Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania

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ABSTRACT

A new Miocene fauna of amphibians and squamate reptiles from Tauţ, Arad district, W Romania, is described. The Taut vertebrate locality is of early Sarmatian (late middle Miocene) age, biochronologically belonging to the European Mammal zone MN 7+8. The assemblage of marshy-lacustrine taphonomic context yielded one of the most diverse fauna of amphibians and squamate reptiles ever described from the late middle Miocene of Central and Eastern Europe. The taxonomic account includes at least four species of newts, six species of anurans, four species of lizards, one amphisbaenian and five species of snakes. The salamandrid Carpathotriton and the palaeobatrachid Palaeobatrachus cf. hiri, both with long aquatic phase, represent common taxa with those known from late middle Miocene of Mátraszőlős, N Hungary, indicating somewhat similar paleoecological conditions. Beside aquatic and periaquatic forms (some newts, Latonia, Palaeobatrachus, Pelophylax, Natrix), other taxa probably inhabited the surrounding terrestrial environments with azonal vegetation (Hyla cf. arborea) and areas covered with scrubs and forests (Geckonidae indet., Ophisaurus sp., Hierophis cf. hungaricus, Macrovipera sp.). Pelobates, Blanus cf. gracilis and Scolecophidia indet., were subterranean dwellers. A number of taxa (e.g., Triturus cf. marmoratus, Ophisaurus, Blanus cf. gracilis) indicate close palaeobiogeographic connections with the western Paratethys and Mediterranean areas. On the other hand, some snakes (e.g., Coronella, Hierophis cf. hungaricus and Macrovipera sp.) appear as Asiatic immigrants. The Taut herpetofauna differs from those of other coeval localities in the area by its abundance in water preferring amphibian groups, by presence of amphisbaenians and by lack of crocodiles as well.

KEY WORDS
Amphibia,
Reptilia,
Lacertilia,
Serpentes,
Amphisbaenia,
Miocene,
Romania.

RÉSUMÉ

Amphibiens et reptiles squamates du Miocène moyen tardif de Tauţ, Roumanie. Une nouvelle faune d'amphibiens et reptiles squamates du Miocène de Tauţ, d'Arad district, Roumanie occidentale, est décrite. Le gisement de vertébrés de Taut d'âge Sarmatien inférieur (Miocène moyen tardif) se place, du point de vue biochronologique, dans la zone européenne mammifère MN 7+8. Ce gisement de contexte marécageux, a fourni une des faunes d'amphibiens et squamates d'âge Miocène moyen tardif d'Europe Centrale et de l'Est les plus diverses décrites jusqu'à présent. La faune comprend au moins quatre espèces d'urodèles, six espèces d'anoures, quatre espèces de lézards, un amphisbaenidé et cinq espèces de serpents. Carpathotriton et le palaeobatrachidé Palaeobatrachus hiri, deux taxons aux phases de vie aquatiques longues, sont également présents dans le Miocène moyen de Mátraszőlős (nord de la Hongrie) et indiquent des conditions palaeoécologiques similaires pour les deux gisements. A côté des formes aquatiques et périaquatiques (quelques tritons, Latonia, Palaeobatrachus, Pelophylax, Natrix), les autres taxons sont des habitants de milieux à végétation azonale (Hyla cf. arborea) et de régions à arbres et arbustes (Geckonidae indet., Ophisaurus sp., Hierophis cf. hungaricus, Macrovipera sp.). Blanus cf. gracilis, Pelobates et le Scolecophidia indet. sont des formes fouisseuses. La composition faunique (e.g., Triturus cf. marmoratus, Ophisaurus, Blanus cf. gracilis) indique des connexions paléogéographiques étroites avec les régions de la Paratéthys occidentale et méditerranéenne. Mais quelques serpents (e.g., Coronella, Hierophis cf. hungaricus et Macrovipera sp.) sont venus d'Asie. L'herpétofaune de Taut est différente de celles des autres gisements du même âge de cette région, par sa richesse dans les groupes d'amphibiens principalement aquatiques, par l'existence d'amphisbaenidés et par l'absence de crocodiles.

MOTS CLÉS
Amphibia,
Reptilia,
Lacertilia,
Serpentes,
Amphisbaenia,
Miocène,
Roumanie.

INTRODUCTION

Late middle Miocene (MN 7+8) faunas of terrestrial vertebrates were rarely reported from Romania. Apart from reports of occasional megamammalian occurrences (Codrea 2000) the only published data come from the localities of Tauţ and Comăneşti (Arad County, W Romania) (Feru et al. 1979, 1980; Rădulescu & Samson 1988; McNulty et al. 1999). Recently, two new locality complexes were described from Tăşad (Hír et al. 2002) and Subpiatră (Bihor County, W Romania) (Hír & Venczel 2005; Venczel et al. 2005). The only reports on herpetofaunas come from the latter two localities (Hír et al. 2002; Hír & Venczel 2005; Venczel et al. 2005).

The Tauţ vertebrate locality is located in the Migieşului Valley, south of Tauţ village (Arad district,

western Romania). The occurrence of terrestrial-lacustrine deposits from this site was pointed out by Istocescu first (1971) and Istocescu & Istocescu (1974); the outcrop of narrow extent consists from tufaceous green clays enclosing rare shells of *Planorbis* Müller, 1774 and *Helix* Linnaeus, 1758. The above authors correlated the age of these layers with the Volhynian substage of the Sarmatian, which may correspond to the lower part of the Sarmatian (late middle Miocene) (Grigorescu & Kazár 2006). Based on micromammals, Feru *et al.* (1980) assigned the Tauţ locality to the MN 8 of the European Neogene Mammal zones system (Mein 1975).

During a survey on the microvertebrate fossils from the collections of the Speleological Institute "Emil Racoviță" (ISER), Bucharest, we found a huge amount of herpetological material from Tauţ,

collected by M. Feru, C. Rădulescu and P. Samson in 1979. The material has never been mentioned in any papers of the above authors. However, some of the large discoglossid bones were already sorted out and partially restored probably by C. Rădulescu and P. Samson (pers. obs.). The fauna includes at least 10 species of amphibians and 10 species of squamate reptiles which may have belonged to 14 different families. Up to present, such a diversified late middle Miocene (MN 7+8) herpetofaunal assemblage has never been described from the eastern part of Central Europe. Accordingly, the Taut locality represents an important landmark in the evolution of herpetofaunas for this time interval.

In this paper we provide a detailed description of the amphibians and squamates coming from the above locality, and discuss the palaeobiogeographic and palaeoenvironmental implications of the described fossils.

MATERIAL AND METHODS

The disarticulated bones of amphibians and reptiles were sorted out by one of us (MV) from a large amount of dissociated microvertebrate remains, labeled and stored collectively with the micromammalian teeth, already published by Feru et al. (1979). The dissociated skeletal remains of newts and frogs include a series of skull bones, vertebrae, parts of the pelvic girdle and of the extremities. The lizard materials mainly consist of jaws and vertebrae, while those of limbless lizards include vertebrae and osteoderms; the amphisbaenian and snake remains comprise primarily vertebrae and very few cranial bones. All the remains described in this paper are curated in the ISER. The standard anatomical orientation system is used throughout this paper; the anatomical terminology of salamanders follows Sanchiz (1998a), that of frogs follows Špinar (1972), that of lizards follows Roček (1984) and that of snakes follows Rage (1984).

ABBREVIATIONS

Speological Institute "Emil Racoviță", **ISER**

MTC Țării Crișurilor Museum, Oradea;

CL centrum length; **CMT** coldest month temperature; CW centrum width;

MAP mean annual palaeoprecipitation; MAT

mean annual temperature.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758 Order CAUDATA Scopoli, 1777 Family SALAMANDRIDAE Goldfuss, 1820 Genus Chelotriton Pomel, 1853

Chelotriton paradoxus Pomel, 1853 (Figs 1; 2)

MATERIAL EXAMINED. — One nasal (ISER Tt-0300), four parietals (ISER Tt-0301/1-4), one squamosal (ISER Tt-0302), one quadrate (ISER Tt-0303), two dentaries (ISER Tt-0304/1 and 2), five vertebrae (ISER Tt-0306/-1-5), four humeri (ISER Tt-0307/1-4), one ischium (ISER Tt-0308), five femurs (ISER Tt-0309/1-5), seven ribs (ISER Tt-0310/1-7).

DESCRIPTION

Nasal

The medial margin of the only available specimen (ISER Tt-0300) is broken off. In dorsal view the bone is densely sculptured with prominent tubercles, which are sometimes confluent at their base. In ventral view there is a high bony wall which delimitates the nasal capsule mesially.

Parietal

In dorsal view the outline of the bone is oblongshaped with an elevated dorsal region of roughly triangular shape. The latter is covered with small, prominent, and sometimes confluent tubercles, separated by deep grooves pierced by small pores. Medially the tubercles are rather diminutive but become more prominent anteriorly and laterally featuring a dished surface. However, in specimens ISER Tt-0301/1 and 2 the tubercles on the lateral side are completely fused producing a bony wall with denticulate dorsolateral margin (Fig. 1A, B). The posterolateral surface of the parietal is smooth displaying an anterolateral concavity, which delimits medially the temporal fenestra. There is a relatively small anterior surface which in living

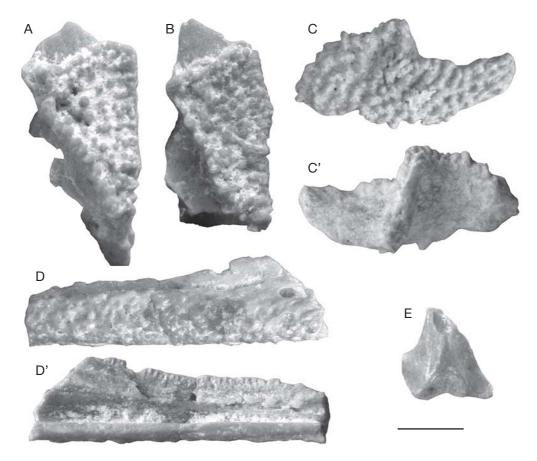


Fig. 1. — Chelotriton paradoxus Pomel, 1853: **A, B**, left parietals, dorsal views; **A**, ISER Tt-0301/1; **B**, ISER Tt-0301/2; **C**, **C'**, right squamosal (ISER Tt-0302/1); **C**, right lateral view; **C'**, medial view; **D, D'**, left dentary (ISER Tt-0304/1); **D**, left lateral view; **D'**, medial view; **E**, left quadrate (ISER Tt-0303/1), anterior view. Scale bar: 2 mm.

animal was covered by the posteroventral margin of the frontal.

Ouadrate

The only specimen lacks the otic process (Fig. 1E). The quadrate is widened ventrally and provided with a quadrate crest of moderate height ending in a distinct spur-like process facing laterally.

Squamosal

The single available specimen (ISER Tt-0302) lacks the ventral ramus, while the remaining dorsal part is flattened mediolaterally with the lateral surface covered by a prominent sculpture (Fig. 1C, C'). The posterior ramus is distinctly widened and in living animal its medial side contacted the *crista parotica* of the prootic. The anterior ramus is somewhat longer and thinner, and was articulated with the posterolateral process of the frontal, forming a complete fronto-squamosal arch.

