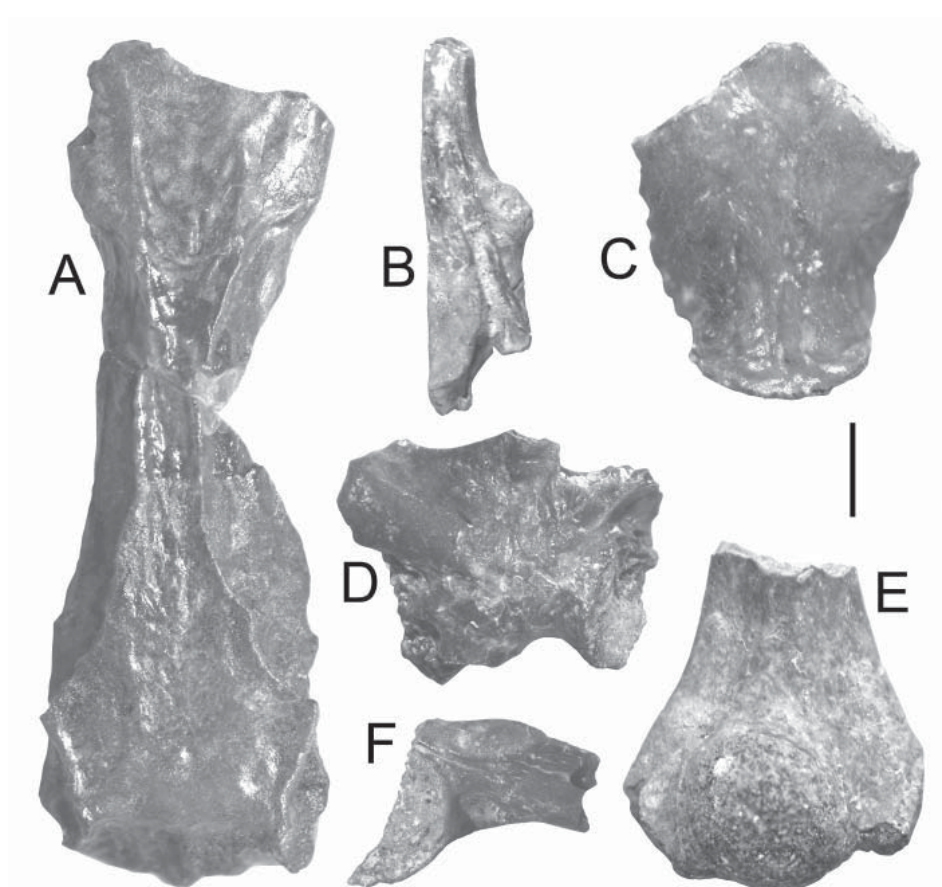


Figure 2. *Palaeobatrachus* sp. from Subpiatra 2/2. A: MTC 23195 frontoparietal in dorsal view; B: MTC 23590/1 prearticular in posteromedial view; C: MTC 23586/1 atlantal centrum in ventral view; D: MTC 23625 scapula in ventral view; E: MTC 23585/1 distal humeral fragment in ventral view; F: MTC 23589 fragmentary ilium in lateral view.

Scale equals 2 mm.

Description and comments. MTC 23588/2 represents the only available sphenethmoid in which the rostrum, the posterior margin and latero-ventral part

are broken off. The bone is slightly flattened dorso-ventrally and elongated antero-posteriorly. The surface of the lamina supraorbitalis is concave dorsally and finely striated, in living animal serving as a contact area for the overlying frontoparietal. The orbitonasal foramen for *ramus medialis nervi ophthalmici* is situated dorsolaterally to the olfactory canal.

The *ramus postchoanalis* in the only available vomer is broken off. The dorsal surface of the bone is grooved, while posteroventrally three vomeral tooth positions are preserved.

The premaxilla in both specimens is strongly damaged with the alary process and part of the palatine process broken off. MTC 23584/1 belonged to a larger individual with six tooth positions preserved. The smaller specimen (MTC 23584/2) in dorsal or ventral views has an oval shape with only three tooth positions preserved.

There are two small maxillary fragments with all teeth broken off. MTC 23587/1 has on its labial surface a faintly developed longitudinal striation and preserves relatively prominent *processus nasalis maxillae*. In the tooth row there are several osseous knobs preserved between the bases of teeth.

MTC 23587/3 represents the proximal fragment of a dentary with the mentomeckelian bone completely fused to the lingual margin. The bone is flattened labio-lingually and is toothless with thin edged dorsal margin.

The prearticular in all specimens is more or less damaged at their anterior and posterior sections. The bone is slightly S-shaped with the anterior portion curved medially. The coronoid process in all the individuals is rather small, rounded, with the surface sculptured by pits and ridges (Fig. 2: B).

MTC 23195, belonging to a rather large individual, is the only frontoparietal recovered from Subpiatră 2/2. At first only the posterior part of the bone was found (see Hir & Venczel 2005, Plate I: Fig. 1, 2; Venczel *et al.* 2005, Plate 1: Fig. 3). Later I have identified the anterior frontoparietal section and since both fragments displayed a comparable morphological pattern (e.g. same height and width of parasagittal ridges), and similar surface of fracture as well, the two parts were agglutinated (Fig. 2: A). The frontoparietal table is widened posteriorly and bordered laterally and posteriorly by distinct ridges. The parasagittal ridges in the mid dorsal section are prominent and situated close to each other producing medially an elongated, irregularly concave depression. In the anterior section the parasagittal ridges diverge from each other and both rami are forked anterolaterally.

