



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

A contribution to the herpetofauna from the late Miocene of Gritsev (Ukraine)



Une contribution à l'étude de l'herpétofaune de la fin du Miocène de Gritsev (Ukraine)

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ABSTRACT

Excavations in the locality Gritsev (karstic fillings of the upper Miocene age in a limestone quarry in Shepetovsky District, Khmelnytsky Region, Ukraine) revealed, since 1983 when excavations started, a rich vertebrate fauna that includes also amphibians and lizards. The material is rich enough to assess individual and developmental variation within some taxa (e.g., *Pseudopus pannonicus*). Although the fragmentary nature of the disarticulated bones does not sometimes allow precise taxonomic assignment, morphological differences in, e.g., dental characteristics suggest the presence of some other ones, not formally named forms. Thus, the list of the amphibian and reptilian taxa from Gritsev is by far not complete, but their osteological characteristics are representative to such a degree that they can provide information for comparisons with other European Miocene herpetofaunas.

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R É S U M É

Des fouilles dans la localité de Gritsev (remplissages karstiques du Miocène supérieur, dans une carrière de calcaires du district de Shepetovsky, région de Khmelnytsky, Ukraine) ont révélé, depuis le commencement des fouilles en 1983, une riche faune de vertébrés, qui comporte aussi des amphibiens et de lézards. Le matériel est suffisamment riche pour pouvoir établir des variations au niveau des individus et de leur développement au sein de plusieurs taxa (e.g., *Pseudopus pannonicus*). Bien que la nature fragmentaire des os désarticulés ne permette pas toujours une assignation taxonomique précise, des différences morphologiques dans les caractéristiques dentaires suggèrent la présence d'autres formes non dénommées formellement. Ainsi, la liste des taxa d'amphibiens et de reptiles de Gritsev n'est de loin pas complète, mais leurs caractéristiques ostéologiques sont représentatives à un degré tel qu'elles peuvent fournir quelques informations permettant de réaliser des comparaisons avec d'autres herpétofaunes miocènes d'Europe.

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1. Introduction

At the beginning of the process of formation of the European herpetofauna into its today's state, it experienced a profound turnover generally known as the “Grande Coupure,” which was caused by a drop of temperature at the end of the Eocene (it can be noted that this boundary occurred simultaneously with the beginnings of the ice sheet coverage of Antarctica). The worldwide cooling was thus responsible for regression of seas, when Europe changed from an archipelago to a more compact landmass. In addition, the Turgai Strait was closed, which opened the way for immigration (mainly of mammals) from Asia. As a result, a large number of the Eocene taxa disappeared and were replaced by new ones, which were either immigrants or evolved here from their endemic predecessors (e.g., Rage, 1984).

Taken only anurans as an example, a typical genus that disappeared at the Eocene/Oligocene boundary was *Thaumastosaurus* (Holman and Harrison, 2002, 2003; Laloy et al., 2013; Rage, 2012, 2016; Rage and Roček, 2007; Roček and Lamaud, 1995; Vasilyan, 2018). There could have been also others, not so well represented, as suggested by *Opisthocoelellus* (one articulated skeleton from MP 13 of Geiseltal; Kuhn, 1941, and another one from the Eocene/Oligocene boundary of Bechlejovice; Špinar, 1976).

In contrast, *Palaeobatrachus* can be mentioned as an example of those anurans that occurred in Europe before and during the Eocene, but survived the crisis at the end of the Eocene and adapted themselves to new conditions. Its Eocene representatives *P. tobiensis* from Messel and another one from Kučlín were small and probably still more terrestrial than aquatic (Wuttke et al., 2012). Similar were tiny forms from Bechlejovice and Sieblos, i.e. still close to the Eocene/Oligocene boundary. However, typical representatives of *Palaeobatrachus* from the Oligocene were much larger (e.g., *P. gigas*) and, within evolutionary constraints given by their permanent life in water, deviated from their Eocene predecessors.

Another widely distributed Eocene form, which during the Oligocene gradually evolved into a morphologically different taxon, was *Eopelobates*. Whereas *E. wagneri* was still a typical representative of this genus (e.g., by shape of the frontoparietal and by its pitted sculpture), the late Oligocene *Pelobates decheni* had its sculpture intermediate between *Eopelobates* and *Pelobates*, and post-Miocene forms exclusively had pustular sculpture (Roček et al., 2014).

Among those anurans that appeared only after the Eocene/Oligocene boundary is *Latonia*, known by its large Miocene representatives with co-ossified secondary sculpture on the dermal bones of the skull roof. Its earliest findings may be from the earliest Oligocene of Aubreton 1, France (MP21), judging by a large urostyle typical for this genus (Rage and Roček, 2003), but doubtless evidence provided by complete, articulated skeletons are known only from the late Oligocene of Vertaizon (Roček, 1994). Another distinct group of frogs that appeared in the early Oligocene are “green frogs”, currently referred to as *Pelophylax*. Their earliest record is from MP 22 of Möhren 13, Germany (Sanchíz et al., 1993). Thus, the Oligocene is marked by

the emergence of the present-day anuran genera *Pelobates*, *Pelophylax* (and probably *Discoglossus*, if taxonomic status of *D. troscheli* would be confirmed).

The gradual diversification of European herpetofauna, as exemplified by anurans, culminated in the early Miocene, when Eurasia became connected to Africa, and when a warm and wet climate was established after a comparatively cold and dry late Oligocene. At this period, the European herpetofauna was the most diversified, including new genera *Bombina*, *Pelodytes*, *Bufo*, *Hyla* (Rage and Roček, 2003), and the earliest representative of “brown frogs” (Böhme, 2001). Since the early Miocene, the diversity of the European anuran fauna has been steadily decreasing and it may be supposed that similar trends occurred also in the caudates and lizards.

The locality Gritsev (Hrytsiv) stratigraphically fits into this period. Its fossil content is represented by karstic fissure fillings in reef-forming limestones, which contain isolated bones. These karstic fillings were stratigraphically attributed, according to Korotkevich et al. (1985), to the lower (Novomoskovsky) horizon of the middle Sarmatian (upper Miocene, Vallesian, MN 9a). The quarry is on the right bank of the Khomora River, about 3 km west of the village Gritsev (Hrytsiv) in the Shepetovsky District, Khmelnytsky Region, Ukraine (49°58'N; 27°10'E; Semenov, 2001). The karstic genesis of the taphocenosis was proposed by Rosina and Semenov (2012). Preliminary accounts of lizards and snakes from Gritsev may be found in Zerova (1985, 1987, 1989, 1992, 1993), Lungu et al. (1989), Szyndlar and Zerova (1990), and Ivanov (1997a, 1997b, 1997c, 1999). Relatively recently, a giant salamander was reported from this locality (Vasilyan et al., 2013).

In the last decades, many localities stratigraphically close to Gritsev that yielded amphibian and reptile fossils were discovered. This not only allowed faunal comparisons and considerably extended our knowledge of evolution of European herpetofauna, but also improved our knowledge of anatomical features of those fossil taxa that are preserved only fragmentary. Examples of the localities that yielded herpetofaunas coeval or of similar stratigraphic age as Gritsev and, at the same time, are geographically not too distant from it are Gratkorn and Atzelsdorf, Austria (Böhme and Vasilyan, 2014; Tempfer, 2008), Rudabánya, Hungary (Roček, 2004), Tauț and Subpiatră, Romania (Hír and Venczel, 2005; Venczel and Știucă, 2008; Venczel et al., 2005), Karpov Yar, Moldova (Skutschas and Bannikov, 2009), Volchaya Balka and Solnechnodonsk, Russia (Syromyatnikov and Roček, 2018; Tesakov et al., 2017) and some others.