Dentary

ISER Tt-0304/1 lacks both the anterior and posterior portions (Fig. 1D, D'). It is strongly curved medially and, except the dental parapet which is smooth, the labial surface is sculptured by low crests and shallow pits or grooves. The Meckel's groove is widely opened. ISER Tt-0304/2 represents an anterior portion of a dentary with the meckelian groove closed, provided with a higher dental parapet

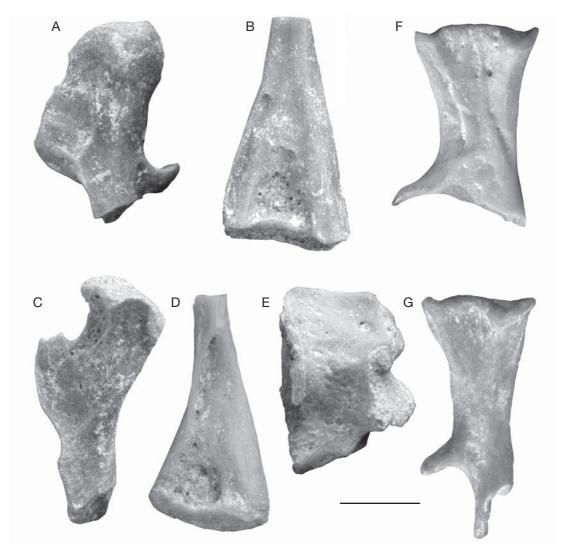


Fig. 2. — Chelotriton paradoxus Pomel, 1853: **A**, proximal fragment of humerus (ISER Tt-0307/1); **B**, distal fragment of humerus (ISER Tt-0307/2); **C**, proximal fragment of femur (ISER Tt-0309/1); **D**, distal fragment of femur (ISER Tt-0309/2); **E**, ischium (ISER Tt-0308); **F**, rib (ISER Tt-0305/1); **G**, same (ISER Tt-0305/2); **A**, **C**, lateral views; **B**, **D**, **E**, ventral views; **F**, **G**, posterior views. Scale bar: 2 mm.

than that of ISER Tt-0304/1 and with the labial surface only slightly sculptured.

Vertebrae

All the presacral vertebrae are strongly damaged. ISER Tt-0306/1 preserves the centrum and the transverse processes (= rib bearers), while the neural lamina is broken off. The centrum is opisthocoelous and rather

short. The subcentral surface is slightly convex and flattened, penetrated by several small foramina. The transverse processes are wholly interconnected by a bony lamina. The posterior portion of the anterior zygapophyseal crest joins the lamina interconnecting the transverse processes. An isolated neural spine, forked posteriorly and bearing a dorsal sculpture might have had belonged to this taxon also.

Ribs

All ribs assigned to *Chelotriton paradoxus* are flattened antero-posteriorly, provided with two articular surfaces and with a rather prominent dorsal spine (Fig. 2F, G).

Humerus

Only proximal and distal fragments were available for study. ISER Tt-0307/1 (Fig. 2A) has a rounded proximal articular surface which is continued in a rather prominent ventral humeral crest. The dorsal humeral crest is only partially preserved displaying a rather prominent and dorsally recurved process. The distal fragments are strongly widened and provided with a rather shallow ventral cubital fossa penetrated by several small foramina (Fig. 2B).

Ischium

The only specimen assigned to this taxon is rather robust, thickened at the level of the acetabulum (Fig. 2E). The medial margin is straight, while the ischiadic plate is pierced by a small foramen; the ischiadic process is broken off.

Femur

All specimens are rather fragmentary, consisting of proximal and distal fragments (Fig. 2C, D). In lateral view the proximal section of the femur is curved ventrally, provided with a rather robust femoral head. The trochanter possesses a spur-like process connected to the extremely prominent *crista trochanterica*. The distal part of the femur is bent dorsally, expanded distally, and provided with a well-defined distal fossa.

REMARKS

The material described closely resembles *C. paradoxus* and the morphological diversity of the available specimens does not exceed the limits of the intraspecific variations. The secondary sculpture which covers a number of cranial bones, consisting of densely distributed tubercles, strongly differs from that of *C. robustus* Westphal, 1980, known from the Eocene of Germany, in which the sculpture on cranial bones consists of broad pits delimited by prominent ridges (Westphal 1980). In the extant *Tylototriton* Anderson, 1871 the parietal sculpture

is not at all so extensive (e.g., see Haller-Probst 1998) than observed in the Taut specimens. In fact, the morphology of the sculptured elements, especially those of parietals with highly elevated sculptured surface and that of the dentary bearing also a smooth dental parapet, approaches the condition observed by Roček (2005) in *Chelotriton* sp. – type I, described from the late Miocene (MN 9) of Rudabánya locality. The quadrate spur of the only fragmentary specimen is present not only in Chelotriton but also in the extant Echinotriton Nussbaum & Brodie, 1982 and in some members of Tylototriton (Haller-Probst 1998). However, a somewhat smaller quadrate process is present in several Recent Salamandra salamandra (Linnaeus, 1758) examined by us (e.g., MTC 24030, 24031, 24032). The development of the anterior zygapophyseal crest seems to be variable within *Chelotriton*: whereas the only specimen from Taut exhibits the condition seen in cf. Chelotriton, reported from the late early Miocene (MN 4) of Béon 1, France (Rage & Bailon 2005), in presacral vertebrae of C. pliocenicus Bailon, 1989, known from the late Pliocene (MN 16) of Balaruc II, France, the anterior zygapophyseal crest joins the lower rib bearer (= parapophysis) (Bailon 1989).

Genus Carpathotriton Venczel, 2008

Carpathotriton sp. (Fig. 3)

MATERIAL EXAMINED. — One frontal (ISER Tt-0330), one squamosal (ISER Tt-0331), six angulo-prearticulars (ISER Tt-0333/1-6), two dentaries (ISER Tt-0332/1 and 2), six atlases (ISER Tt-0334/1-6), 35 presacral vertebrae (ISER Tt-0335/1-35), four humeri (ISER Tt-0336/1-4), one ischium (ISER Tt-0337), three femurs (ISER Tt-0338/1-3).

DESCRIPTION

Frontal

The dorsal surface is smooth except some sculpture near the supraorbital margin. The anterior portion of the dorsal surface exhibits a groove bordered by two ridges suggesting a contact with the dorsal process of the premaxillary (Fig. 3A). The posterolateral

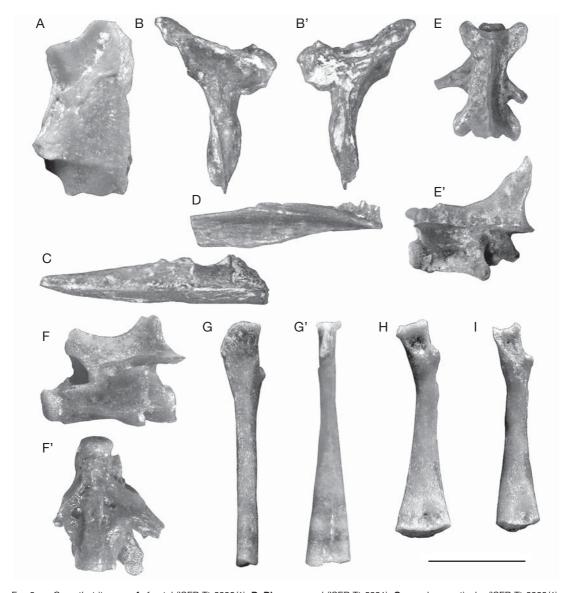


Fig. 3. — Carpathotriton sp.: **A**, frontal (ISER Tt-0330/1); **B**, **B'**, squamosal (ISER Tt-0331); **C**, angulo-prearticular (ISER Tt-0333/1); **D**, dentary (ISER Tt-0332/1); **E**, **E'**, presacral vertebrae (ISER Tt-0335/1); **F**, **F'**, same (ISER Tt-0335/2); **G**, **G'**, humerus (ISER Tt-0336/1); **H**, femur (ISER Tt-0338/1); **I**, same (ISER Tt-0338/2); **A**, **E**, **G'**, dorsal views; **C**, **E'**, **F**, **G**, left lateral views; **B**, right lateral view; **B'**, **D**, medial views; **F'**, **H**, **I**, ventral views. Scale bar: 2 mm.

process of the frontal is broken off but we assume that it might have been rather long and formed a complete fronto-squamosal arch. A low crest runs from the medial margin of the posterolateral process toward the posteromedial margin of the frontal delimiting a less elevated posterior area.

Squamosal

The ventral ramus is relatively long, while the anterior ramus is somewhat shorter than the posterior one (Fig. 3B, B'). The anterior ramus is widened distally for the articulation with the posterolateral process of the frontal.

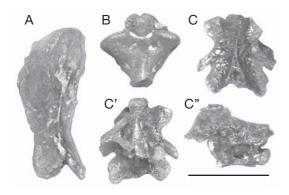


Fig. 4. — Lissotriton sp.: **A**, frontal (ISER Tt-0350); **B**, atlas (ISER Tt-0351); **C-C"**, presacral vertebra (ISER Tt-0352/1); **A**, **C**, dorsal views; **B**, **C'**, ventral views; **C"**, right lateral view. Scale bar: 2 mm.

Angulo-prearticular

The bone is elongated and provided with a moderately low coronoid process; the lateral flange is low and borders the Meckel's groove lingually (Fig. 3C).

Dentary

The only specimen (ISER Tt-0332/1) is rather fragmentary with the anterior and posterior portions broken off. The dental row is extremely short when compared to the toothless posterior ramus, a feature that is unparalleled in other salamandrids (Fig. 3D).

Atlas

In anterior view, the articular surfaces are faintly convex and circular in shape. The odontoid process is relatively wide and slightly concave dorsally; the atlantal cotyle is circular in shape.

Presacral vertebrae

All the vertebrae are opisthocoelous and provided with spinal nerve foramina. The neural arch is vaulted and provided with an extremely high neural spine (in most specimens it is completely broken off) (Fig. 3E-F'). The subcentral lamina projects ventrolaterally and is connected to the lower rib bearer (= parapophysys); the subcentral foramina are of variable size. The transverse processes are widely spaced while the rib articulating surface is relatively small and rounded.

Humerus

The head of the humerus is moderately widened and connected to a well-defined ventral humeral crest. The dorsal humeral crest is weakly defined forming a triangular bony lamina. The humeral shaft is elongated and slender with the distal extremity moderately widened (Fig. 3G, G').

Femur

In lateral view the bone is slightly sigmoid shaped with a moderately widened femoral head, a rather shallow ventral depression and a relatively short trochanter (Fig. 3H). The distal part of the femoral shaft is moderately widened and there is a shallow distal fossa.

REMARKS

For the first time, Carpathotriton was found in the late middle Miocene (MN 7) of Mátraszőlős, Hungary; it was then identified erroneously as Archaeotriton von Meyer, 1859 (Gál et al. 2000). The basis of this assignment was its extremely high neural spines of presacral vertebrae. However, a more detailed morphological study and the phylogenetic analysis indicates that it might have belonged to a more advanced stock of salamandrids reminiscent of some recent Asiatic newts (e.g., Cynops Tschudi, 1838, Pachytriton Boulenger, 1878, Paramesotriton Chang, 1935). Furthermore, some features (e.g., the extremely high neural spines of the trunk vertebrae, limb bones only slightly widened distally, long toothless posterior ramus of dentary) indicate that it might have had a long aquatic phase and a peculiar feeding mechanism (Venczel 2008).