The medial rami enclose a concavity with the pineal foramen. In ventral view, there is an elongated depression delimited by sharp bony lamellae, which in living animal cover the frontoparietal fenestra.

In all three atlas+axis, the neural lamina is broken off. The centrum is strongly flattened; the condyloid fossae are incompletely separated from each other. The ventral surface displays a longitudinal striation (Fig. 2: C).

The only scapula is rather fragmentary with its anterior and medial margins broken off (Fig. 2: D). It is rather short and uncleft, while on its dorsal surface a deep fossa is preserved.

The humerus in the available specimens preserves a fragmentary distal humeral shaft only (Fig. 2: E). The *epicondylus medialis* and the *epicondylus lateralis* are situated nearly symmetrical to each other. However, the lateral condyle is always larger than the medial one. The ventral cubital fossa is lacking.

The supraacetabular part, the posterior margin of the acetabulum and the iliac shaft in both available ilia is broken off. The preacetabular region is reduced and there is a small preacetabular fossa (Fig. 2: F). The dorsal protuberance has an ovaloid surface and presumably was divided in two tubercles. The only evidence for the latter feature is observed on the posterodorsal margin of MTC 23589, which preserves a small anterior section of the posterior tubercle only.

The morphology of the frontoparietal strongly differs from that of *Palaeobatrachus hiri*, known from the Middle Miocene localities of Mátraszőlős 1 and 2, and Sámsonháza, northern Hungary (Venczel 2004), in which the frontoparietal is strongly widened backward. At the same time the growth of parasagittal ridges on the frontoparietal table of *P. hiri* exhibit a wide range of intraspecific variations. On the other hand in *Palaeobatrachus robustus*, known from the earliest Miocene of France (Hossini & Rage 2000), the frontoparietal is only slightly widened posteriorly and the frontoparietal table lacks for parasagittal ridges. A third species, namely *Pliobatrachus langhae*, is known from the Pliocene and early Pleistocene of Central Europe. Unfortunately the type material of *Pliobatrachus*, consisting of a synsacrum and an urostyle, described by Fejérváry (1917) from the Early Biharian of Betfia (Romania) is lost. Notwithstanding, Sanchiz & Mlinarski (1979) and Sanchiz (1998b) extended the generic diagnosis of *Pliobatrachus* and assigned new skeletal elements to this form (e.g. frontoparietal, maxilla, premaxilla, sphenethmoid, parasphenoid, mandible, vertebrae, scapula, coracoid, humerus, ilium). According to the previous mentioned authors the frontoparietal

in *Pliobatrachus* is strongly convex dorsally and bears well-defined parasagittal ridges delimiting medially a dorsal anterior U-shaped groove (*i. e.* comparable to MTC 23195). On the other hand Hodrova (1982) reported from the Early Pliocene (MN 15) of Ivanovce several frontoparietals with faintly defined parasagittal ridges and with the posterior section of bone of variable width (*e.g.* see Hodrova 1982, Fig. 1: d-g and Plate I: 1-2). Thus, a revision of the late Neogene palaeobatrachids in the next future is on large requirement.

Pelobates sp.

Material examined: **SP 2/1R**: 1 ilium (MTC 23546).

Description and comments. MTC 23546 represents a preacetabular region and part of the iliac shaft; the iliac crest is of low height. Typical for *Pelobates* is the occurrence of a so-called spiral groove (*sensu* Evans & Milner 1993) part of which could be observed extending around the base of the iliac blade from dorsomedial to ventrolateral. There is no sign of a dorsal protuberance, which is variably developed in the genus *Pelodytes*, or sometimes absent (Sanchiz *et al.* 2002).

Bufo cf. *viridis*

Material examined: **SP 2/1R**: 2 fragmentary ilia (MTC 23608/1-2).

Description and comments. The best preserved specimen is MTC 23608/1 which exhibits parts of the acetabular region and the iliac shaft (Fig. 3: C). The dorsal protuberance is prominent, divided in 2-3 tubercles, and positioned above the anterior half of the acetabulum. The iliac crest is low, while the preacetabular fossa is well defined.

The morphology and position of the dorsal protuberance as well as the presence of a distinct preacetabular fossa are distinctive for recent *Bufo viridis*. In *B. bufo* the preacetabular fossa is lacking, while in *B. calamita* the ventrolateral margin of the iliac shaft produces a salient crest, the so-called “lamina calamita” (Sanchiz 1977). At the same time in the latter forms the dorsal protuberance is not differentiated in smaller tubercles.

A bufonid frog from the Astaracian (MN 6) of Devinska Nova Ves (= Neudorf)

had been described under the name of *B. priscus* by Špinar *et al.* (1993), while *B.* (= *Palaeophrynos*) *gessneri* is known from the Astaracian (MN 7-8) of Oehningen, Germany (Sanchiz 1998b). However, according to Rage & Roček (2003) the latter two forms might be synonyms of *B. viridis*.



Figure 3. Anurans from Subpiatra 2/1 (C-F) and Subpiatra 2/2 (A, B). A: prearticular (MTC 23597/1) of *Hyla* cf. *arborea* in posteromedial view; B: fragmentary ilium (MTC 23597/2) of *Hyla* cf. *arborea* in lateral view; C: fragmentary ilium (MTC 23608) of *Bufo* cf. *viridis* in lateral view; D: fragmentary squamosal (MTC 23611) of *Rana* (*Pelophylax*) sp. in medial view; E: fragmentary ilium (MTC 23600/1) of *Rana* (*Pelophylax*) sp. in lateral view; F: fragmentary prearticular (MTC 23610/1) of *Rana* (*Pelophylax*) sp. in posteromedial view.