The aim of this study is to add caudates, anurans, and some lizards to the list of fossil taxa from this locality and, because of a large number of the material belonging to *Pseudopus pannonicus*, to assess the individual variation of some skeletal elements of this fossil species.

2. Material and methods

The fossil material described in this paper belongs to the collections of the Institute of Zoology, Department of the Paleozoology, of the Ukrainian Academy of Sciences in Kiev (the current official name of the institution is given

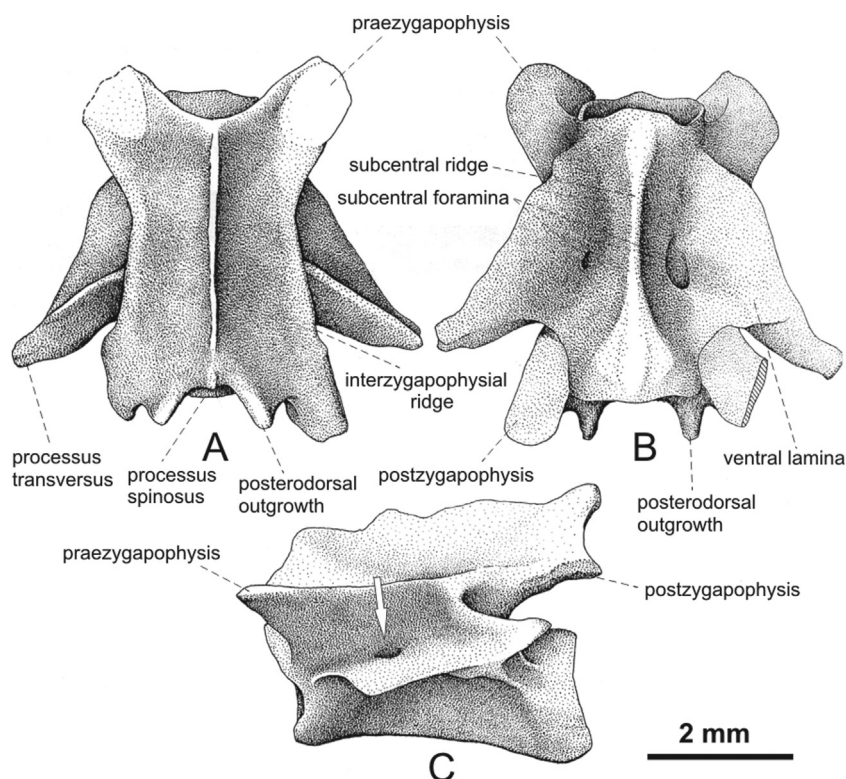


Fig. 1. *Mioproteus caucasicus* Estes and Darevsky, 1977, 1977. A–C. Trunk vertebra (NMNHU-P 2064) in dorsal (A), ventral (B) and lateral (C) views. The subcentral foramen in C is marked by an arrow.

Fig. 1. *Mioproteus caucasicus* Estes et Darevsky, 1977. A–C. Vertèbre de tronc (NMNHU-P 2064) en vues dorsale (A), ventrale (B) et latérale (C). Le foramen central en C est marqué d'une flèche.

below). Because the material was not catalogued, the catalogue numbers were provided by Dr. Galina Zerova, former researcher at the paleozoological department. The material collected in 1983 was catalogued as IZANK 1962–2105, in 1987 as IZANK 2106–2176, in 1985 as IZANK 2177–2601, and in 1990 as IZANK 2602–3550. Thus, 1515 specimens were available for this study. However, because the Department of Paleozoology was then moved to the National Museum of Natural History of the National Academy of Sciences, the catalogue numbers should now bear the abbreviation NMNHU-P (National Museum of Natural History, Ukraine).

Osteological terminology of the Caudata follows that of Francis (1934). The terminology of the cranial epidermal scales in anguids follows that of Meszoely (1970: 93), bone terminology of the lacertids and anguids that of Fejérváry-Lángh (1923) and Roček (1984), and partly (morphology of vertebrae) also that of Hoffstetter and Gasc (1969).

Institutional abbreviation: IZANK – Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kiev; NMNHU-P – National Museum of Natural History, Ukraine, paleontological collections.

3. Results

Systematic part.

Amphibia Linnaeus, 1758.

Caudata Scopoli, 1777.

Proteidae Bonaparte, 1831.

Mioproteus caucasicus Estes and Darevsky, 1977.

Material: 1 trunk vertebra (NMNHU-P 2064 – Fig. 1).

Description: The centrum is amphicoelous. In dorsal view, the neural arches are slightly depressed in the middle of their antero-posterior length, running out in a thin, but well prominent median crest. The anterior margin of the neural arches (rimming the neural canal) is elevated almost to the same level as the median crest. The posterior margin of the neural arches project in posterodorsal outgrowths; this seemingly results in a bifurcated spinal process but, in fact, these outgrowths are separated from the spinal process, which is only an indistinct knob. The interzygapophysial ridge is moderately deflected dorsally. The transverse processes taper towards their blunt end and bear a prominent ridge on their dorsal surface, which runs low posterolaterally.

In ventral aspect, the centrum is compressed in the middle of its length, which is also reflected in a deep median subcentral ridge whose margin almost reaches the level of the ventral surfaces of the cotyles. The transverse processes are connected with the centrum by the ventral lamina. Anterolaterally, the lamina extends to the margin of the transverse process, and is depressed along its incorporation to the centrum. This depression is pierced by a large subcentral foramen on either side, which opens on the dorsal surface of the horizontal lamina anterior to the basis of the processus transversus, covered by the

interzygapophysial ridge in dorsal view (marked by an arrow in Fig. 1C).

Remarks: The specimen conforms to the basic morphological features of *Mioproteus caucasicus* described from the late Miocene deposits of the Belaya River near Maikop in northern Caucasus (Estes and Darevsky, 1977) and is of a similar age. Vertebrae from the Pliocene of the locality of Węże in Poland, described as *Mioproteus wezei* by Estes (in Młynarski et al., 1984: 210–212), differ mainly in the shape of the posterior bifurcation of the dorsal median crest. Whether these differences reflect taxonomic differences or individual variation can be decided only based on more numerous material.

Geographic and stratigraphic occurrence: Arkalyk, central Kazakhstan, middle Miocene (Malakhov, 2003); Belaya River near Maikop and Volchaya Balka, Northern Caucasus, upper Miocene (Estes and Darevsky, 1977; Tesakov et al., 2017); Ambach (MN 5), Dieshof (MN 5–6), Hitzhofen (MN 5), Oggendorf (MN 6), Unterhausen 2 (MN 5–6), all southern Germany (Estes and Schleich, 1994); Rudabánya, Hungary, upper Miocene (Roček, 2004); Mokrá-Western Quarry, Czech Republic, lower Miocene (as *Mioproteus* sp.; Ivanov, 2008).

Salamandridae Goldfuss, 1820.

Chelotriton paradoxus Pomel, 1853.