Genus Lissotriton Bell, 1839

Lissotriton sp. (Fig. 4)

MATERIAL EXAMINED. — One frontal (ISER Tt-0350), one atlas (ISER Tt-0351), eight presacral vertebrae (ISER Tt-0352/1-8).

DESCRIPTION

Frontal

The dorsal surface bears a fine sculpture formed by shallow ridges and pits (Fig. 4A). The supraorbital

margin is low; parallel to the latter, a deep and widening furrow is directed anteriorly. The relatively short posterolateral process tapers distally, and its posterior edge only slightly exceeds the posterior margin of the frontal. This morphology is suggestive of an incomplete or a somewhat weak frontosquamosal arch.

Atlas

In the single specimen only the centrum is preserved. The subcentral surface is slightly concave, triangle-shaped and provided with two relatively large subcentral foramina (Fig. 4B). The articular surface of the paired atlantal condyles is of circular shape. The odontoid process is partially divided exhibiting two shallowly convex ventrolateral articular surfaces of oval shape. The atlantal cotyle is circular.

Presacral vertebrae

All the specimens are small sized with relatively short and opisthocoelous centrum (Fig. 4C-C"). The neural arch is moderately vaulted and provided with a relatively high neural spine forking posteriorly. The dorsal margin of the latter structure is not widened laterally.

REMARKS

Based on the available material, the above taxon may be securely placed in the genus *Lissotriton*. Among members of *Lissotriton* the postfrontal process is rather long in *L. helveticus* (Razoumovsky, 1789) and L. boscai (Lataste, 1879) but is relatively short in L. montandoni (Boulenger, 1880) and L. vulgaris (Linnaeus, 1758), the later displaying a morphology fairly similar with that of ISER Tt-0350. The size and morphology of the trunk vertebrae, with relatively high neural arch and well-developed neural spine forking posteriorly, support also the taxonomic assignment of the above fossils. Lissotriton roehrsi (Herre, 1955), an extinct member of the genus, known from the early to late Miocene of Central Europe (Sanchiz 1998a; Böhme & Ilg 2003), differs from the other ingroup taxa by having a relatively high neural spine provided with a distinct dorsal enlargement of the dorsal margin. Furthermore, Sanchiz (1998a) reported numerous skeletal remains assigned to *Lissotriton* (= *Triturus*)

roehrsi from the late early Miocene (MN 4) of Obersdorf, Austria. The frontals are provided with a relatively long postfrontal process and with an extensive sculptured dorsal surface differing clearly from the Tauţ specimen.

The earliest fossil record of the genus *Lissotriton* might be from the late early Miocene (MN 4) of Béon 1, France, described under the name *Triturus* aff. *T. helveticus* by Rage & Bailon (2005) and Obersdorf, Austria (Sanchiz 1988a), suggesting an already wide distribution of this group during late early Miocene.

Genus Triturus Rafinesque, 1815

Triturus cf. *marmoratus* (Fig. 5)

MATERIAL EXAMINED. — One oticooccipital (ISER Tt-0360), one parietal (ISER Tt-0361), eight presacral vertebrae (ISER Tt-0362/1-8), one humerus (ISER Tt-0363), one femur (ISER Tt-0364).

DESCRIPTION

Oticooccipital

The only available specimen belonged to a largesized adult individual (Fig. 5A, A'). In dorsal view, the crista muscularis is extremely prominent and runs sinuously from the posterodorsal margin of the prootic process to the anteromedial border of the otic capsule. This crest marks the medial limit of the squamosal attachment. The occipital condyle is prominent and of rounded shape with the medial and lateral margins bent posteriorly. The postotic foramen is dorsoventrally elongated and lies between the occipital condyle and fenestra ovalis. The latter structure is of roughly oval shape, delimited by a well-defined bony collar. In ventral view, the basal process is rather prominent and situated anteromedially to the fenestra ovalis. The palatal foramen is observed medially in the close vicinity of the basal process.

Parietal

The parietal is roughly rectangular with some damages on its anterior and posteromedial margin (Fig. 5B). The dorsal surface lacks any sculpture.

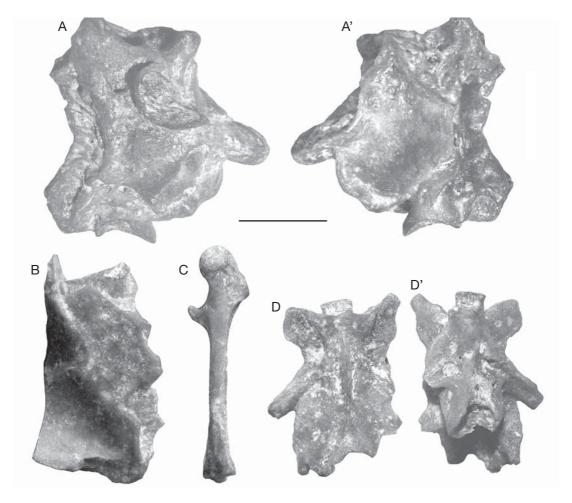


Fig. 5. — *Triturus* cf. marmoratus: **A**, **A'**, oticooccipital (ISER Tt-0360); **B**, parietal (ISER Tt-0361); **C**, humerus (ISER Tt-0363); **D**, **D'**, presacral vertebra (ISER Tt-0362/1); **A**, **D'**, ventral views; **A'**, **B**, **D**, dorsal views; **C**, left lateral view. Scale bar: 2 mm.

The anteromedial portion is elevated and delimited by a transversely running crest; the less elevated posterolateral section is slightly bent laterally. The nearly vertically positioned anterolateral wall is pierced by a small foramen.

Presacral vertebrae

The vertebrae belonged to relatively small to medium sized individuals. In lateral view the centrum is slightly bent ventrally; the centrum length in four largest vertebrae ranges between 2.89-3.08 mm (mean = 2.98). The neural arch is flattened and provided with a relatively long neural spine of variable height. In its

anterior section the neural spine arises progressively in ISER Tt-0362/1 (Fig. 5D, D'), but more abruptly in few other specimens (e.g., ISER Tt-0362/2-4). The dorsal margin of the neural spine is never thickened. The transverse processes in all the specimens are damaged, but their remnants suggest that they were closely spaced. The subcentral lamina is moderately wide, connected to the lower rib bearer and pierced by several foramina of moderate or small size.

Humerus

The head of the humerus is rounded and connected to a well-developed ventral humeral crest

(Fig. 5C). The dorsal humeral crest is reduced to a spur-like process which is slightly inclined dorsally. The humeral shaft is relatively slender but strongly widened near its distal extremity and provided with a deep ventral cubital fossa of elongated triangular shape. The entepicondyle is slightly larger than the ectepicondyle.

Femur

Specimen ISER Tt-0364 represents a proximal femoral shaft. The head of the femur is only slightly curved dorsally, while the trochanter is rather short and acute-angled; part of the well-defined *crista trochanterica* is preserved on the anteroventral margin of the femur.

REMARKS

The above described specimens are comparable morphologically to Recent *T. marmoratus* (Latreille, 1800), even if the sizes of the presacral vertebrae are much smaller than those coming from adult *T. marmoratus* individuals (Haller-Probst & Schleich 1994). The neural spine of the presacral vertebrae is distinctly higher than in the members of the *T. cristatus* group (i.e. *T. cristatus* (Laurenti, 1768), *T. dobrogicus* (Kiritzescu, 1903) and *T. karelinii* (Strauch, 1870)).

Order ANURA Fischer von Waldheim, 1813 Family DISCOGLOSSIDAE Günther, 1858 Genus *Latonia* Meyer, 1843

Latonia gigantea (Lartet, 1851)

MATERIAL EXAMINED. — Two premaxillae (ISER Tt-0370/1 and 2), eight maxillae (ISER Tt-0371/1-8), five frontoparietals (ISER Tt-0372/1-5), one presacral vertebra (ISER Tt-0373), one coracoid (ISER Tt-0374), one humerus (ISER Tt-0375), two ilia (ISER Tt-0376/1 and 2).

DESCRIPTION

Premaxilla

The anterior surface of the premaxilla is smooth (Fig. 6B, B'). The alary process is relatively wide and convex dorsally. The palatine process is well developed; there are 18 tooth positions preserved on the premaxilla.

Frontoparietal

The best preserved specimen, representing a posterior half of a frontoparietal, belonged to a relatively large sized individual (Fig. 6A, A'). The dorsal surface is broad and covered by a dense secondary sculpture; the tubercules tend to form rows near the posterior and lateral margins. The ventral surface exhibits the posterior part of frontoparietal incrassation, which is roughly circular. The latter structure is bordered laterally by prominent bony laminae diverging posteriorly, which represents the pars contacta (Roček 1994).

Maxilla

Most specimens are fragmentary and represent different maxillary parts (Fig. 6C-F'). The processus zygomaticomaxillaris was presumably rather high as suggested by ISERTt-0371/1 (Fig. 6C, C'). The labial surface is covered by secondary sculpture formed by prominent tubercles which stay dispersed or usually constitute confluent rows. The extent of labial sculpture displays a wide ontogenetic variation. In smaller (i.e. younger) individuals the sculpture covers only the posterior maxillary region as seen in ISER Tt-0371/2 (Fig. 6F, F'), but in larger (i.e. older) specimens it usually reaches the level of the palatine process. The pterygoid process is prominent and projects posteromedially. The posterior depression is usually shallow and limited anteriorly by a transversal bony ridge at the level of the pterygoid process. The horizontal lamina is rather wide and convex lingually. The tooth row extends posteriorly to the level of the pterygoid process, but in some specimens (e.g. ISER Tt-0371/3) is just finished at that level (Fig. 6E).

Presacral vertebra

The only available specimen (ISER Tt-0373) is opisthocoelous and provided with well-developed interzygapophyseal ridges and a low neural ridge (Fig. 7A, A'). However, a distortion is observed: the neural ridge is shifted rightwards, while the right postzygapophysis is positioned more anteriorly with its long axis oriented more laterally than that of the left side.

Coracoid

In the only available fragmentary specimen, the shaft is slightly curved and provided with a low ridge on

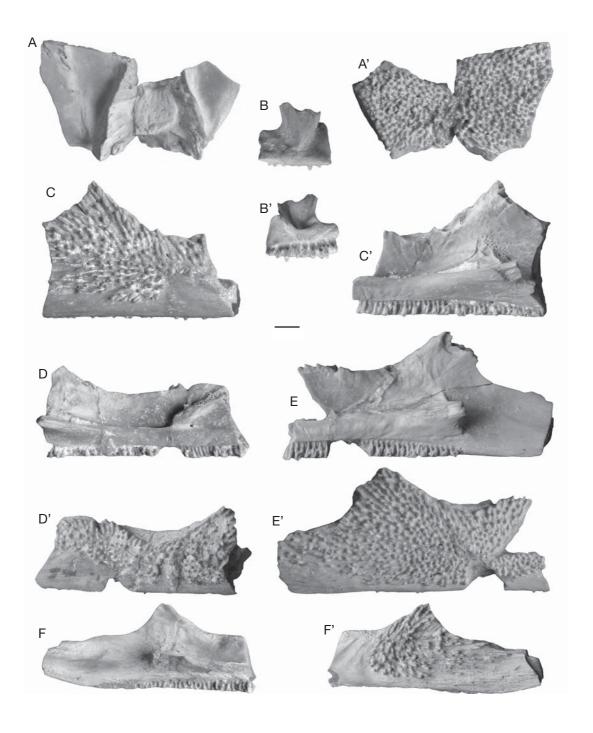


Fig. 6. — Latonia gigantea (Lartet, 1851): **A, A'**, frontoparietal (ISER Tt-0372/1); **B, B'**, premaxilla (ISER Tt-0370/1); **C, C'**, maxilla (ISER Tt-0371/1); **D, D'**, same (ISER Tt-0371/2); **E, E'**, same (ISER Tt-0371/3); **F, F'**, same (ISER Tt-0371/4); **A, B'**, ventral views; **A'**, **B**, dorsal views; **C**, **E'**, right lateral views; **C'**, **D, E, F**, medial views; **D'**, **F'**, left lateral views. Scale bar: 2 mm.