Scale equals 2 mm.

Hyla cf. arborea

Material examined: **SP 2/2**: 1 prearticular (MTC 23597/1), 3 ilia (MTC 23597/2-4).

Description and comments. The prearticular is slender and slightly S-shaped; some damage can be observed on the anterior and posterior margins (Fig. 3: A). The *pars spatulata* is posteroventrally trended, while the meckelian groove is extremely shallow and exposed laterally. The posterior part of the coronoid process is slightly concave dorsally and has three or four tiny tubercles on its anterodorsal portion.

The ilium in the three available specimens is damaged in a various degrees. The supraacetabular region is small with the posterior margin posterodorsally trended. The ventral margin of the preacetabular region is extremely thin. The iliac crest is faint. The dorsal protuberance is prominent, laterally expanded and has an oval shape (Fig. 3: B).

All the above features are retrieved in Recent *Hyla arborea* too. In *H. meridionalis* the dorsal protuberance is more or less rounded (Holman 1992, Bailon 2000).

Rana (Pelophylax) sp.

Material examined: **SP 2/1R**: 6 frontoparietals (MTC 23547/1-3, 23609/1-3), 1 squamosal (MTC 23611), 4 premaxillae (MTC 23548/1-3, 23601/1), 18 maxillae (MTC 23549/1-15, 23601/2-4), 10 prearticulars (MTC 23550/1-4, 23602/1-4, 23610/1-2), 2 trunk vertebrae (MTC 23554/1-2), 4 sacral vertebrae (MTC 23551/1-2, 23554/3-4), 2 humeri (MTC 23552, 23553), 270 ilia (MTC 23555/1-90, 23556/1-90, 23600/1-10, 23612/1-80).

Description and comments. The frontoparietal in all specimens consists of small fragments exposing ventrally the area with the frontoparietal incassation; the latter structure is almost of circular shape. The frontoparietal table is smooth and slightly concave dorsally and a faint longitudinal crest is developed laterally.

The distal part of the alary process of premaxilla and the posterior margin of the *pars palatina* in all three specimens is broken off. The labial surface is smooth and slightly convex. The number of tooth positions in the best-preserved specimen is 13.

The maxilla in all the specimens is rather fragmentary. The labial surface is smooth with moderately high *pars facialis*. The *pars dentalis* is toothed while the *lamina horizontalis* is thickened with convex lingual margin.

In all specimens only the posterior part of the prearticular, preserving the coronoid process and *pars spatulaeformis praearticularis*, was available for study. The bone is moderately widened and labiolingually compressed. The Meckel's groove is rather shallow and exposed laterally. The coronoid process is well developed and lamellar with the posterior portion concave dorsally and with the lingual margin wrinkled (Fig. 3: F).

The only available squamosal (MTC 23611) preserves a relatively short posterior ramus with its posterodorsal part damaged, while the distal part of the anterior ramus (*i. e. processus zygomaticus*) and that of the ventral ramus (*i. e. processus posterolateralis*) is broken off (Fig. 3: D). The bony lamina on the medial side of the ventral ramus is relatively low.

In both presacral vertebrae (MTC 23554/1 and 2) the neural arch is broken off; the centrum is slightly flattened and exhibits a biconcave shape. The sacral vertebra is biconvex with a single condyle forward and two condyles backward. On the anterior medial margin of the condyle there is a *fossa* representing the remnant of the notochord.

The humeri are fragmentary with the distal sections preserved only. The medial crest in MTC 23552 is distinctly larger than that of MTC 23553, which may be interpreted either as an ontogenetic variation, or a sexual dimorphism. The *epicondylus medialis* in both specimens is well developed.

The ilia are damaged in a various degrees. The supraacetabular and the preacetabular regions are roughly of similar expansion and the ilioischadic junction is moderately thick. The acetabulum is round shaped with prominent posterodorsal and anteroventral acetabular rims. The supraacetabular fossa is deep. The dorsal protuberance is prominent, provided with thin dorsal margin, expanded above the level of the iliac crest. In large specimens the lateroventral margin of the dorsal protuberance is thickened bearing a distinct anteroventral overhang (Fig. 3: E). The iliac crest is thin and high.

Based on the registered material, the ilium is the most frequent skeletal element at Subpiatra 2/1R and the overwhelming part belonged to postmetamorphic individuals of small size.

Order CROCODYLIA Gmelin, 1789
Family CROCODYLIDAE Cuvier, 1807

Diplocynodon sp.

Material examined: **SP 2/1R**: 13 fragmentary osteoderms (MTC 23557/1-5, 23558/1-3, 23616/1-5), 47 isolated teeth (MTC 23559/1-20, 23560/1-15, 23615/1-10, 23626/1-2). **SP 2/1L**: 1 osteoderm (MTC 23617). **SP 2/2**: 1 isolated tooth (MTC 23598).

Description and comments. The teeth are more or less conical and slightly curved lingually bearing fine striations and distinct mesiodistal crista (Fig. 4: A, C). Two small specimens (MTC 23604/1 and 2) are distinctly compressed labiolingually with some constriction at their base (Fig. 4: B). MTC 23598 is the only crocodilian tooth recovered from Subpiatră 2/2. It is also compressed labiolingually and recurved with well-developed mesiodistal crista, and with a constriction at the tooth base.