Material. 1 maxilla (NMNHU-P 2799 – Fig. 2C and D); 1 (?) squamosals (NMNHU-P 3505, doubtfully 3504 and 3506); 1 quadrate-quadratejugal (NMNHU-P 3503 – Fig. 2A and B); 1 left frontal (NMNHU-P 3507 – Fig. 2E and F); 1 atlas (NMNHU-P 3329 – Fig. 3A–C); 3 trunk vertebrae (NMNHU-P 3500 – Fig. 3D and E, 3501, 3502); 1 isolated dorsal plate (NMNHU-P 2102); 43 ribs (NMNHU-P 3467–3487, 3488 – Fig. 4A, 3489 – Fig. 4B, 3490, 3491 – Fig. 4C, 3492 – Fig. 4D, 3493 – Fig. 4E, 3494 – Fig. 4F, 3495, 3496 – Fig. 4G, 3497 – Fig. 4H, 3498 – Fig. 4I, 3499 – Fig. 4J, 3536–3537).

Description (for a description of the articulated skull, see Roček and Wuttke, 2010, figure 2A₅ and Schoch et al., 2015). In outer view, the maxilla (NMNHU-P 2799, Fig. 2C) is covered with irregular pustular ornamentation, except for that part of its surface rimming the lamina dentalis. This tooth-bearing edge is clearly delimited from the lower margin of the processus posterior maxillae, which is toothless. The margo orbitalis is a thin horizontal lamella, the outer surface of which is pustular, whereas its dorsal surface and inner margin are smooth and, if the inner margin is viewed from above, it is moderately concave. The lamella gradually tapers toward the level of the posterior margin of the orbit. Viewed from the inner side (Fig. 2D), there is still another lamina (called palatal lamina) within the posterior part of the bone that, however, is separated from the orbital lamella. Above the palatal lamina, there is a large and antero-posteriorly elongated concavity, which is pierced by a large foramen in its anterior part. Besides this foramen, there is a low edge within the concavity, arising close to the mentioned foramen and running parallel to the orbital lamina. The bone runs out posteriorly into two outgrowths. The ventral is at the level of the palate, the dorsal one takes part in the articulation with the squamosal. There is a constricted groove on the inner surface of the bone connecting the space adjacent to the posterior part of the bone

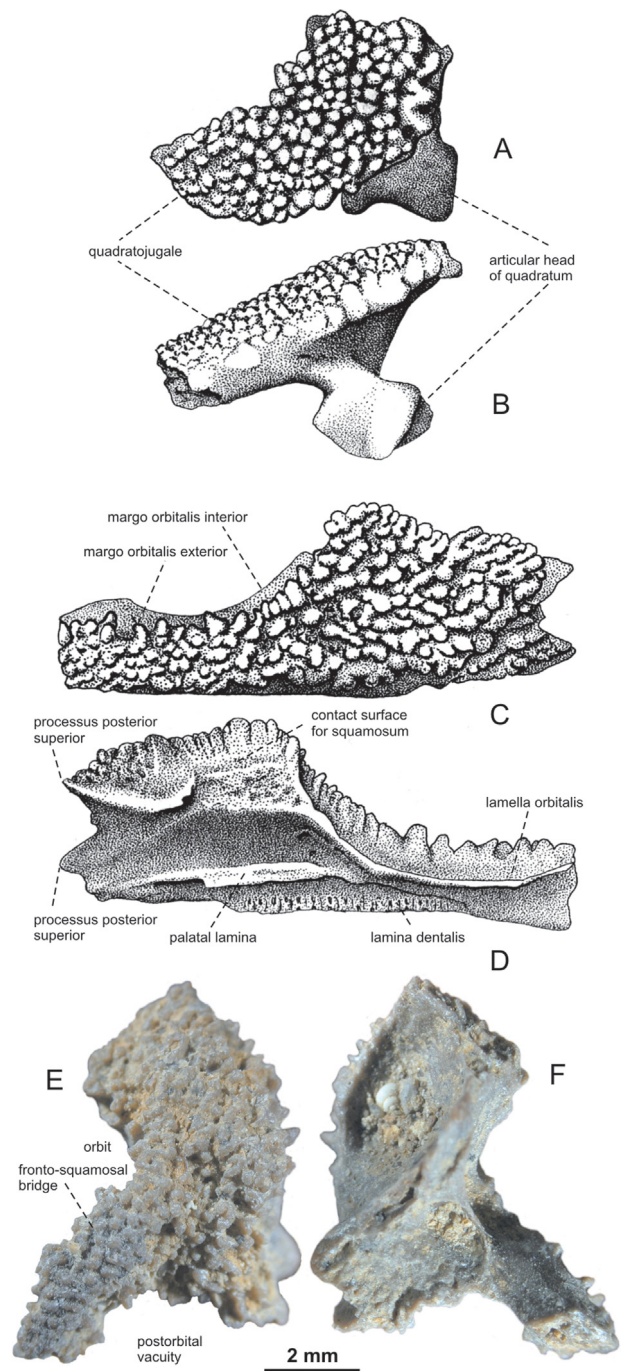


Fig. 2. *Chelotriton paradoxus* Pomel, 1853. A–B. Left quadrate-quadratejugal complex (NMNHU-P 3503) in posterolateral (A) and ventral (B) views. C–D. Left maxilla (NMNHU-P 2799) in outer (C) and inner (D) views. E–F. Left frontal (NMNHU-P 3507) in outer (E) and inner (F) aspects (NMNHU-P 3507). All specimens are at the same scale.

Fig. 2. *Chelotriton paradoxus* Pomel, 1853. A–B. Complexe quadrate-quadratejugal gauche (NMNHU-P 3503) en vues postérolatérale (A) et ventrale (B). C–D. Maxillaire gauche (NMNHU-P 2799) en vues extérieure (C) et intérieure (D). E–F. Frontal gauche sous ses aspects extérieur (E) et intérieur (F) (NMNHU-P 3507). Toutes les spécimens sont à la même échelle.