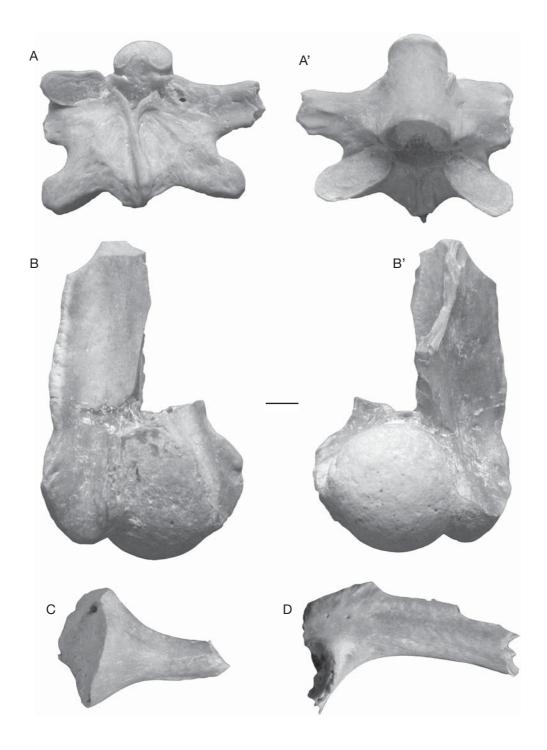


Fig. 7. — Latonia gigantea (Lartet, 1851): $\bf A$, $\bf A'$, presacral vertebra (ISER Tt-0373); $\bf B$, $\bf B'$, humerus (ISER Tt-0375); $\bf C$, coracoid (ISER Tt-0374); $\bf D$, ilium (ISER Tt-0376/1); $\bf A$, $\bf B$, dorsal views; $\bf A'$, $\bf B'$, $\bf C$, ventral views; $\bf D$, right lateral view. Scale bar: 2 mm.

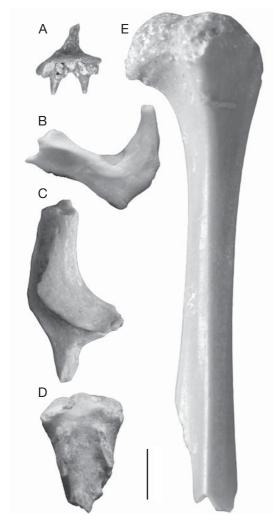


Fig. 8. — Palaeobatrachus cf. hiri: A, premaxilla (ISER Tt-0381), posterior view; B, nasal (ISER Tt-0380), ventral view; C, pterygoid (ISER Tt-0384), dorsal view; D, urostyle (ISER Tt-0385), dorsal view; E, tibiofibula (ISER Tt-0386), posteromedial view. Scale bar: 2 mm

its posterior surface (Fig. 7C). The *pars glenoidalis* is strongly dilated with a rounded shape.

Humerus

ISER Tt-0375 represents the fragmentary distal shaft of a humerus which belonged to an extremely large individual (Fig. 7B, B'). The distal humeral ball is rounded and is slightly shifted laterally; the medial epicondyle is rather prominent.

Ilium

ISER Tt-0376 lacks the supraacetabular region and most part of preacetabular region (Fig. 7D). A small preacetabular fossa is present. The tuber superior is well defined without a lateral projection. The iliac crest was rather high.

REMARKS

The material of *L. gigantea* recovered from Tauţ, mostly consisting of skull bones, belonged almost exclusively to specimens of relatively large size. These remains are easily distinguishable from L. ragei Hossini, 1993, another large discoglossid within the stratigraphic range of *L. gigantea* (Böhme & Ilg 2003), because despite its similarly large size lacks a secondary sculpture. In L. seyfriedi Meyer, 1843, known from the late middle Miocene (MN 8) of Oehningen (Germany) only (Roček 1994), the holotype and all the referred specimens are imbedded in the sediment by their dorsal side. Consequently it is not known if its skull bones bear or not a secondary sculpture. However, if the latter character would be present in *L. seyfriedi*, then *L. gigantea* will become a junior synonym of the former. Thus, only further investigation of the type material would answer this taxonomic problem.

Family PALAEOBATRACHIDAE Cope, 1865 Genus *Palaeobatrachus* Tschudi, 1839

Palaeobatrachus cf. hiri (Fig. 8)

MATERIAL EXAMINED. — One nasal (ISER Tt-0380), one premaxilla (ISER Tt-0381), one pterygoid (ISER Tt-0384), one urostyle (ISER Tt-0385), one clavicle (ISER Tt-0382), one tibiofibula (ISER Tt-0386).

DESCRIPTION

Nasal

The bone is flattened and sickle-shaped with deeply concave anterior margin (Fig. 8B). The anterior process is tapering, while the lateral process is somewhat enlarged. The dorsal surface is smooth, whereas on the ventral surface of the lateral process a low crest is observed delimiting posteriorly an oval depression.

Premaxilla

ISER Tt-0381 represents a left premaxilla of a small individual. In dorsal view, the bone has a roughly rhomboid shape. The premaxillary alary process is thin and has a vertical orientation with its distal section damaged (Fig. 8A). Fine longitudinal striations on the premaxillary anterolateral side suggest that in living animal it was overlapped by the maxilla. The palatine process is relatively wide and horizontal. The number of tooth positions is four; the two preserved teeth are conical and slightly curved posteriorly. At the base of each tooth position there is a deep hole delimited laterally by two osseous knobs.

Pterygoid

The specimen is rather fragmentary with the tips of all three pterygoidal rami damaged (Fig. 8C). The anterior ramus was presumably rather long and exhibits at its dorsomedial surface a moderately deep *sulcus pterygoideus*; the medial tubercle is weakly developed. Near the base of the medial and posterior ramus the bone is considerably widened.

Urostyle

In ISER Tt-0385, the neural lamina and the posterior portion of the shaft are broken off (Fig. 8D). The specimen displays a bicotylar condition with the ventral cotylar margins projecting anteriorly; vestige of a putatively small intercotylar process is also present.

Clavicle

ISER Tt-0382, belonging to a rather small individual, is the only specimen referable to this taxon. The bone is strongly curved and somewhat depressed dorsoventrally. A rather small *processus scapularis* is situated above the *facies glenoidalis claviculae*, the latter contributing to the formation of *cavitas glenoidalis* for the humeral head (Špinar 1972). The medial extremity is also missing but it exhibits posteriorly a rather shallow *sulcus pro cartilagine precoracoidalis*.

Tibiofibula

ISER Tt-0386 is a fragmentary tibiofibula, preserving the proximal part of the diaphysis with the epiphysis

completely ossified; it belonged to a rather old individual (Fig. 8E). The *condylus medialis* and the *condylus lateralis* are well differentiated (the former projects more dorsally), while the *crista ossis cruris* is rather prominent near the proximal extremity of the *condylus medialis*.

REMARKS

The available remains closely resemble those of *P. hiri* Venczel, 2004, known from the middle Miocene (MN 6) of Sámsonháza and from the late middle Miocene (MN 7) of Mátraszőlős, N Hungary. The assignment mainly rests on the morphology of nasal, the shape of which is reminiscent not only of *P. hiri*, but to some extent of P. laubei Bieber, 1881. The latter is known from the lower Oligocene (MP 21) of Suletice, Czech Republic (Špinar 1972), and contrary to P. hiri its frontoparietal (unknown at Taut) is devoid of parasagittal ridges. The specimens from both Mátraszőlős and Tauţ localities exhibit a similarly shaped notch on the ventral surface of the lateral ramus of the nasal (this feature is unknown in P. laubei). Actually, the latter structure could represent the articulation surface with the maxillary nasal process, which is rounded labially (see Venczel 2004: text-fig. 3H). However, the number of premaxillary tooth positions in the Taut specimen is lower (4) than in those of P. hiri (6-10), which might result from ontogenetic variation.

> Family PELOBATIDAE Bonaparte, 1850 Genus *Pelobates* Wagler, 1830

Pelobates sp. (Fig. 9)

MATERIAL EXAMINED. — Three maxillae (ISER Tt-0390/-1-3), one squamosal (ISER Tt-0391), one presacral vertebra (ISER Tt-0392), one scapula (ISER Tt-0393), one ilium (ISER Tt-0394).

DESCRIPTION

Maxilla

The bone is covered on its labial surface by a pit and ridge sculpture (Fig. 9A-B'). Most ridges tend to have a longitudinal orientation; they are less elevated and even absent near the orbital margin and

on the *pars dentalis*. In a smaller individual (ISER Tt-0390/3) the sculpture is less prominent.

Squamosal

The only specimen preserves most part of the *processus* posterolateralis, a minute fragment of the *lamella alaris* and the base of the *processus zygomaticus*. The *processus* posterolateralis is strongly curved laterally and displays a medial groove delimited by bony lamellae. The remnants of the *lamella alaris* and *processus zygomaticus* is covered dorsally by a pit and ridge sculpture.

Presacral vertebra

The only vertebra is procoelous with a relatively short centrum; the cotyle and condyle are slightly flattened dorsoventrally. In dorsal view the anterior margin of the neural arch is deeply indented, while the tip of the neural spine does not exceed the posterior margin of the postzygapophyses (Fig. 9C). The spinal nerve foramen is absent.

Ilium

The bone is fragmentary and most of the acetabular part is broken off (Fig. 9D). The iliac shaft is curved ventrally and slightly medially and the iliac crest is reduced to a ridge of very low height. A weak waisting is observed between the acetabulum and the iliac shaft; the remnant of the so-called spiral groove (Evans & Milner 1993) is also present.

REMARKS

The morphology and pattern of sculpture on the maxilla and squamosal is highly typical for the genus *Pelobates*. On the other hand, due to the fragmentary state of the available material a more precise assignment of the fossils was not possible.

Family BUFONIDAE Gray, 1825 Genus *Bufo* Laurenti, 1768

> Bufo cf. viridis (Fig. 10)

MATERIAL EXAMINED. — One prooticooccipital (ISER Tt-0400), one squamosal (ISER Tt-0401), one premaxilla (ISER Tt-0402), one maxilla (ISER Tt-0403), four prearticulars (ISER Tt-0404/1-4), one atlas (ISER

Tt-0405), two presacral vertebrae (ISER Tt-0406/1 and 2), four urostyles (ISER Tt-0407/1-4), three humeri (ISER Tt-0408/1-3), three ilia (ISER Tt-0409/1-3).