The osteoderms are rather fragmentary. However, the available specimens suggest that at least a part of them might have had a rectangular shape. The outer surface bears an ornament with pits of various size and grooves (Fig. 4: D), while the inner surface is nearly smooth, penetrated by small foramina. The margins are flattened bearing a denticular suture.

Based on the available fossil record the genus *Diplocynodon* was rather frequent in Central Europe up to the Early/Middle Badenian, but practically disappeared in younger formations (Böhme & Ilg 2003). The abrupt climatic deterioration as well as the resulted stronger temperature gradient in Europe (around 14-13.5 Ma) caused regional extinction of a number of thermophilous ectotherms in Central Europe (Böhme 2003), which continue to survive in the southern regions only.

Order SQUAMATA Merrem, 1820
Suborder LACERTILIA Owen, 1842
Family GEKKONIDAE Gray, 1825

Gekkonidae indet.

Material examined: **SP 2/2**: 1 dentary (MTC 23592/1), 1 vertebra (MTC 23592/2).

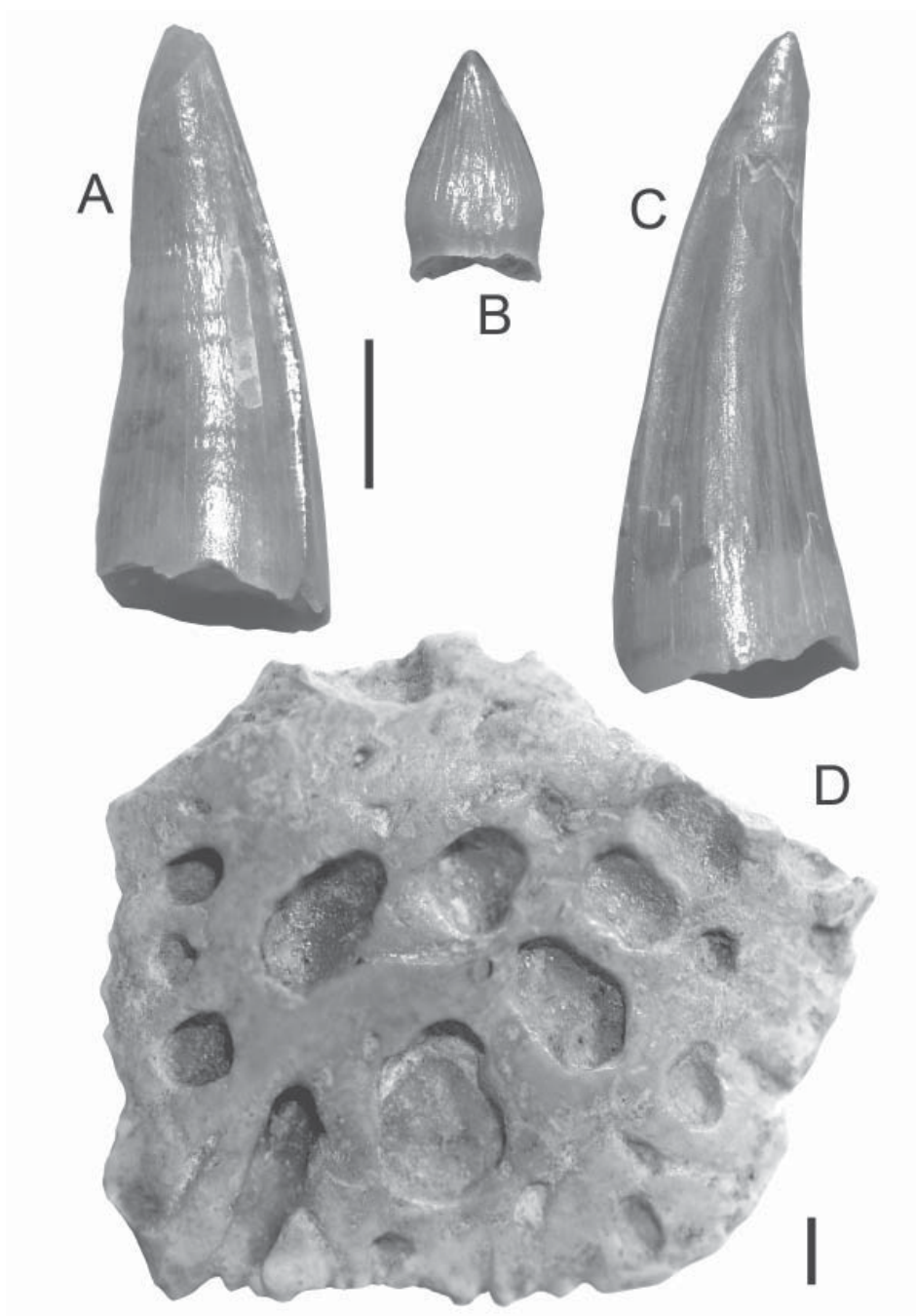


Figure 4. *Diplocynodon* sp. from Subpiatra 2/1. A, B, C: isolated teeth (MTC 23560/2, 23626, 23560/1); D: osteoderm (MTC 23617) in dorsal view. Scale equals 2 mm.