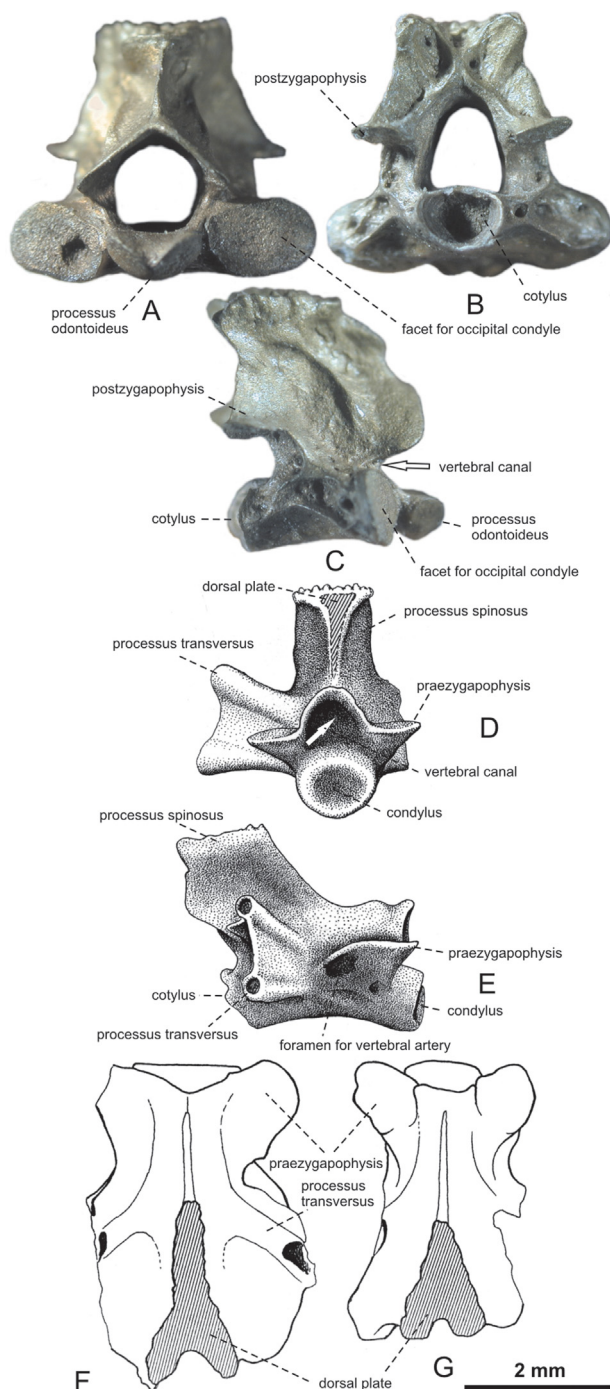


Fig. 3. *Chelotriton paradoxus* Pomel, 1853. A–C. Atlas (NMNHU-P 3329) in anterior (A), posterior (B), and lateral (C) views (C reversed for comparisons with E). D–E. Trunk vertebra (NMNHU-P 3500) in anterior (D) and dextral (E) views. Hatched area – broken surface, broken line – restored anterior margin of processus spinosus. F–G. Trunk vertebrae (F – NMNHU-P 3501, G – NMNHU-P 3502) in dorsal view, to show the variation in shape of the dorsal plate (hatched).

Fig. 3. *Chelotriton paradoxus* Pomel 1853. A–C. Atlas (NMNHU-P 3329) en vues antérieure (A), postérieure (B) et latérale (C). D–E. Vertèbre de tronc (NMNHU-P 3500) en vues antérieure (D) et dextre (E). Zone hachurée – surface brisée, ligne brisée – marge antérieure restaurée du processus spinosus. F–G. Vertèbres de tronc (F – NMNHU-P 3501, G – NMNHU-P 3502) en vue dorsale, pour montrer la variation de forme de la plaque dorsale hachurée.

with the postorbital space. The tooth row was obviously rather short, extending from about the mid-length of the orbit to the middle distance between the orbit and the posterior end of the bone. The anterior part of the maxilla was toothless.

The quadratojugal-quadrato complex (NMNHU-P 3503, Fig. 2A and B) seems to be complete, as can be judged by its anterior margin, which contacts the posterior end of the maxilla. On its inner surface, there is a prominent, thin, vertical lamina terminated ventrally by an articular head; most probably, this is the quadrato and the sculptured portion of the bone is the quadratojugal. This is supported by condition in the articulated specimen of *Chelotriton paradoxus* from Enspele (Roček and Wuttke, 2010, figure 2A₅, A₆) and also in the specimen from Rott (Hellmund and Böhme, 1987, figure 1A) from which it is obvious that its maxillary arch was complete and that there was an independent element in the posterolateral corner of the skull between the squamosal and the posterior part of the maxilla.

The shape of the frontal and the portion of the fronto-squamosal bridge belonging to it (Fig. 2E and F) may be recognized after the natural margin of the bone facing into the orbit. It is obvious that the postorbital vacuity was large.

Other dermal cranial elements (NMNHU-P 3530–3535) are also characteristic by dense pustular sculpture similar to that on the dorsal horizontal extension of the vertebral spinal process. Because the inner parts of these bones are usually broken off, the identification of these bones is difficult.

The atlas (Fig. 3A–C) is high, its dorsal plate is short and wide, and lacks transverse processes (i.e. it bears no ribs). Anteriorly, it has two flat and vertical facets for articulation with occipital condyles. Between them is a well prominent median odontoid process, which bears two ventrolateral facets (for articulation with the bottom of the foramen magnum; Francis, 1934). The neural arches meet above the vertebral canal in almost the right angle, from where a thin median crest protrudes dorsally. The cotyle is deep, with thin margins, and the postzygapophyses have almost horizontal facets.

The trunk vertebrae (NMNHU-P 3500, 3501) were originally amphicoelous, but the anterior concavity was obliterated with bone and cartilage in some individuals, with only a shallow depression (Fig. 3D). However, NMNHU-P 3502 has a deep anterior cotyle, with no sign of osseous tissue fillings. In all trunk vertebrae, the transverse process consists of the dorsal and ventral cylindrical parts united by a thin bony lamina (Fig. 3E). If viewed from above, the transverse processes of both sides diverge posteriorly. The processus spinosus is high and thin lamina bifurcated posteriorly along the whole of its height, and dilated at its top in a horizontal plate (Fig. 3F and G). The plate is covered by an irregular pit-and-ridge sculpture, with each pit perforated by a small foramen. The median part of the plate between both posterior rami is distinctly depressed. The plate considerably vary both in size and shape. It continues anteriorly by a gradually lowering lamina. There is a large foramen below the posterior part of the praezygapophysis that can be homologous with the vertebralarterial foramen of Francis (1934, pl. III, figure 15). Besides this large foramen, there is an additional one below the anterior part of

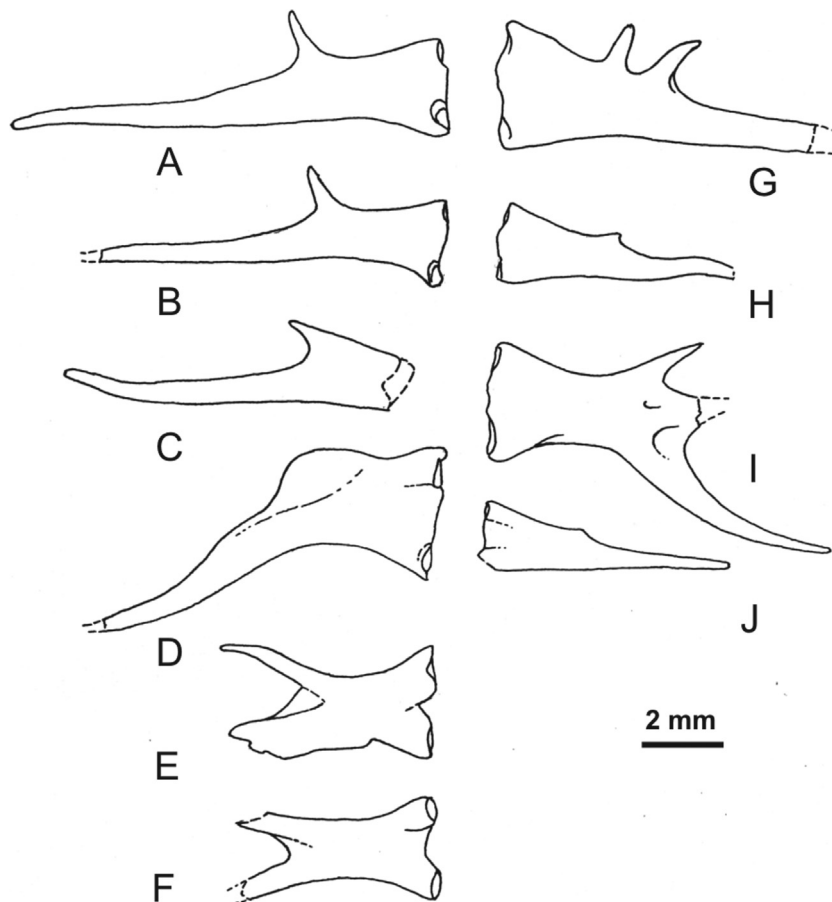


Fig. 4. *Chelotriton paradoxus* Pomel, 1853. Variation in shape of ribs. **A–F** Left ribs in posterior view. **G–J** Right ribs in posterior view (**A** – NMNHU-P 3488; **B** – NMNHU-P 3489; **C** – NMNHU-P 3491; **D** – NMNHU-P 3492; **E** – NMNHU-P 3493; **F** – NMNHU-P 3494; **G** – NMNHU-P 3496; **H** – NMNHU-P 3497; **I** – NMNHU-P 3498; **J** – NMNHU-P 3499).