DESCRIPTION

Prooticooccipital

The fragment preserves a fused prootic and exoccipital which might have belonged to a rather large individual (Fig. 10A). The medial margin, roughly parallel to the supraorbital canal, exhibits a fracture line where the frontoparietal was fused. The *tectum supraorbitale* is rather small and has a smooth dorsal surface. The supraorbital canal is rather shallow and somewhat constricted in its posterior portion.

Squamosal

The *lamella alaris* of the squamosal is square-shaped, while the zygomatic process is rather thin and tapering distally (Fig. 10B). The distal part of the posterolateral process is broken off but indicates that this structure was rather thin.

Premaxilla

The bone is toothless with smooth and slightly convex *pars dentalis* (Fig. 10C). The alary process is relatively high and thin. In dorsal view, an arch-like crest runs from the anterodorsal part of the alary process to the lateral region of the *pars dentalis*. The *lamina horizontalis* is moderately wide.

Maxilla

The anterior part of the only specimen (ISER Tt-0403) is broken off. The posterior portion has a relatively low *pars facialis*, but it is provided with a relatively wide *lamina horizontalis* with its lingual margin directed slightly dorsally (Fig. 10D). The *pars dentalis* is toothless but exhibits a sharp *crista dentalis*.

Prearticular

The bone is faintly S-shaped and in all the specimens the anterior and posterior parts are broken off. The coronoid process is moderately developed and has a concave dorsal surface (Fig. 10E). The paracoronoid crest is relatively long and comparable in shape to that of recent *Bufo viridis* Laurenti, 1768 (see also Bailon & Hossini 1990). The Meckel's groove is rather shallow and faces laterally.

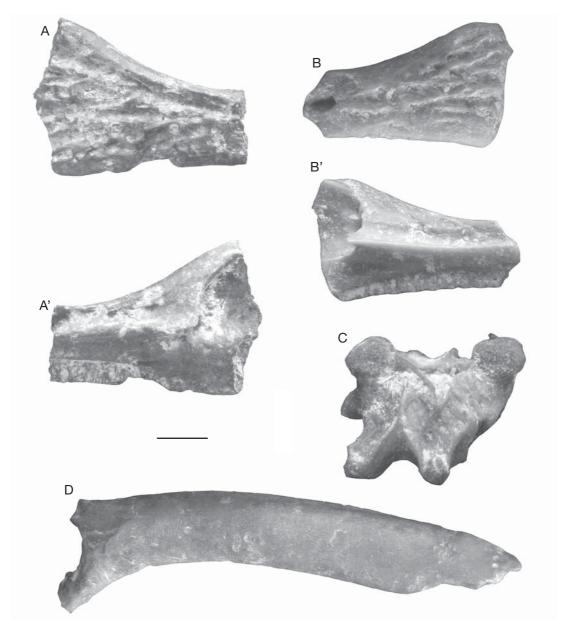


Fig. 9. — *Pelobates* sp.: **A, A'**, maxilla (ISER Tt-0390/1); **B, B'**, same (ISER Tt-0390/2); **C**, presacral vertebra (ISER Tt-0392); **D**, ilium (ISER Tt-0394); **A, D**, right lateral views; **A'**, **B'**, medial views; **B**, left lateral view; **C**, dorsal view. Scale bar: 2 mm.

Atlas

The neural arch in the only specimen is broken off (Fig. 10F). The centrum is short and dorsoventrally flattened, and the two cotyles are separated completely, corresponding to type II of Lynch (1971).

Presacral vertebrae

In both specimens the neural arch is broken off (Fig. 10G, H). The centrum is procoelous and dorsoventrally flattened. The transverse processes are broken off distally.



Fig. 10. — *Bufo* cf. *viridis*: **A**, prooticooccipital (ISER Tt-0400); **B**, squamosal (ISER Tt-0401); **C**, premaxilla (ISER Tt-0402); **D**, maxilla (ISER Tt-0403); **E**, prearticular (ISER Tt-0404/1); **F**, atlas (ISER Tt-0405); **G**, presacral vertebra (ISER Tt-0406/1); **H**, same (ISER Tt-0406/2); **I**, ilium (ISER Tt-0409/1); **J**, urostyle (ISER Tt-0407/1); **K**, humerus (ISER Tt-0408/1); **A**, **E**, **F**, **H**, **J**, dorsal views; **I**, left lateral view; **B**, **D**, medial views; **C**, posterior view; **G**, **K**, ventral views. Scale bar: 2 mm.

Urostyle

The distal portion of the only specimen is lacking. The proximal part is somewhat enlarged and provided with two well-separated and oval-shaped cotyles (Fig. 10J). The dorsal margin of the neural crest is slightly damaged but was presumably of

moderate height. The neural canal was moderately large.

Humerus

The single available specimen preserves only the distal part of the diaphysis (Fig. 10K). The distal

humeral ball is strongly widened and slightly shifted laterally; there is a shallow ventral cubital fossa. The lateral crest is reduced to a keel.

Ilium

Both the supraacetabular and preacetabular regions are moderately extended (Fig. 10I). The tuber superior is compressed mediolaterally and divided in two or three tubercles situated above the anterior margin of the acetabular rim. The preacetabular fossa is well defined.

REMARKS

The earliest bufonid in the Old World is known from the late Palaeocene (MP 6) of Cernay, France (Rage 2003). Afterward they apparently disappeared from Europe but reappeared again in the early Miocene (Rage & Roček 2003) and have become more frequent since the middle Miocene onwards (Böhme & Ilg 2003). The earliest fossil record of B. viridis is known from the late early Miocene (MN 4) of Spain (Sanchiz 1998b), France (Bailon & Hossini 1990) and Germany (Böhme & Ilg 2003). Bufo gessneri (Tschudi, 1838) and *B. priscus* Špinar, Klembara & Meszaros, 1993 are other representatives of the socalled narrow-headed toads, known from the middle Miocene of Central Europe (Spinar et al. 1993; Sanchiz 1998b). According to Rage & Roček (2003), the latter forms are closely similar to *B. viridis* and therefore synonymy cannot be excluded.

> Family HYLIDAE Gray, 1825 Genus *Hyla* Laurenti, 1768

> > *Hyla* cf. *arborea* (Fig. 11A-C)

MATERIAL EXAMINED. — One prearticular (ISER Tt-0410), five ilia (ISER Tt-0411/1-5).

DESCRIPTION

Prearticular

The bone is faintly S-shaped with both the anterior and posterior margins broken off. The coronoid process is elongated, relatively narrow and provided with small tubercles on its medial margin (Fig. 11C).

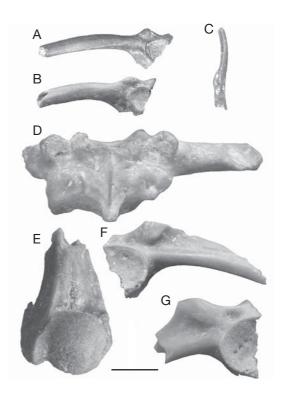


Fig. 11. — **A-C**, *Hyla* cf. *arborea*; **A**, ilium (ISER Tt-0411/1); **B**, same (ISER Tt-0411/2); **C**, prearticular (ISER Tt-0410); **D-G**, *Pelophylax* sp.; **D**, presacral vertebra (ISER Tt-0421/1); **E**, humerus (ISER Tt-0422/1); **F**, ilium (ISER Tt-0423/1); **G**, same (ISER Tt-0423/2); **A**, **B**, **G**, left lateral views; **C**, **D**, dorsal views; **E**, ventral view; **F**, right lateral view. Scale bar: 2 mm.

Ilium

The supraacetabular region of the ilium is distinctly smaller than the preacetabular region (Fig. 11A, B). The tuber superior, of roughly oval shape, is prominent and projects laterally. The iliac shaft is curved ventrally and strongly compressed mediolaterally; the iliac crest is reduced to a faint ridge.

REMARKS

The assignment of the above remains to *Hyla* cf. *arborea* is based on their close resemblance with those of Recent species. On the other hand, *H. arborea* (Linnaeus, 1758) may be easily distinguished from *H. meridionalis* Boettger, 1874 by the morphology of the ilium, in the latter the iliac *tuber superius* having a rounded shape (Holman 1992). Moreover, the spread of *H. meridionalis* in southwestern

Europe may have happened rather recently (Recuero et al. 2007).

The oldest fossils referable with some doubts to Hylidae are known from the Maastrichtian of India (Prasad & Rage 1995, 2004), while the first record of the genus *Hyla* in Europe is from the late early Miocene (MN 4) of Austria (Sanchiz 1998a). Several fossils from the late middle Miocene (MN 7) of Mátraszőlős, Hungary were already assigned to *H. cf. arborea* by Venczel (2004).

Family RANIDAE Rafinesque-Schmaltz, 1814 Genus *Pelophylax* Fitzinger, 1843

Pelophylax sp. (Fig. 11D-G)

MATERIAL EXAMINED. — Two premaxillae (ISER Tt-0420/1 and 2), one presacral vertebra (ISER Tt-0421/1), one sacral vertebra (ISER Tt-0421/2), three humeri (ISER Tt-0422/1-3), seven ilia (ISER Tt-0423/1-7).

DESCRIPTION

Premaxilla

The anterior surface is smooth and flat with a well-defined lateral crest. The tip of the alary process in both specimens is broken off. The *lamina horizontalis* is well developed, but the *pars palatina* is broken off. The number of preserved tooth positions is 11 and 12 respectively.

Presacral vertebra

The centrum is procoelous and relatively short with the condyle flattened dorsoventrally. The neural arch is of non-imbricate type and provided with a low but distinct neural crest. The only preserved transverse process is straight and tends to widen distally (Fig. 11D). Based on the latter character it is assumed that the specimen represents the third presacral vertebra.

Sacral vertebra

The centrum is procoelous and displays two posterior condyles for the articulation with the urostyle. The neural arch is extremely short and provided with a low keel extending laterally to the dorsal surfaces of the transverse processes. Distally the

latter structures are broken off but were presumably rather slender.

Humerus

Only distal parts of humeri are preserved. The distal humeral ball is round and there is a well-developed ventral cubital fossa (Fig. 11E). In ISER Tt-0422/1 the *epicondylus medialis* as well as the *crista medialis* is distinctly larger than in ISER Tt-0422/2. The latter two attributes may be related to sexual dimorphism.

Ilium

Based on the morphology of ISER Tt-0423/1, the supraacetabular and the preacetabular regions are roughly of equal height. The acetabulum is nearly circular with the acetabular rim projecting above the preacetabular region and the preacetabular fossa is absent or extremely shallow (Fig. 11F, G). The tuber superior is high and positioned anterodorsally to the acetabulum. In ISER Tt-0423/2 the tuber superior is damaged but its ventral margin is produced in a distinct overhang delimiting dorsally the *fossula tuberis superioris*. The iliac crest is thin and it was presumably high, but in all the available specimens its dorsal margin is lacking.

REMARKS

All the above remains show a close morphological resemblance with those of the genus *Pelophylax* (Frost *et al.* 2006). The variation observed in the shape and thickness of the ventral margin of the tuber superior is also reminiscent of specimens described from the late middle Miocene (MN 7) of Mátraszőlős, Hungary under the name *Rana esculenta* synklepton (Venczel 2004).

Class REPTILIA McCartney, 1802 Order SQUAMATA Merrem, 1820 Suborder LACERTILIA Owen, 1842 Family GEKKONIDAE Gray, 1825

Geckonidae indet. (Fig. 12A)

MATERIAL EXAMINED. — Two dentaries (ISER Tt-0430/1 and 2).