Description and comments. The only available dentary fragment belonged to a small sized individual. The meckelian groove is completely closed, while the subdental shelf is of considerable width. The dentition is of pleurodont type. The teeth are small and of similar size and provided with monocuspid tips. The number of tooth positions in the dentary fragment is 11.

The centrum of the only available vertebra is biconcave and slightly bent downward, provided with two tiny subcentral foramina. The paradiapophyses are small and oval shaped.

Family LACERTIDAE Bonaparte, 1831

Lacertidae indet. sp. 1

Material examined: **SP 2/1R**: 2 frontals (MTC 23561), 1 premaxilla (MTC 23613/1), 10 maxillae (MTC 23562, 23563, 23613/2-8), 2 dentaries (MTC 23564), 1 vertebra (MTC 23565); **SP 2/2**: 1 maxilla (MTC 23593/1), 1 frontal (MTC 23593/2).

Description and comments. The frontal is paired with the posterior section moderately widened. The dorsal surface of the frontal fragments is sculptured by small pits distributed irregularly; the *sulcus interfaccialis posterior* is rather shallow.

The dorsal part of the labial surface of the vertical wall of maxilla is sculptured by pits, furrows and tubercles, while the lower part is smooth and pierced by a row of *foramina pro rami nervorum alveolarium superiorum*; there are several smaller foramina situated dorsally to the main row (Fig. 5: A). The implementation of teeth in the maxillae and dentaries is pleurodont; the tooth neck is somewhat compressed mesiodistally. The tooth crown is labiolingually compressed and bicuspid with a central main cusp and a mesial lateral cusp.

The size and morphology of the remains is reminiscent of some smaller lacertids (e. g. *Podarcis*), but a closer assignment is actually not possible.

Lacertidae indet. sp. 2

Material examined: **SP 2/1R**: 6 dentaries (MTC 23566/1-3, MTC 23567/2-3, 23614), 1 maxilla (MTC 23567/1); **SP 2/2**: 1 dentary (MTC 23594/1), 1 frontal (MTC 23594/2).