Fig. 4. *Chelotriton paradoxus* Pomel, 1853. Variation de forme des côtes. **A–F** Côtes gauches en vue postérieure. **G–J** Côtes droites en vue postérieure (**A** – NMNHU-P 3488; **B** – NMNHU-P 3489; **C** – NMNHU-P 3491; **D** – NMNHU-P 3492; **E** – NMNHU-P 3493; **F** – NMNHU-P 3494; **G** – NMNHU-P 3496; **H** – NMNHU-P 3497; **I** – NMNHU-P 3498; **J** – NMNHU-P 3499).

the praezygapophysis, directed anteriorly. The ventral and lateral surfaces of the centrum are pierced by several other foramina that vary in size and position.

The ribs (Fig. 4) are bicipital, usually with one or rarely two dorsal spines. The spine is poorly developed in posterior ribs, whereas in anterior ribs it may attain the length of the rib itself, as can be judged by condition in articulated skeletons found in other localities (e.g., Enspel, Rott; Hellmund and Böhme, 1987; Roček and Wuttke, 2010).

Comparisons. The vertebrae of *Chelotriton* from Gritsev fit into the variation range of those from the locality Coderet that include also the neotype of *Chelotriton paradoxus* Pomel, 1853. On the other hand, they differ from *Chelotriton pliogenicus* Bailon, 1989 in the fact that they have no zygosphen – zygantrum articulation.

Remarks. *Chelotriton paradoxus* was established by Pomel (1853), based on vertebrae from the Oligocene (MP 27) of Chauffours (Puy-de-Dôme, France), and from the terminal Oligocene (MP 30) or lower Miocene (MN 2a) of Langy (Allier, France). He did not mention any particular specimen and his collection is now lost, but from his brief

description in which he mentioned a broad, rough plate on the neurapophyses, one can easily recognize the characteristic feature of the species. Herre (1949) then published the first illustrations of the vertebra and Estes and Hoffstetter (1976) gave the list of diagnostic characters, namely that the articulation cotyles (“rib-bearers”) of the transverse processes are well separated and the spinal process is deep, with a dermal horizontal plate mostly covered by pustular ornamentation at the top. Estes (1981) then designated as the neotype one trunk vertebra from the late Oligocene (MP 30) of Coderet (Allier, France), which is practically of the same age as Chauffours. The neotype is deposited in the “Institut de paléontologie” in Paris (MNHN Cod 12) (Rage 1994, pers. comm.). Further diagnostic characters were added when taxonomic identity of complete, articulated skeletons (e.g., *Heliarchon furcillatus* Meyer, 1860) were recognized, and when further skeletons were recovered, which made it possible to assess variation (Schoch et al., 2015).

Geographic and stratigraphic occurrence of the genus *Chelotriton*. England: Hordle Cliff (upper Eocene, MP 17)

(Milner et al., 1982); Spain: Rubielos de Mora, Las Planas IV-A, (lower Miocene) (Estes, 1981); France: Chaffours, Antoinet, Boningen, Coderet, Langy (late Oligocene, MP 30 – lower Miocene, MN 2a) (Estes, 1981; Rage, 1984, tab.1; Rage and Hossini, 2000), Peulblanc (lower Miocene) (Estes, 1981), La Grive St. Alban, Sansan (Middle Miocene) (Rage and Hossini, 2000); Balaruc II (upper Pliocene, MN16) (Bailon, 1989); Austria: Gratkorn (middle Miocene) (Böhme and Vasilyan, 2014); Germany: Enspel, Gaimersheim, Herrlingen, Rott (upper Oligocene) (Estes, 1981; Hellmund and Böhme, 1987; Roček and Wuttke, 2010), Florersheim, Weisenau, Grafenmühle (lower Miocene) (Estes, 1981), Randeck Maar (lower – middle Miocene, MN5) (Schoch and Rasser, 2013; Schoch et al., 2015); Wintershof-West, Wintershof-Ost, Schneithelm, Erkertshofen (middle Miocene) (Estes, 1981), Öhningen (upper Miocene, Astaracian, MN 7) (Westphal, 1978); Poland: Opole (middle Miocene, Astaracian, MN 7) (Młynarski et al., 1982); Romania: Tauț (upper middle Miocene, MN7 + 8) (Venczel and Știucă, 2008); Russia: Volchaya Balka and Gaverdovsky (upper Miocene, MN 11) (Tesakov et al., 2017); Ukraine: Gritsev (upper Miocene, middle Sarmatian, MN 9a) (this paper).

In addition, *Chelotriton robustus* was described from the Middle Eocene (MP 11) of Messel, Germany (Westphal, 1982), but even if it bears sculptured horizontal plates on its vertebrae, its taxonomic status should be revised.

Anura Fischer, 1813.

Alytidae Fitzinger, 1843.

Latonia Meyer, 1843.

Latonia sp. (Fig. 5).

Material. One prooticoccipital (NMNHU-P 3340 – Fig. 5A–C); 1 premaxilla (NMNHU-P 3300 – Roček, 1994, pl. 1, figure 2); 6 maxillae (NMNHU-P 2085 – Fig. 5I, NMNHU-P 2087 – Fig. 5D, NMNHU-P 2079 – Fig. 5E, NMNHU-P 3308 – Fig. 5F, Roček, 1994, pl. 1, figure 3; NMNHU-P 3319 – Fig. 5G, NMNHU-P 3334 – Fig. 5H); 5 frontoparietals (NMNHU-P 2078 – Fig. 5J, NMNHU-P 3306 – Fig. 5M, NMNHU-P 3339 – Fig. 5L, Roček, 1994, pl. 1, figures 6 et 7; NMNHU-P 3452 – Fig. 5K, NMNHU-P 3541); 2 squamosals (NMNHU-P 3341 – Fig. 5N, Roček, 1994, pl. 1, figure 1; NMNHU-P 3539 – Fig. 5O); 5 angulars (NMNHU-P 3309, NMNHU-P 3317 – Fig. 5P, NMNHU-P 3331 – Fig. 5S, NMNHU-P 3332 – Fig. 5Q, Roček, 1994, pl. 1, Figs. 4 and 5; NMNHU-P 3333 – Fig. 5R); 2 centra of V_1 (NMNHU-P 2168 – Fig. 6B, NMNHU-P 3301 – Fig. 6A, Roček, 1994, pl. 1, figure 10); 2 presacral vertebrae (NMNHU-P 3305 – Fig. 6F–I, Roček, 1994, pl. 1, figure 12; NMNHU-P 3327, Fig. 6C–E); 1 urostyle (NMNHU-P 3315 – Fig. 6J, Roček, 1994, pl. 1, figure 8); 2 ilia (NMNHU-P 2840 – Fig. 6N, NMNHU-P 3326 – Fig. 5T); 1 ischia (NMNHU-P 3318 – Roček, 1994, pl. 1, figure 11).