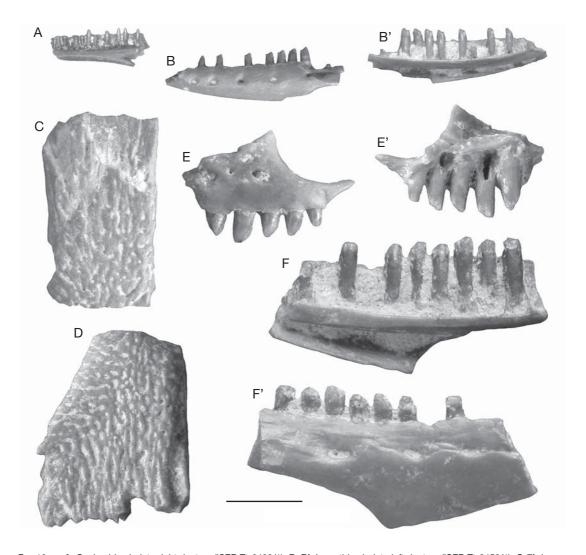


Fig. 12. — **A**, Geckonidae indet., right dentary (ISER Tt-0430/1); **B**, **B**', Lacertidae indet., left dentary (ISER Tt-0450/1); **C-F**', *Lacerta* sp.; **C**, frontal (ISER Tt-0441/1), **D**, same (ISER Tt-0441/2); **E**, **E**', right maxilla (ISER Tt-0442/1); **F**, **F**', right dentary (ISER Tt-0443/1); **A**, **B**', **E**', **F**, medial views; **B**, left lateral view; **C**, **D**, dorsal views; **E**, **F**', right lateral views. Scale bar: 2 mm.

DESCRIPTION

The two available specimens represent different sized individuals. The Meckel's groove is completely closed and there is a relatively wide subdental shelf. The insertion of teeth is of pleurodont type and less than half of the tooth projects above the dental parapet. The teeth are rather small and provided with unicuspid tooth crown. The number of tooth positions in the available dentaries is 13 and 16 respectively.

Family LACERTIDAE Bonaparte, 1831 Genus *Lacerta* Linnaeus, 1758

Lacerta sp. (Fig. 12C-F')

MATERIAL EXAMINED. — One parietal (ISER Tt-0440), two frontals (ISER Tt-0441/1 and 2), seven maxillae (ISER Tt-0442/1-7), four dentaries (ISER Tt-0443/1-4).

DESCRIPTION

Parietal

ISER Tt-0440 preserves the posterior portion of parietal only. The dorsal surface is sculptured as small pits, while in ventral view there is a relatively long *facies trapezoideus* bordered by the medial laminae of the exoccipital processes.

Frontal

The sculpture on the dorsal surface is formed by small pits and low ridges which trend anteroposteriorly; near the lateral margin the ridges run laterally or anterolaterally (Fig. 12C, D).

Maxilla

ISER Tt-0442/1 preserves the anterior part of a maxillary fragment with the *crista dentalis* and lower part of vertical wall of maxilla (Fig. 12E, E'). In lateral view, two superior alveolar foramina and two additional openings are present and there is an extremely small surface displaying a labial sculpture; five tooth positions are preserved. The teeth are pleurodont and the tooth crowns have bicuspid tips. The main cusps are positioned distally while the mesial cusps are of much smaller size. The striations of the tooth crown are restricted to the lingual side of the main cusps.

Dentary

The meckelian groove is widely open throughout the dentary length. The symphysis in ISER Tt-0443/1 extends to the fourth mandibular length. The dentition, except the first three mandibular teeth, is with bicuspid tips. The subdental shelf in the first mandibular portion is reduced (up to the level of the 12th-13th tooth position) with the lingual surface of the horizontal lamina flattened (Fig. 12F, F'). From the level of the 13th-14th tooth position the subdental shelf widens moderately and the horizontal lamina displays a convex lingual margin. In lateral view, the labial surface of the fragmentary dentaries is strongly convex and smooth, displaying a row of three or four foramina pro rami nervorum alveolarium inferiorum. An elongated and only partially preserved shallow groove, situated parallel to the posterior part of the dental parapet, marks the attachment with the coronoid. The tooth shaft is more or less cylindrical

and projecting about one third above the tooth parapet. The tooth crown is bicuspid with morphology similar to that observed in maxillae.

Remarks

The available specimens belonged to large sized individuals comparable to *L. viridis* (Laurenti, 1768)-*L. trilineata* Bedriaga, 1886. Unfortunately these remains are unsuitable for a more precise assignment.

Lacertidae indet. (Fig. 12B, B')

MATERIAL EXAMINED. — Six dentaries (ISER Tt-0450/-1-6).

DESCRIPTION

All the available dentaries belonged to relatively small individuals. The bone is slender with the meckelian groove opened throughout the dentary length and moderately enlarged posteriorly. The horizontal lamina is relatively thin and it tapers posteriorly; the subdental shelf is of moderate width. The labial surface is smooth and slightly convex. In ISER Tt-0450/1 a number of six foramina pro rami nervorum alveolarium inferiorum are preserved. From the level of the posteriormost foramen the imprint for the attachment of the coronoid is observed. The anterior teeth are unicuspid, while the remaining ones are distinctly bicuspid. The shape of the tooth shaft is more or less cylindrical and more than one third of the tooth height projects above the dental parapet.

REMARKS

The size and morphology of the above dentaries approaches those seen in smaller lacertids, including the extinct genera *Miolacerta* Roček, 1984, known from the late early Miocene (MN 4) of Dolnice, Czech Republic (Roček 1984) and *Edlartetia* Augé & Rage, 2000, described from the middle Miocene (MN 6) of Sansan, France (Augé & Rage 2000). However, the dentary in *Miolacerta* is devoid of imprint for the coronoid attachment, and typically bears tricuspid teeth, while in *Edlartetia* the teeth are narrowed below the apex (Rage & Bailon 2005).

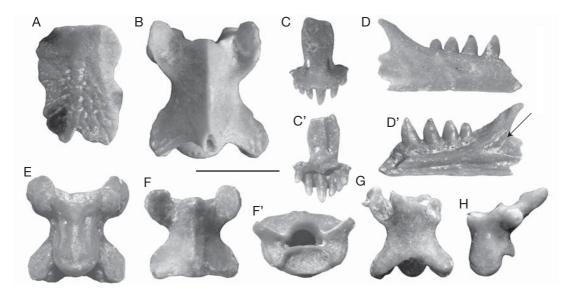


Fig. 13. — **A**, **B**, *Ophisaurus* sp.; **A**, osteoderm (ISER Tt-0461/1); **B**, trunk vertebra (ISER Tt-0460/1); **C**-**F**', *Blanus* cf. *gracilis*; **C**, **C**', premaxilla (ISER Tt-0470); **D**, **D**', dentary (ISER Tt-0471/1), the arrow indicates the surangular fragment; **E**, vertebra (ISER Tt-0472/1); **F**, **F**', same (ISER Tt-0472/2); **G**, Scolecophidia indet., trunk vertebra (ISER Tt-0480/1); **H**, same (ISER Tt-0480/2); **A-C**, **F**, **G**, dorsal views; **C**', **E**, **H**, ventral views; **D**, right lateral view; **D**', medial view; **F**', anterior view. Scale bar: 2 mm.

Family ANGUIDAE Gray, 1825 Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp. (Fig. 13A, B)

MATERIAL EXAMINED. — Ten vertebrae (ISER Tt-0460/-1-10), 14 osteoderms (ISER Tt-0461/1-14).

DESCRIPTION

Vertebrae

The vertebrae belonged to individuals of various sizes. The ventral surface of the centrum is slightly convex while the subcentral margins are slightly concave. Shallow anteroposterior grooves pass on the subcentral foramina, delimiting a median more elevated subcentral area. The interzygapophyseal ridges are better developed in the vicinity of the zygapophyses featuring an X-shape to the vertebrae (Fig. 13B). The haemal processes in all caudal vertebrae are broken off.

Osteoderms

The osteoderms are small, relatively thin and of rectangular shape. The outer surface displays a

distinct medial ridge and a series of bifurcating and confluent tubercles are developed on the lateral sides of the osteoderm (Fig. 13A). A specimen (ISER Tt-0461/2) displays a uniting line which indicates that it was constituted from two consecutive osteoderms.

REMARKS

The morphology and size of trunk vertebrae approaches the condition seen in cf. Ophisaurus morphotype I, described from the late early Miocene (MN 4) of Dolnice, Czech Republic (Roček 1984) and that of Ophisaurus sp., described from the late Miocene (MN 13) of Polgárdi, Hungary (Venczel 2006: fig. 2C, D). Furthermore, some resemblance with the trunk vertebrae of Anguis Linnaeus, 1758 may be evidenced too. However, the latter never displays longitudinal grooves delimiting a medial keel. In the genus Pseudopus Merrem, 1820 the centrum is more flattened and widened anteriorly (Rage & Bailon 2005) and the osteoderms are more thickened in the middle. The osteoderms in Anguis have an oval or irregular shape and are devoid of bony keel on their sculptured surface.

Family BLANIDAE Kearney, 2003 Genus *Blanus* Wagler, 1830

Blanus cf. gracilis (Fig. 13C-F')

MATERIAL EXAMINED. — One premaxilla (ISER Tt-0470), four fragmentary dentaries (ISER Tt-0471/1-4), 60 vertebrae (ISER Tt-0472/1-60).

DESCRIPTION

Premaxilla

The only specimen belonged to a small sized individual (Fig. 13C, C'). The anterodorsal surface of the premaxilla is strongly convex and the nasal process is rather high (its distal portion is broken off) with a flat surface. The base of the nasal process displays a weak waisting and laterally it is pierced by two large foramina of oval shape. The inner surface of the nasal process is provided with a prominent medial keel tapering distally. In each side of the keel, near the base of the nasal process, there is a dorsal large foramen and a ventral smaller one. However, on the right side the bony wall between the foramina is not complete. It is worth to mention that a connection exists between the outer and inner foramina. The maxillary process is broken off on both sides, while the lamina horizontalis is rather thin. The dentition is distinctly proterodont with a rather large median tooth and successively decreasing posterolateral teeth. The number of tooth positions in the premaxilla is seven. The teeth are cylindrical and have small circular resorption pits at their base. The tooth crown is monocuspid and bears faintly developed lingual and labial crests which show an anterolingual and posterolabial orientation respectively.

Dentary

The dentaries belonged to individuals of different size. In ISER Tt-0471/1 and 2, which preserve the anterior part of the tooth row, the Meckel's groove opens at the level of the first tooth position, and widens posterior to the fifth tooth position. The symphyseal process, situated at the level of the second tooth position, is relatively short and flattened dorsoventrally. The *crista splenialis* is rounded lingually and delimits a weakly defined subdental shelf. The ventral margin of the posterior third of

the crista splenialis bears an elongated imprint left by the splenial. The coronoid process is relatively large and slanting posterodorsally. ISER Tt-0471/1 demonstrates that the dorsoposterior limit of the coronoid process is higher than the largest mandibular tooth (Fig. 13D, D'). The surangular process is also well defined but its posterior terminus in all the specimens is broken off. ISER Tt-0471/1 preserves a small remnant of the anterior part of surangular in the original position. The dentition is heterodont with eight teeth in a complete dentary. The first and second teeth are broken off on all the dentaries, but they were presumably smaller than the third tooth. The latter is distinctly larger than the fourth tooth, while beginning from the fifth tooth their size decreases posteriorly. The teeth are conical with smooth apex and they are slightly recurved; some of them preserve a faintly developed anteroposterior crest.