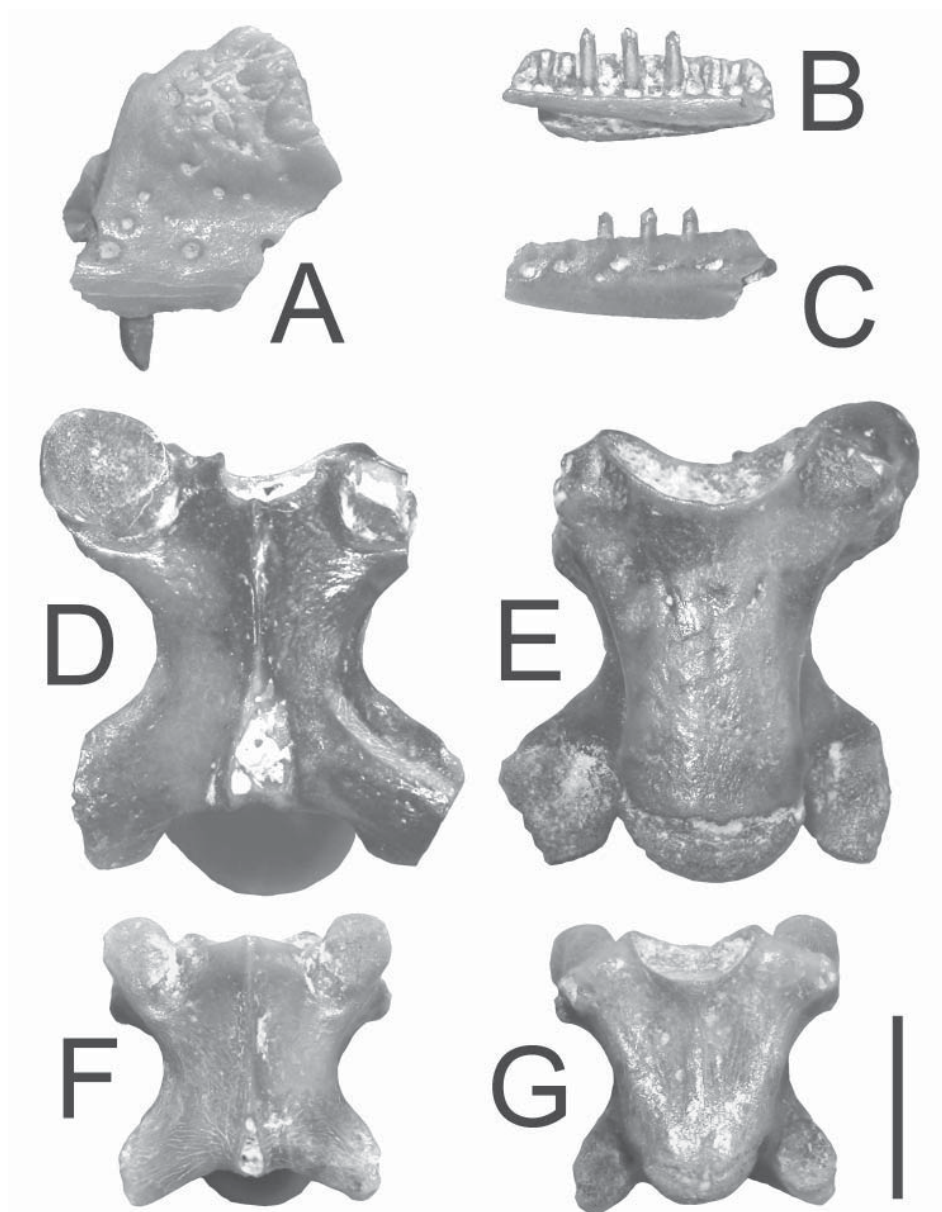


Figure 5. Lizard remains from Subpiatra 2/1 R. A: fragmentary maxilla (MTC 23613/2) of Lacertidae indet. sp. 1 in labial view; B, C: fragmentary dentary (MTC 23614) of Lacertidae indet. sp. 2 in lingual (B) and labial (C) views; D, E: MTC 23618/1 trunk vertebra of *Ophisaurus* sp. in dorsal and ventral views; F, G: MTC 23618/2 trunk vertebra of *Ophisaurus* sp. in dorsal and ventral views. Scale equals 2 mm.

Description and comments. The single fragmentary frontal (MTC 23594/2) belonging to a small individual preserves a sculpture formed by grooves and ridges; near the orbital margin a tubercular ornament is preserved. The *sulcus interfacialis posterior* is rather shallow.

The lamina horizontalis on the dentary is somewhat widened at its anterior third but becomes rather thin in the posterior section (Fig. 5: B). The meckelian groove is opened throughout the mandibular length. The subdental shelf is shallow. The dentition is pleurodont with cylindrical teeth. The tooth crown is labiolingually compressed with bicuspid tips. The main cusp is situated central while the lateral cusp is located mesially. MTC 23567/2 and MTC 23614 preserve on their labial sides, a well-marked facet for the coronoid attachment (Fig. 5: C). The remains are comparable in size with that of *Miolacerta tenuis*, but in the latter there is no sign of coronoid attachment (Roček 1984).

Ophisaurus sp.

Material examined: **SP 2/1R**: 810 osteoderms (MTC 23569, 23570, 23619), 1 jugal (MTC 23571), 1 pterygoid (MTC 23572), 24 vertebrae (MTC 23573/1-10, 23574/1-10, 23618/1-4); **SP 2/2**: 1 maxilla (MTC 23595/1), 4 osteoderms (MTC 23595/2-5), 10 vertebrae (MTC 23596/1-10).

Description and comments. The pterygoid fragment preserves a toothed portion with denticles of various sizes arranged in two rows.

The jugal is rather robust with the maxillary and temporal processes broken off, while the zygomatic process is rather short. The labial surface is sculptured with longitudinal grooves, pits and ridges.

The single maxillary fragment available lacks the vertical wall of maxilla and all functional teeth from the tooth row are broken off. However, a small recurved and cone-shaped replacement tooth, bearing a mesiodistal crest could be observed in the tooth row.

The osteoderms are variable in size displaying flat or slightly concave inner surface and usually provided with several small pits and a shallow medial groove. Their outer surface is convex and displays a smaller smooth margin and a larger sculptured surface. There is a prominent medial keel, bordered by a series of isolated or sometimes confluent tubercles.

The trunk vertebrae are flattened dorsoventrally and of variable size; the centrum has a flattened or a slightly convex subcentral surface provided with two subcentral foramina. The subcentral margins are also variable in shape: in some specimens these structures are slightly divergent (e. g. MTC 23618/1, Fig. 5: D, E), somewhat approaching the condition seen in the genus *Anguis*; in other specimens (e. g. MTC 23618/2, Fig. 5: F, G) the subcentral ridges are prominent flanking a concave subcentral surface, while the subcentral margins are strongly divergent forward. The caudal vertebrae are slender and provided with distinct haemapophyses near the ventral surface of the condyle.

Unfortunately the available material is not distinctive enough for a more advanced assignment.

Family VARANIDAE Gray, 1827

Varanidae indet.

Material examined: **SP 2/1R**: 8 isolated teeth (MTC 23575/1-4, 23620/1-4).

Description and comments. The isolated teeth are slightly curved posteriorly and labiolingually compressed with their bases broken off. A striation is obvious at the tooth base, while the posterior tooth margin bears a fine serration.

In the Central Paratethys area, based on the fossil records, the varanids survived up to the early Pliocene (Fejérváry 1918, Tempfer 2004, Venczel 2006).

SERPENTES Linnaeus, 1758

Infraorder SCOLECOPHIDIA Duméril & Bibron, 1844

Scolecophidia indet.

Material examined: **SP 2/1R**: 1 vertebra (MTC 23576).

Description and comments. The vertebra is damaged with its anterior part of the neural lamina (including the zygosphenes) broken off. The centrum is flattened, devoid of haemal keel and provided with two tiny subcentral foramina. The lateral surface of the paradiapophyses is damaged having a nearly circular shape. The neural arch is flattened dorsoventrally and there is no trace of a neural spine. The