Description. The only available part of the neural endocranium (that portion of the skull that ossifies from cartilaginous primordium) is the prooticoccipital. It basically corresponds to that described in Roček (1994), namely in the fact that the prominent ductus semicircularis posterioris is manifested on the posterodorsal surface of this complex as a thin, prominent crista terminated abruptly on both its ends (Fig. 5A–C). The contact area for the frontoparietal (Fig. 5C) suggests that the crista continued from the processus paraoccipitalis of the frontoparietal, which

bears a similar crest (Fig. 5L). The contact area for the palatoquadrate is as large as the occipital condyle or larger (Fig. 5B). In the anterior aspect, there is a distinct horizontal groove, termed the sulcus venae jugularis.

All maxillae are incomplete, but because all these fragments preserve that part of the bone that is strengthened by the posterior end of the lamina horizontalis, one can observe the sculptured area on the outer surface of the bone at the level of the processus zygomaticomaxillaris. In addition, these fragments belonged to individuals of different ages, from a juvenile (Fig. 5D) to an adult (Fig. 5I). It follows from this developmental sequence that ornamentation appears and spreads only during the growth of an individual, from faint, indistinct tubercles to densely tubercular, well delimited fields. Very characteristic for *Latonia* is a groove running dorsoventrally through this tubercular field; however, it is not clear whether it occurs in all individuals.

The frontoparietals are too fragmentary to determine general shape of the bone, but all diagnostic features of the genus *Latonia* are preserved – the tubercular sculpture of the dorsal surface of the bone which anteriorly tends to fuse into parallel and slightly divergent ridges, extensive tectum supraorbitale, and typical frontoparietal incassation consisting of the anterior and posterior parts. The pars contacta, which is a prominent ridge that inserts onto the braincase walls, is deep and slightly deflected laterally, so it fits by its medial surface into the contact area on the prooticoccipital (Fig. 5B and C). The posterior slanting face of the frontoparietal is pierced by two tiny foramina below the extended horizontal roof, one on each side of low, vertical median crest. Besides, it is well seen in posterior view that the sculpture is distinctly separated from the flat dorsal surface of underlying bone, sometimes even by a thin layer of tiny pores (marked by an arrow in Fig. 5L). This suggests that the sculpture is a secondary ossification. Similar pores leading to the dividing layer occur also on the dorsal surface between the tubercles.

Both squamosals (Fig. 5N and O) have a longitudinal crista on their posterolateral process, but they differ from one another in the fact that the smaller one has its lamella alaris smooth, whereas the larger one has its zygomatic process covered with tubercular or vermicular sculpture. Most probably it continued onto the sculptured area on the zygomaticomaxillary process of the maxilla.

The angulars of *Latonia* bear very distinctive features, some of which can be used as diagnostic of the genus (Fig. 5P–S). First of all, they are provided with a flat, horizontal, dorsoventrally compressed outgrowth, usually termed the processus paracronoideus, although, judging by its position, it may be considered homologous with the processus cronoideus of other frogs. Besides that, however, there is another process located closer to the jaw joint and directed vertically. It is usually called the processus cronoideus. Thus, *Latonia* has two processes instead of one. In juveniles (Fig. 5P), both processes are already developed but in much lesser degree. Finally, there is a distinct recess in the bottom of Meckel's groove (marked by arrows in Fig. 5Q–S), which is at about the level of the processus cronoideus. One can also mention a distinct depression on the medial surface of the posterior part of the angulars,

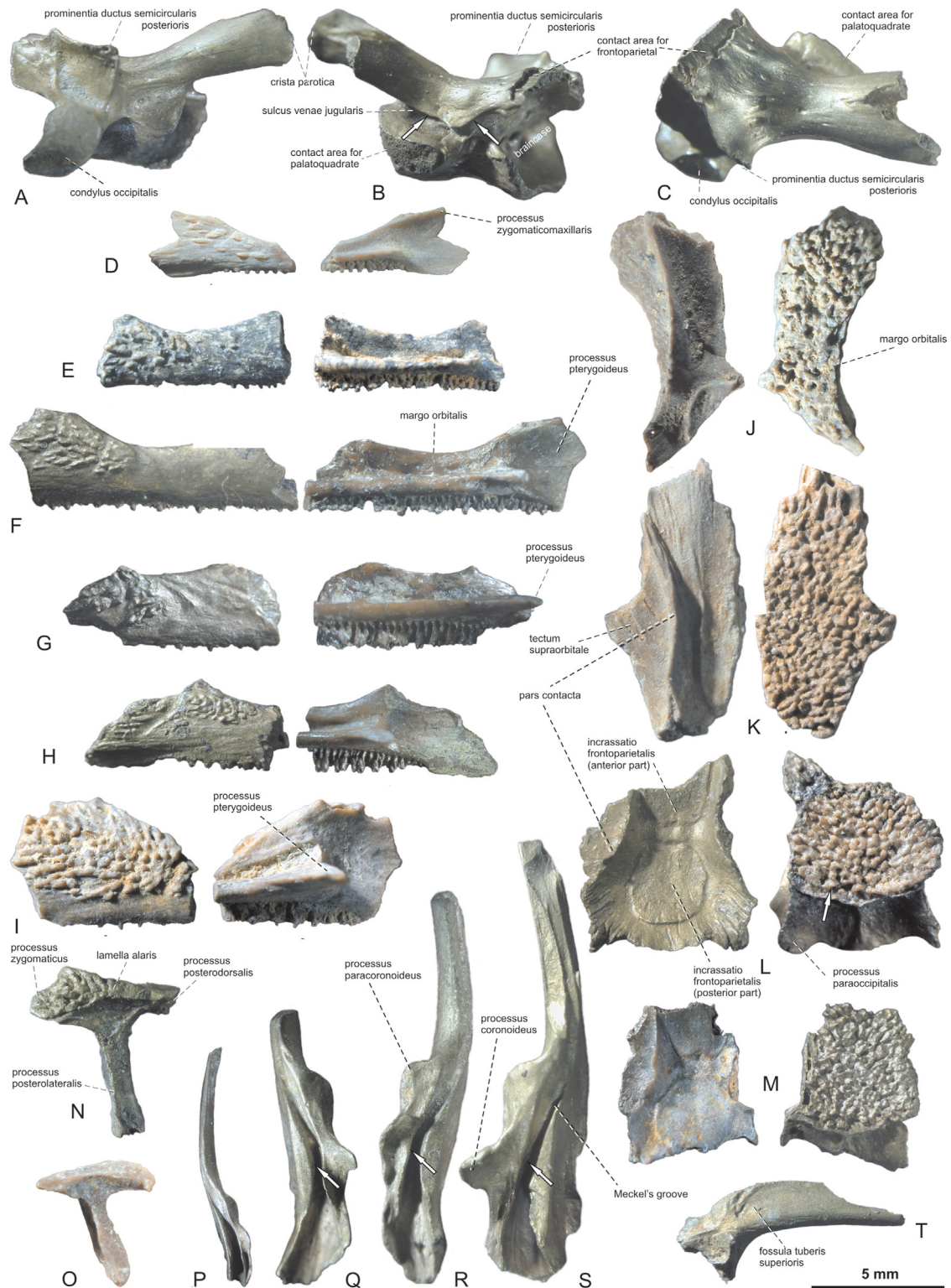


Fig. 5. *Latonia* sp., cranial elements. **A–C.** Right oticooccipital (NMNHU-P 3340) in posterior (**A**), anterior (**B**), and dorsal (**C**) aspects. The white arrows in **B** mark the groove for vena jugularis. **D–I.** Developmental variation of sculpture on right maxilla (**D** – NMNHU-P 2087, **E** – NMNHU-P 2079, **F** – NMNHU-P 3308, **G** – NMNHU-P 3319, reversed for comparisons, **H** – NMNHU-P 3334, **I** – NMNHU-P 2085) in labial (left) and lingual (right) aspect. (**D** is the youngest individual from the series, **I** the oldest one.) **J–M.** Frontoparietals (**J** – NMNHU-P 2078; **K** – NMNHU-P 3452; **L** – NMNHU-P 3339; **M** – NMNHU-P 3306). **N–O.** Left squamosals (**N** – NMNHU-P 3341; **O** – NMNHU-P 3539). The arrow in **L** marks the border between the sculpture and the flat surface of the