On the labial side of ISER Tt-0471/2 three alveolar foramina are observed. The first foramen opens between the levels of the first and second tooth positions, the second one opens between the third and fourth teeth, while the third one opens at the level of the seventh tooth position.

Vertebrae

All the available specimens belonged to small individuals, the centrum length in 12 measured trunk vertebrae ranging between 1.7 and 2.03 mm. The vertebrae are flattened dorsoventrally. The ventral surface of the centrum is flat or slightly convex and provided with two subcentral foramina. In few specimens, which probably belonged to the anterior region of the vertebral column, a faintly defined subcentral keel is observed (Fig. 13E), while another specimen preserves a well-developed and posteriorly hooked hypapophysis. The lateral margins of the centrum are parallel but the centrum slightly widens near the condyle. The condyle and cotyle are flattened dorsoventrally. The neural ridge is more or less present in all the specimens, finishing in a somewhat widened posterior tuberosity (Fig. 13F, F'). In several larger vertebrae there is a tuberosity situated near the anterior margin of the neural arch, while another one is placed near the posterior margin of the neural arch. The zygosphene-

zygantrum complex is lacking and the neural arch exhibits a convex or pointed anterior margin. The synapophyses, situated below the prezygapophyses, are of hemispherical shape. The pre- and postzygapophyses are of oval shape and the prezygapophyseal processes are lacking.

REMARKS

The morphology of the dentary differs from that of Palaeoblanus Schleich, 1988, the latter being provided with a distinctly larger first tooth (Schleich 1988; Böhme 1999), but it closely resembles that of the extant genus Blanus. Another fossil blanid species was described under the name Omoiotyphlops gracilis Roček, 1984 from the late early Miocene (MN 4) of Dolnice, Czech Republik (Roček 1984). The diagnosis given and the morphology of the figured specimens concord with that of the genus Blanus. In fact, the small lingual process near the top of the coronoid process, which has been used by Roček (1984) to diagnose O. gracilis, is variably present in Recent Blanus also. From the same locality, a premaxilla (DP FNSP 317) described by Roček (1984) and assigned to Squamata, family indet. II (see Roček 1984: 61, text-fig. 5) quite probably belonged to Blanus (= Omoiotyphlops) gracilis too.

If the above assignment is correct, then *B. gracilis* appears as the most widely distributed European blanid. After Böhme (2002) *Palaeoblanus* and *Blanus* were contemporaneous at least during MN 3-MN 5, or even over a much longer period (MP 30-MN 5).

Suborder SERPENTES Linnaeus, 1758 Infraorder SCOLECOPHIDIA Duméril & Bibron, 1844

Scolecophidia indet. (Fig. 13G, H)

MATERIAL EXAMINED. — Five fragmentary trunk vertebrae (ISER Tt-0480/1-5).

DESCRIPTION

All the vertebrae are of small size; the centrum length of the largest one is 1.64 mm. The centrum lacks

a haemal keel and it is provided with one or two subcentral foramina (Fig. 13H). The neural arch is depressed, devoid of neural spine (Fig. 13G); the synapophyses are undivided and have a hemispherical shape. The zygosphenal roof in all the specimens is damaged, but some of them preserve small lateral lobes. The prezygapophyses are elongated anteroposteriorly. The prezygapophyseal processes, preserved in two specimens only, equal in length the diameter of the prezygapophyseal articular facets. The paracotylar foramina are lacking in all the vertebrae. The cotyle and the condyle are depressed dorsoventrally.

REMARKS

All the above described morphological features are shared by members of Typhlopidae Merrem, 1820, Leptotyphlopidae Stejneger, 1892 and Anomalepididae Taylor, 1939, consequently the available material cannot be assigned within scolecophidians.

Infraorder ALETHINOPHIDIA Nopcsa, 1923 Family COLUBRIDAE Oppel, 1811 Genus *Coronella* Laurenti, 1768

> Coronella miocaenica Venczel, 1998 (Fig. 14)

MATERIAL EXAMINED. — Four fragmentary trunk vertebrae (ISER Tt-0490/1-4).

DESCRIPTION

All the vertebrae are of minute size. The centrum length of the largest specimen is 3.45 mm, while the centrum width is 2.38 mm (centrum length/centrum width ratio = 1.45). The centrum is elongated; the neural arch is moderately vaulted and provided with a longer than high neural spine. The dorsal margin of the latter structure is not thickened and both the anterior and posterior margins are overhanging. The posterior margin of the neural arch lacks epizygapophyseal spines. The zygosphene lacks a medial lobe, or it is provided with a rather indistinct medial and two small lateral lobes. The anterior portion of the haemal keel is rather prominent and thin, while the posterior part diminishes in

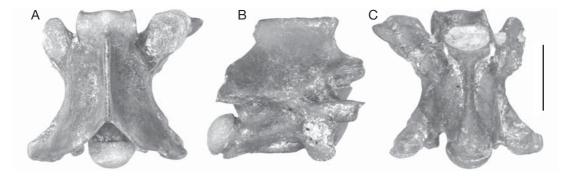


Fig. 14. — Coronella miocaenica Venczel 1998, presacral vertebra (ISER Tt-0490/1): **A**, dorsal view; **B**, right lateral view; **C**, ventral view. Scale bar: 2 mm.

height and becomes spatulate-shaped. Tiny paired tubercles are present on the subcotylar lips. The subcentral ridges are weakly defined. The prezygapophyseal articular facets are of oval shape, while the prezygapophyseal processes are extremely short and with obtuse extremities. The paradiapophyses are evidently differentiated into diapophyses and parapophyses. The latter structures are noticeably longer than the diapophyses.

REMARKS

The vertebral morphology of the above fossils closely resembles that of *Coronella miocaenica*, known from the late Miocene (MN 13) of Polgárdi 4, Hungary (see Venczel 1998: fig. 6a-e). The centrum length/centrum width ratio approaches also the intraspecific variation of this species (1.02-1.42 in specimens coming from Polgárdi 4U). The neural arch in the extant *C. austriaca* Laurenti, 1768 is more flattened and provided with a somewhat lower neural spine.

The genus *Coronella* is considered closely related to Old World rat snakes (Dowling & Duellman 1978; Utiger *et al.* 2002; Nagy *et al.* 2004). There is some evidences that the ancestry of the above groups could have differentiated in tropical Asia during late Eocene and afterward dispersed among others to the western Palearctic during Oligocene times (Burbrink & Lawson 2007). As a result the genus *Coronella* could have reached the European continent at an earlier date than considered before (Venczel 1998). Unfortunately, remains of *Coronella*, except those from a number of Quaternary localities

(Szyndlar 1991), were rarely reported from Europe. Nevertheless, small sized colubrids, reminiscent of *Coronella*, were described from a number of European Tertiary localities but referred to other genera (e.g., *Texasophis* Holman, 1977 and *Hispanophis* Szyndlar, 1985) (Rage & Holman 1984; Szyndlar 1985, 1987, 1991, 1994; Gál *et al.* 1999; Ivanov 2000). Conceivably, a detailed revision of all these remains should indicate (at least in some cases) a putatively early presence of the genus *Coronella* in the European Tertiary.

Genus Hierophis Fitzinger, 1843

Hierophis cf. *hungaricus* (Fig. 15)

MATERIAL EXAMINED. — One fragmentary compound bone (ISER Tt-0500), 35 vertebrae (ISER Tt-0501/1-35).

DESCRIPTION

Compound bone (surangular + prearticular + articular)

The only specimen preserves a small fragment from the posterior half of the bone (Fig. 15A). The medial flange projects dorsally and apparently had a considerable height. The mandibular fossa is relatively wide because the dorsal margin of the lateral flange is bent laterally; the latter has a deeply concave lateral surface; the supraangular crest is well developed.

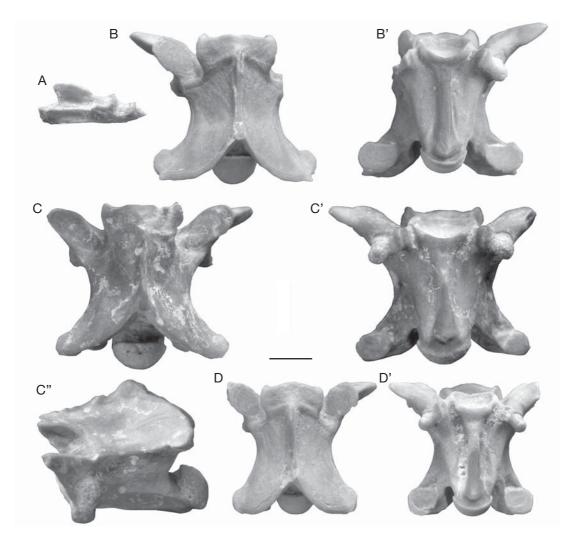


Fig. 15. — Hierophis cf. hungaricus: A, left compound bone (ISER Tt-0500); B, B', trunk vertebra (ISER Tt-0501/1); C-C", same (ISER Tt-0501/2); D, D', same (ISER Tt-0501/3); A, C", left lateral; B, C, D, dorsal views; B', C', D', ventral views. Scale bar: 2 mm.

Vertebrae

The available vertebrae belonged to medium-sized individuals. The neural arch is moderately vaulted and in few vertebrae the posterolateral margins of the neural lamina possess a small epizygapophyseal spine (Fig. 15B, B'). In most vertebrae the neural spine is broken off, but its remnants in a few specimens indicate that it was longer than high and provided with an anterior overhang. The zygosphene was slightly crenate with an indistinct median lobe. The prezygapophyseal articular facets are of elongated

or oval shape; the prezygapophyseal processes are pointed distally and shorter than the diameter of the prezygapophyseal articular facets (Fig. 15B-D'). The paradiapophyses are clearly differentiated into diapophyseal and parapophyseal portions which are roughly of equal length. The centrum of the trunk vertebrae is moderately elongated. In 10 measured vertebrae the centrum length ranges between 4.05 and 5.9 mm, while the centrum width is between 2.84 and 4.63 mm. The centrum length/centrum width ratio range is between 1.23-1.45

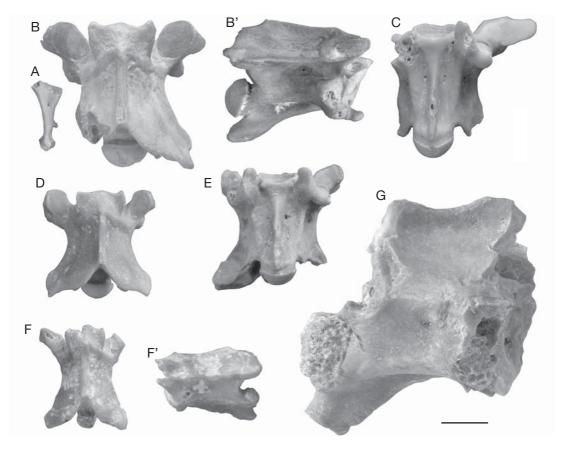


Fig. 16. — **A-F'**, *Natrix* cf. *rudabanyaensis*; **A**, quadrate (ISER Tt-0502); **B**, **B'**, presacral vertebra (ISER Tt-0503/1); **C**, same (ISER Tt-0503/2); **D**, same (ISER Tt-0503/3); **E**, same (ISER Tt-0503/4); **F**, **F'**, posterior presacral vertebra (ISER Tt-0503/5); **G**, *Macrovipera* sp., presacral vertebra (ISER Tt-0504); **A**, **B**, **D**, **F**, dorsal views; **B'**, **G**, right lateral views; **C**, **E**, ventral views; **F'**, left lateral view. Scale bar: 2 mm.