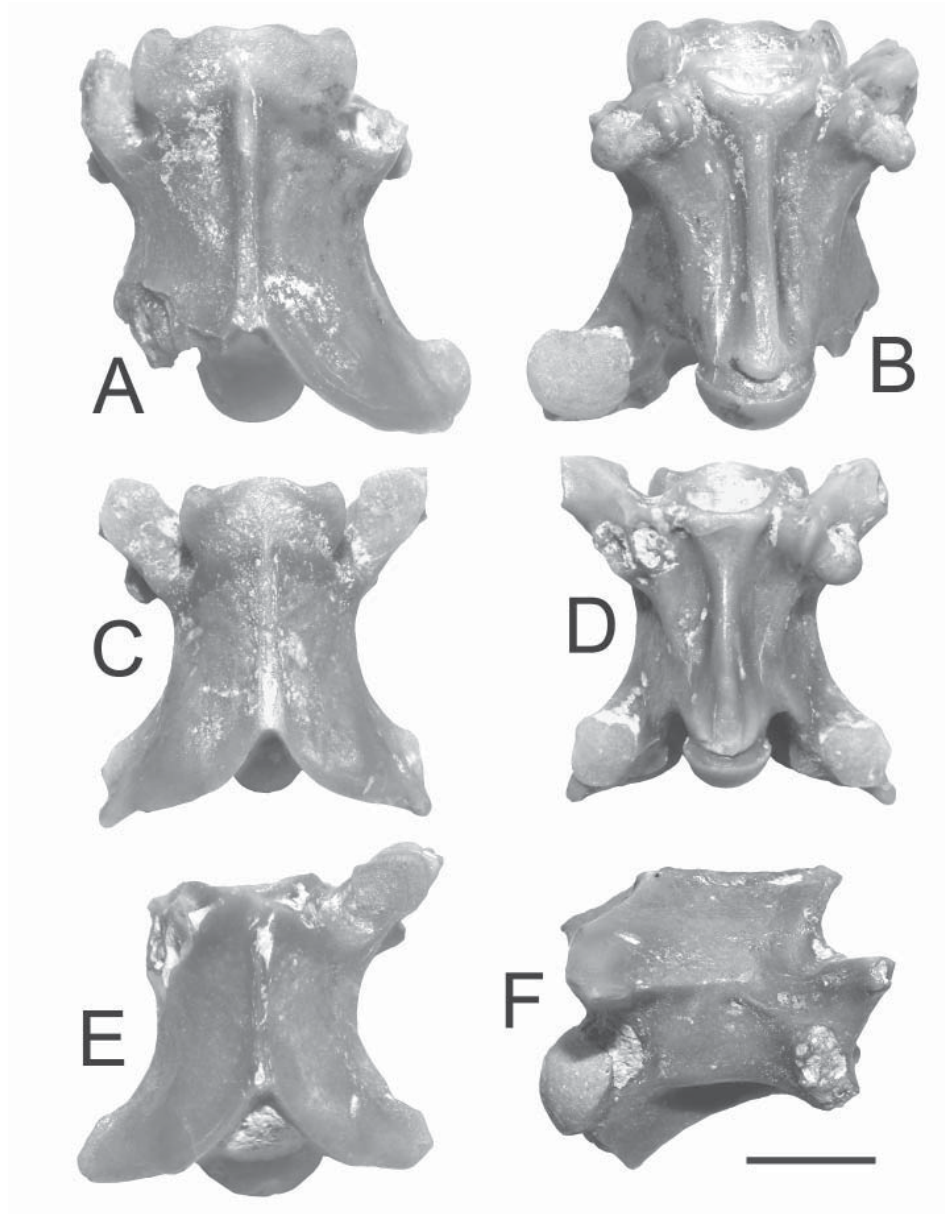


Figure 6. Snake vertebrae from Subpiatră 2/1R. A, B: trunk vertebra of Colubrinae indet. (MTC 23578/1) in dorsal and ventral views; C, D: presacral vertebra of *Natrix* sp. (MTC 23577/1) in dorsal and ventral views; E, F: presacral vertebra of *Vipera* sp. (MTC 23579/1) in dorsal and lateral views. Scale equals 2 mm.

posterior margin of the neural lamina is also damaged, but on the right posterior side the zygantum is preserved.

Members of Typhlopidae, Leptotyphlopidae and Anomalepididae share the above-observed morphological characters. As a matter of fact, the material in hand is inappropriate for assignment below suborder level. The presence of Scolecophidia in the Central European territory could be documented up to the early Pleistocene (Venczel 2000). The only actual representative of the family Typhlopidae is *Typhlops vermicularis*, which now inhabits the south-eastern area of Europe (Szyndlar 1991).

Infraorder ALETHINOPHIDIA Nopcsa, 1923
Family COLUBRIDAE Oppel, 1811

Natrix sp.

Material examined: **SP 2/1R**: 6 presacral vertebrae (MTC 23577/1-3, 23623/1-3).

Description and comments. The best preserved specimen (MTC 23577/1) represents a presacral vertebra in which the dorsal margin of the neural spine, the prezygapophyseal processes, the distal portion of the hypapophysis and those of the parapophyseal processes are broken off (Fig. 6: C, D). The vertebral centrum is 4 mm long and 2.61 mm wide (CL/CW = 1.53). The neural arch is moderately vaulted. The posterolateral margin of the neural lamina produces a well-defined epizygapophyseal spine. The anterior margin of the zygosphenes is crenate with a relatively wide medial lobe. The pre- and postzygapophyseal articular facets are of oval shape. The paradiapophyses are distinctly separated into parapo- and diapophyseal portions. The subcentral crest is better defined in the close proximity of parapophyses only. The cotyle and the condyle are circular in shape. Further specimens (MTC 23577/2 and 3) preserve part of the centrum only. However, in both the shape of the hypapophysis is sigmoidal.

The size and measurements of the only presacral vertebra approaches the condition seen in *Natrix sansaniensis* (CL/CW = 1.4-1.6), and *N. rudabanyaensis* (CL/CW = 1.4-1.7) (see Szyndlar 2005), but it is too fragmentary to be assigned to one of the above-mentioned forms.