which is delimited ventrally by a distinct horizontal ledge terminated abruptly at its posterior end.

Both atlases (V_1) are incomplete, with their neural arches broken off (Fig. 6A and B). They have a distinct median ridge on their ventral surface (probably less distinct in younger individuals than in older ones). The articular facets for the occipital condyles are either close to one another (Fig. 6A) or widely separated (Fig. 6B). It is difficult to decide whether this is due to developmental or individual variation.

One of the three rib-bearing vertebrae (probably V_3 or V_4 judging by inclination of the articular facets of the transverse processes) is NMNHU-P 3305 (Fig. 6F–I). The transverse processes are markedly broadened at their ends, with their contact facets slightly directed posteroventrally. In ventral view, the centrum is moderately constricted in the middle of its length. The neural arches meet in a low median ridge, which continues on a prominent, posterodorsally directed spinal process (broken off in NMNHU-P 3305). The posterior presacral vertebrae are represented by NMNHU-P 3327 (Fig. 6C–E), which can be V_5 , according to inclination of the only preserved transverse process. One rib is available (Fig. 6M), obviously belonging to a fully-grown adult, not only because of its large size, but also because it is coalesced with the fragment of the transverse process. It belongs to V_3 , as evidenced by its uncinate process (ribs on V_3 are the only ones which bear uncinate processes).

The only urostyle available (NMNHU-P 3315, Fig. 6J) is apparently from a juvenile. It is bicotylar, with a pair of dorsoventrally compressed, triangular transverse processes. On the dorsal side, there is a deep median groove extending posteriorwards from the level of the posterior margins of the transverse processes. The anterior orifice of the vertebral canal opens anterodorsally. There is no horizontal edge on the lateral sides of the shaft; this, however, can be due to developmental variation.

The large humerus NMNHU-P 2839 (Fig. 6L) extends medially in a thin but large crista medialis and less extensive crista lateralis. On its ventral surface, it bears a rounded ventral crista from which another rounded ridge splits medially, so that a deep groove arises between them. The crista ventralis continues proximally, giving rise to a medially deflected lamina, which partly overlaps the groove (marked by arrow in Fig. 6L). These are characteristic features of the humerus of *Latonia* (cf. Roček, 1994, figure 17G), although some variation within this basic scheme undoubtedly exists. NMNHU-P 3316 (Fig. 6K) is the humerus of a juvenile with basically the same morphology.

Fragment of the ilium (NMNHU-P 2840, Fig. 6N) bears a robust tuber superius, which is situated rather obliquely, so that its posterior margin terminates in a small depression above the acetabulum. Here the margin of the acetabulum is indistinct, whereas it is markedly raised in its anterior portion. Due to this, the acetabulum as a whole opens posterolaterally, rather than laterally. Below the anterior part of the tuber superius is a shallow triangular depression on the lateral surface of the bone, usually termed the fossula tuberis superioris. Its bottom is pierced by one or more tiny foramina (marked by arrow in Fig. 6N), which is a typical feature of the ilium in *Latonia*. All these features, including the fossula and several foramina piercing its bottom occur also in juveniles (Fig. 5T).

Comparisons. It is similar to *Latonia seyfriedi* and *L. gigantea* in the fact that the maxilla and lamella alaris squamosi are partly covered with sculpture. Similar to *L. ragei* in that the tooth row extends beyond the level of the pterygoid process. Similar to *L. caucasica* Syromyatnikova et Roček, 2018 in that the prominentia ductus semicircularis posterioris does not extend beyond the level of the occipital condyle.

It differs from *L. ragei* and *L. caucasica* Syromyatnikova et Roček, 2018 by the maxilla and anterior part of the lamella alaris squamosi covered with sculpture (smooth in both mentioned species), and from *L. caucasica* in that the tooth row on the maxilla extends posteriorly beyond the level of the pterygoid process (does not extend beyond that level in *L. caucasica*).

Remarks: The sample from Gritsev includes both fully-grown adults as well as postmetamorphic juveniles. This allows us to reconstruct the development of some characters used in the diagnostics of the currently recognized species, such as the presence or the absence of sculpture on the maxillae and squamosals.

Geographic and stratigraphic occurrence. For a summary of recent data, see Syromyatnikova and Roček (2018).

Palaeobatrachidae Cope, 1865.

Palaeobatrachus Tschudi, 1838.

Palaeobatrachus sp.

Material. Two premaxillae (NMNHU-P 2026, NMNHU-P 3300 – Fig. 7D and E), 4 maxillae (NMNHU-P 2080 – Fig. 7B and C, NMNHU-P 2081 – Fig. 7A, NMNHU-P 2086, NMNHU-P 2088); 3 angulars (NMNHU-P 3321 – Fig. 7H, NMNHU-P 3325 – Fig. 7G, NMNHU-P 3330 – Fig. 7F).

Description. The premaxilla (Fig. 7D and E) has 10 tooth positions, but typical knob-like outgrowths adjacent to their bases are broken off. The median symphysis was straight and the pars palatina runs out posteriorly in a blunt

underlying bone. **P–Q.** Left angulars (**P** – NMNHU-P 3317, **Q** – NMNHU-P 3332). **R–S** Right angulars (**R** – NMNHU-P 3333, **S** – NMNHU-P 3331); the arrows indicate the position of a deep recess in the bottom of Meckel's groove. **T.** Right ilium of juvenile (NMNHU-P 3326). All specimens are at the same scale. **Fig. 5.** *Latonia* sp., éléments crâniens. **A–C.** Oticoccipital droit (NMNHU-P 3340) sous ses aspects postérieur (**A**), antérieur (**B**) et dorsal (**C**). Les flèches blanches en **B** indiquent un sillon pour la veine jugulaire. **D–I.** Variation du développement de la sculpture sur le maxillaire droit (**D** – NMNHU-P 2087, **E** – HU-P 2079; **F** – NMNHU-P 3308; **G** – NMNHU-P 3319, retourné pour comparaison; **H** – NMNHU-P 3334; **I** – NMNHU-P 2085 sous l'aspect labial (à gauche) et lingual (à droite)). (**D**) est l'individu le plus jeune de la série et **I** le plus vieux). **J–M.** Frontopariétaux (**J** – NMNHU-P 2078; **K** – NMNHU-P 3452; **L** – NMNHU-P 3339; **M** – NMNHU-P 3306). **N–O** Squamosaux gauches (**N** – NMNHU-P 3341; **O** – NMNHU-P 3539). La flèche en **L** indique la limite entre la sculpture et la surface plate de l'os sous-jacent. **P–Q.** Angulaires gauches (**P** – NMNHU-P 3317; **Q** – NMNHU-P 3332). **R–S.** Angulaires droits (**R** – NMNHU-P 3333; **S** – NMNHU-P 3331); les flèches indiquent la position d'un profond renfoncement à la base du sillon de Meckel. **T.** Ilium droit de juvénile (NMNHU-P 3326). Tous les éléments sont figurés à la même échelle.