(mean = 1.33). The subcentral ridges are less evident in the middle trunk vertebrae, but are well-defined in those coming from the posterior trunk region. In the mid-trunk vertebrae the haemal keel is flattened and slightly broadened posteriorly but usually rounded and more prominent in the posterior trunk vertebrae (Fig. 15D, D').

REMARKS

The morphology of the fragmentary compound bone is reminiscent of that of *Hierophis* (= *Coluber*) hungaricus (Bolkay, 1913) (Venczel 1994, 1998) and also of Recent *Hierophis gemonensis* (Laurenti, 1768) and *H. viridiflavus* (Lacépède, 1789) (pers. obs.). Variation observed in *H. hungaricus*

(Venczel 1994, 1998) (e.g., height of coronoid process, shape of lateral flange and width of mandibular fossa) seems to be dependent on ontogenetic age (Venczel 1998). The morphology of the trunk vertebrae approaches that observed in *H. hungaricus* from the late Miocene (MN 9) of Rudabánya (Szyndlar 2005) and from the late Miocene (MN 13) of Polgárdi 4 and 5 localities (Venczel 1994, 1998). However, in the Tauţ specimens the centrum length/centrum width ratio (CL/CW) is somewhat lower than in those coming from Rudabánya (CL/CW = 1.3-1.5, mean = 1.4), Polgárdi 4 (CL/CW = 1.23-1.49, mean = 1.36), or Polgárdi 5 (CL/CW = 1.21-1.61, mean = 1.37).

Subfamily NATRICINAE Bonaparte, 1838 Genus *Natrix* Laurenti, 1768

Natrix cf. rudabanyaensis (Fig. 16A-F)

MATERIAL EXAMINED. — One quadrate (ISER Tt-0502), 30 presacral vertebrae (ISER Tt-0503/1-30).

DESCRIPTION

Quadrate

ISER Tt-0502 is slightly damaged at its anterodorsal margin; it might have belonged to a rather small individual (Fig. 16A). In lateral view, the bone widens distally while the quadrate crest is better defined above the *trochlea quadrati*. Dorsally the height of the crest is abruptly reduced merging into the anterior margin of the bone. In posterolateral view the bone is straight, somewhat thinner in the middle portion.

Vertebrae

The vertebral centrum is elongated and provided with a sigmoid hypapophysis. The distal portion of the hypapophysis strongly projects beyond the condyle and displays a rounded tip (Fig. 16B, B'). The subcentral ridge is rather prominent posteriorly to parapophyses (Fig. 16C, E). The neural arch is moderately depressed, provided with large and posterolaterally projecting epizygapohyseal spines (Fig. 16B, D). In most specimens the neural spine is strongly damaged. However, small remnants of this structure indicate that the neural spine was longer than high. The anterior margin of the zygosphene is crenate with three distinct lobes. The prezygapophyseal articular facets are of oval shape, while the prezygapophyseal processes are moderately long, flattened dorsoventrally and obtuse distally. The paradiapophyses are well differentiated into diapophyseal and parapophyseal portions. The parapophyses are provided with a rather long parapophyseal process which has usually an obtuse anterior margin. In 12 measured presacral vertebrae the centrum length ranges between 2.84 and 4.86 mm, while the centrum width is between 1.72 and 3.3 mm. The centrum length/centrum width ratio range is 1.34-1.65 (mean = 1.5). The vertebrae from the posterior presacral region are more depressed dorsoventrally and provided with a low and long neural spine (Fig. 16F).

REMARKS

The fossils from Tauţ closely resemble Natrix rudabanyaensis Szyndlar, 2005 by their relatively small size, moderately developed subcentral ridges, rounded distal hypapophyseal tip and similar centrum length/centrum width ratio (Szyndlar 2005). In N. natrix (Linnaeus, 1758) and N. merkurensis Ivanov, 2002, in both of which the hypapophysis has a rounded tip, the centrum length/centrum width ratio is distinctly higher. In several other members of the genus the hypapophysis is provided with a pointed distal tip (e.g., N. longivertebrata Szyndlar, 1984, N. maura (Linnaeus, 1758), N. sansaniensis (Lartet, 1851), N. tessellata (Laurenti, 1768)), and with variable centrum length/centrum width ratio (Szyndlar 2005). In Neonatrix natricoides Augé & Rage, 2000, known from the middle Miocene (MN 6) of Sansan (sometimes regarded as a member of the genus Natrix [Szyndlar 2005]), the prezygapophyseal processes and the hypapophysis are extremely short, while the neural lamina usually lacks an epizygapophyseal spine (Augé & Rage 2000).

> Family VIPERIDAE Gray, 1825 Genus *Macrovipera* Reuss, 1927

Macrovipera sp. (Fig. 16G)

MATERIAL EXAMINED. — One presacral vertebra (ISER Tt-0504).

DESCRIPTION

The only specimen belonged to a rather large but strongly damaged individual, in which the anterior and posterior portions of the neural arch, the paradiapophyses and the distal part of the hypapophysis are broken off. The centrum length is 8.18 mm, while the centrum width is 6.64 mm (centrum length/centrum width ratio = 1.23). The neural arch is depressed and somewhat tilted posteriorly;

 $\label{eq:Table 1.} \begin{tabular}{ll} TABLE 1. & --- Ecophysiologic index of selected fossil amphibian and reptile taxa from Taut (Romania). \end{tabular}$

Fossil taxa	Ecophysiologic index
Chelotriton paradoxus	0.3918
Lissotriton sp.	0.3918
Triturus cf. marmoratus	0.513
Carpathotriton sp.	1
Latonia gigantea	0.3918
Palaeobatrachus hiri	1
Pelobates sp.	0.0917
Bufo cf. viridis	0
Hyla arborea	0.3918
Pelophylax sp.	0.513
Geckonidae indet.	0.0917
Lacerta sp.	0
Lacertidae indet.	0
Ophisaurus sp.	0
Blanus cf. gracilis	0.0917
Scolecophidia indet.	0.0917
Ecophysiologic index	0.31

the remnants of the neural spine indicate that it was rather long. The remnant of the hypapophysis is directed posteroventrally and presumably was rather long.

REMARKS

The large absolute size of the vertebra and its relatively low centrum length/centrum width ratio is typical for the members of so called "Oriental vipers" (Szyndlar & Rage 2002; Szyndlar 2005). However, for this group of snakes these authors retained the generic name *Vipera* Laurenti, 1768. The oldest "Oriental vipers" appeared in Europe in the late early Miocene (MN 4) and they were present mainly in the southern part of the continent up to late Pliocene times (Szyndlar & Rage 2002).

CONCLUSIONS

The herpetofaunal assemblage described hereinabove from Tauţ is actually one of the most comprehensive fossil records from the Neogene of Romania. At the same time it represents one of the most diversified herpetofauna of late middle Miocene (MN 7+8) age ever described from the territory of Central and Eastern Europe. The composition of the fossil

assemblage, including also other vertebrates as well as helicid and planorbid gastropods, is suggestive of a marshy-lacustrine taphonomic context. However, the peculiarity of the Tauţ fauna, if compared to those from other late middle Miocene localities from Romania (e.g., Subpiatră 2/2 and Tāṣad), is its abundance in water preferring amphibian groups (especially salamandrids), the presence of amphisbaenians, as well as absence of crocodiles.

One of the most diversified groups in the assemblage is the Salamandridae. Except *Carpathotriton*, whose apparent distribution was restricted to the Carpathian Basin, all other taxa were widespread in the continental Europe (e.g., *Chelotriton paradoxus*, *Lissotriton* and *Triturus marmoratus*). Noticeably, *Carpathotriton*, described for the first time from the late middle Miocene (MN 7) of Mátraszőlős, N Hungary (Venczel 2008), beside its extremely high neural spines of presacral vertebrae was provided with an extremely short tooth row in the mandible, indicating an unusual feeding mechanism.

Among frogs, Latonia gigantea was rather common and was probably linked to various types of aquatic habitats, but due to its good jumping ability it ranged also in the azonal vegetation surrounding marshes, lakes and along rivers (Böhme 2002). In contrary, Palaeobatrachus was more closely linked to aquatic environments, and might have had a peculiar ecology, perhaps comparable to those of recent xenopids (Venczel 2004). Further taxa which might have been closely related to aquatic environments are the limnicole ranid frog *Pelophylax* sp. and the natricine snake *Natrix* cf. *rudabanyaensis*. Based on the analogy with Recent species, Bufo cf. viridis could have inhabited extremely various milieus, whereas the genus Pelobates excepting its spawning season had fossorial habits, preferring well-aerated sandy soils. Other burrowing taxa from Taut are the blanid *Blanus* cf. *gracilis* and the Scolecophidia indet. Based on the fossil record, the scolecophidians, similarly to gekkonid, lacertid and anguid lizards, were more widely distributed in the European Neogene, while the blanids were mainly restricted to the southern and western part of the continent (see Böhme & Ilg 2003). The lizards and various snakes (Coronella miocaenica, Hierophis cf. hungaricus and Macrovipera sp.), probably inhabited

at least partly wooded grasslands and rocky biotopes with xerothermic vegetation. *Coronella, H. hungaricus* and *Macrovipera* sp. may be considered Asiatic immigrants, the latter two taxa being recorded also from the younger (MN 9) Rudabánya locality, N Hungary (Szyndlar 2005).

Following the methodology elaborated by Böhme et al. (2006), we calculated the ecophysiologic index of the recorded taxa, excepting those of colubrid and viperid snakes (Table 1). Using the equation proposed by these authors (MAP = $-35.646 + 2402.289 \cdot index$), the MAP for Taut might be 709 mm (average errors ± 250-280 mm). However, the absence of the crocodile Diplocynodon from Taut suggests a lower MAT and CMT than those expected for the late middle Miocene (MN 7+8) localities of Subpiatră 2/2 and Tăşad, W Romania. In the eastern part of Central Paratethys crocodile remains were reported from the middle Miocene (MN 6) of Pińczów, S Poland (Młynarski 1984), Sámsonháza 3, N Hungary (Hír et al. 1998), and Subpiatră 2/1R, W Romania (Venczel 2007). Furthermore, these thermophilous ectotherms were still present in the late middle Miocene (MN 7+8) of Subpiatră 2/2 and Tășad (Venczel 2007), but they were absent from the late middle Miocene (MN 7) of Mátraszőlős (Gál et al. 1999) and Felsőtárkány, N Hungary (Hír et al. 2001). Conceivably, the southward disappearance of *Diplocynodon* may be correlated to the development of a distinct north-south thermal gradient, process which started in Central Europe around 14-13.5 Ma (Böhme 2003). The increasing Asiatic faunal influence, as is reflected in the composition of the Taut fauna, was also accountable for important herpetofaunal alterations onward Sarmatian times.

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