Colubrinae indet. sp.1

Material examined: **SP 2/1R**: 3 vertebrae (MTC 23578/1-2, 23621); **SP 2/2**: 5 vertebrae (MTC 23591/1-5).

Description and comments. The centrum of the largest vertebra reaches 5 mm in length, while its width is 3.34 mm (CL/CW = 1.49) (Fig. 6: A, B). The neural arch is moderately vaulted and the anterior margin of the zygosphen is crenate, the medial lobe displaying a small emargination in the middle. The haemal keel is well defined with rounded and posteriorly slightly widened ventral margin; on the subcotylar lip two tiny tubercles are observed. The paradiapophyses are diminutive with the diapophyseal and parapophyseal portions of roughly equal length. The haemal keel in the specimens from SP 2/2 is prominent with two tiny subcotylar tubercles. The latter condition is present in recent *Hierophis caspius* and the fossil *H. caspioides* too.

Colubrinae indet. sp. 2

Material examined: **SP 2/1R**: 25 vertebrae (MTC No. 23578/3-10, 23599/1-5, 23622/1-12).

The vertebrae are of tiny size, the centrum length never reaching 3 mm in length. The neural arch is moderately vaulted and the neural spine of low or of moderate height without thickening of the dorsal margin. The zygosphen is with three lobes; the parapophyses equals in length or are slightly longer than the diapophyses. The haemal keel in the middle trunk vertebrae is weakly defined. In four well preserved vertebrae the centrum length ranged between 1.98-2.65 mm, while its width between 1.55-2.08 mm; CL/CW ratio is: 1.27-1.38.

Based on size and morphology I can presume the presence of a second colubrid snake (having much smaller dimensions than that of Colubrinae indet. sp. 1) at Subpiatră 2/1R.

Family VIPERIDAE Gray, 1825

Genus *Vipera* Laurenti, 1768

Vipera sp.

Material examined: **SP 2/1R**: 2 presacral vertebrae (MTC 23579/1-2), 4 venom fangs (MTC 23579/3, 23624/1-3).

Description and comments. The best preserved presacral vertebra belonged to a medium sized viperid snake (Fig. 6: E, F). The anterior margin of the neural lamina with the zygosphenes, the left prezygapophysis, and the tips of the hypapophysis and those of the parapophyses are broken off. The neural arch is depressed dorsoventrally; the ventral margin of the hypapophysis is straight and posteroventrally trended. The dorsal margin of the neural spine is broken off but it could have a considerable height. The tips of the paradiapophyses are missing but their remnants are ventrally trended. The centrum length is 4.24 mm, while the centrum width is 2.92 mm (CL/CW = 1.45).

The size and morphology of the above fossil material is reminiscent of the “*Vipera aspis* complex” of the genus *Vipera* (Szyndlar & Rage 2002). The presacral vertebrae in the members of the “*Vipera berus* complex” are comparatively smaller, and provided with low neural spines, while the centrum is more elongated. The vertebrae of the so-called “Oriental vipers” are very large with relatively short centrum, provided with high neural spine and long hypapophysis (Szyndlar 2005).

Concluding remarks

The differences seen in the faunal assemblages of the above-specified localities may be related, beside different geological ages, to dissimilar taphonomical contexts, as well as to their peculiar paleoenvironmental frameworks.

The microvertebrates and land snails of Subpiatră 2/1 were found in 15-20 cm thick sandy clay and silt layers accumulated probably in a freshwater lake or harbor; the fossils had been carried by streams of relatively high energy far enough, as suggested by the attrition of the dissociated bones of large mammals. The deposit is also plentiful in partly silicified wood fragments, fish otoliths, and freshwater ostracods (pers. obs.).

The fossil bearing strata from Subpiatră 2/2 locality consist of 70-90 cm thick dark-brown and yellowish clays (Venczel *et al.* 2005) extremely rich in planorbis shells, and may be interpreted as a marshy-lacustrine deposit. The silicified wood fragments are lacking there.

Megacricetodon distinctly dominates the micromammalian fauna of Subpiatră 2/1, while that from Subpiatră 2/2 by glirids and sciurids (e.g. *Myoglis* and *Spermophilinus*) (Hír & Venczel 2005). This is suggestive for different

paleoenvironments: the micromammals from Subpiatră 2/1 stress out a relatively dry climate and scrubby vegetation, while the abundant green frogs, *Latonia*, *Natrix* sp. and the crocodile *Diplocynodon* are indicative for permanent water sources in the area. *Diplocynodon* evidences a relatively high mean annual temperature (MAT) (Markwick 1998, Böhme 2003). In contrast, the micromammalian assemblage from Subpiatră 2/2 suggests a forested paleoenvironment. The occurrence of *Latonia* and *Palaeobatrachus* in the latter locality is also suggestive of persistence of aquatic habitats, while *Diplocynodon* points to a relatively mild climate too. However, the only *Diplocynodon* tooth from Subpiatră 2/2 and those from the coeval Tășad 1 locality (Hír *et al.* 2002) may represents the last occurrence date (LOD) of this genus in the Central Paratethys area. Beside these, the only known occurrence of *Diplocynodon* is from the late Middle Miocene Anwil locality (Swiss Molasse Basin, early MN 8), (Kälin and Kempf, 2002). At the same time these fossil records documents that at least some isolated populations of *Diplocynodon* could survived up to the early late Sarmatian even in northern Central European regions, contrary than considered before.

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