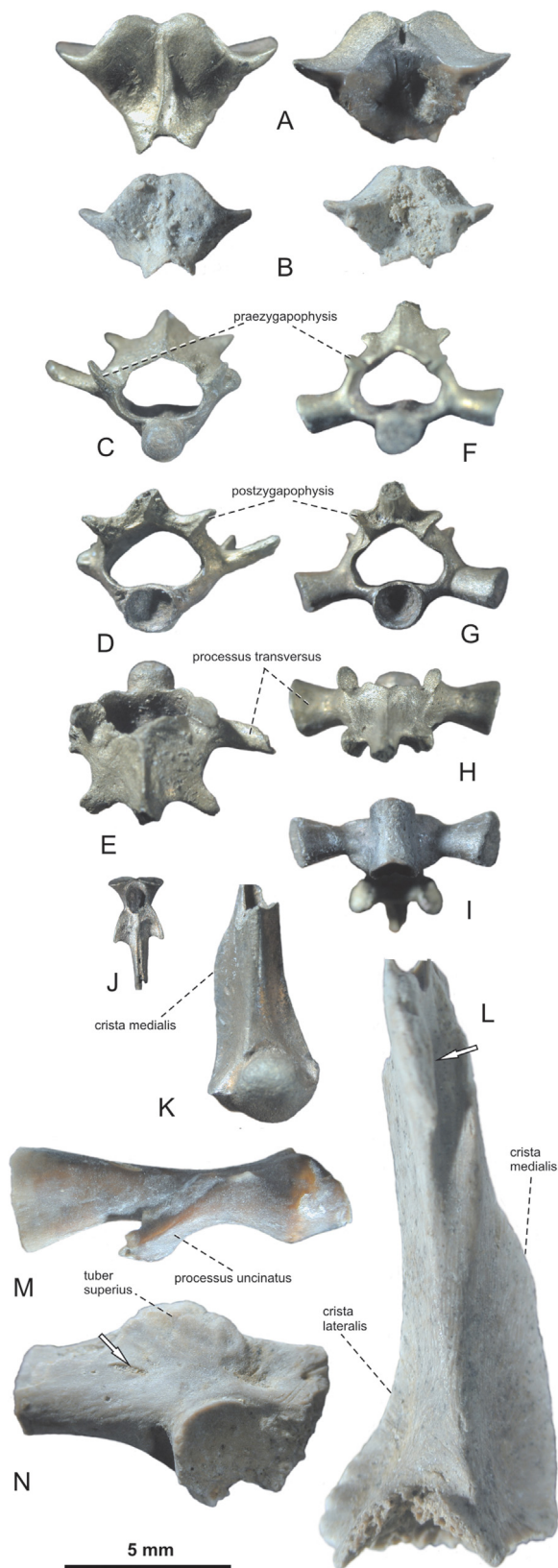


Fig. 6. *Latonia* sp., postcranial elements. **A–B.** Centrum of V_1 with neural arches broken away (**A** – NMNHU-P 3301, **B** – NMNHU-P 2168) in

process. The pars facialis is broken away, but it is apparent that on its inner surface it was deeply concave, with another, narrower concavity separated by a sharp ridge (marked by arrow in Fig. 7E). However, characters that would allow us to assign this premaxilla unambiguously to *Palaeobatrachus* are not preserved, so the determination should be only tentative. It may be inferred from available fragments that the maxilla had at least 15 tooth positions and that the tooth row terminated close behind the level of the posterior margin of the frontal process. The processus posterior is long, with the lamina horizontalis reaching nearly its end. The anterior part of the maxilla is not preserved in the available material, so its contact with the pterygoid cannot be restored. The outer surface of the bone is smooth, only along its lower margin with signs of rugosity. It was pierced by two foramina whereas, on the inner surface of the bone; there was a wide but short canal situated at the transition between the lamina horizontalis and the vertical wall (Fig. 7C). The teeth are conical with blunt tips, which are black, and this dark part is separated from the rest of the tooth by a straight border. Between the bases of neighboring teeth are knob-like outgrowths rather prominent medially; they continue as sharp partitions up to the lower basis of the lamina horizontalis, thus separating rather deep depressions in each tooth position.

Angulars have the coronoid process that bears rugosity on its dorsal surface. The anterior margin of the coronoid process continues as a low ridge to the medial edge of the sulcus Meckeli, where the ridge forms an indistinct process (marked by arrows in Fig. 7F–H).

Comparisons. Because most of currently recognized species of *Palaeobatrachus* were based on articulated skeletons, their comparisons with single, disarticulated bones are difficult. Another reason that prevents taxonomic assignment is osteological uniformity of these water-dwelling anurans.

Pelobatidae Bonaparte, 1850.

Pelobates Wagner, 1830.

Pelobates sp.

ventral (left) and dorsal (right) aspect. **C–E.** (?) V_5 (NMNHU-P 3327) in anterior (**C**), posterior (**D**), and dorsal (**E**) views. **F–I.** V_3 (NMNHU-P 3305) in anterior (**F**), posterior (**G**), dorsal (**H**), and ventral (**I**) views. **J.** Urostyle of juvenile (NMNHU-P 3315) in dorsal view. **K.** Left humerus (NMNHU-P 3316) in ventral view. **L.** Right humerus (NMNHU-P 2839) in ventral view. The arrow marks characteristic, medially deflected lamina overlapping the groove on the ventral surface of the humeral shaft. **M.** Rib of V_3 (NMNHU-P 3538). **N.** Left ilium (NMNHU-P 2840) in lateral view. The arrow indicates the characteristic foramen in the bottom of fossula tuberis superioris. All specimens are at the same scale.

Fig. 6. *Latonia* sp. Éléments post-crâniens. **A–B.** Centre de V_1 avec les arcs neuraux brisés ôtés (**A** – NMNHU-P 3301 ; **B** – NMNHU-P 2168) en vues ventrale (à gauche) et dorsale (à droite). **C–E.** (?) V_5 . NMNHU-P 3327 en vues antérieure (**C**), postérieure (**D**) et dorsale (**E**). **F–I.** V_3 (NMNHU-P 3305) en vues antérieure (**F**), postérieure (**G**), dorsale (**H**) et ventrale (**I**). **J.** Urostyle de juvénile (NMNHU-P 3315) en vue dorsale. **K.** Humérus gauche (NMNHU-P 3316) en vue ventrale. **L.** Humérus droit (NMNHU-P 2839) en vue ventrale. La flèche indique une lamina caractéristique, médialement incurvée, recouvrant le sillon sur la surface ventrale de la tige de l'humérus. **M.** Côte de V_3 (NMNHU-P 3538). **N.** Ilium gauche (NMNHU-P 2840) en vue latérale ; la flèche indique le foramen caractéristique à la base de la fossula tuberis superioris. Tous les éléments sont figurés à la même échelle.

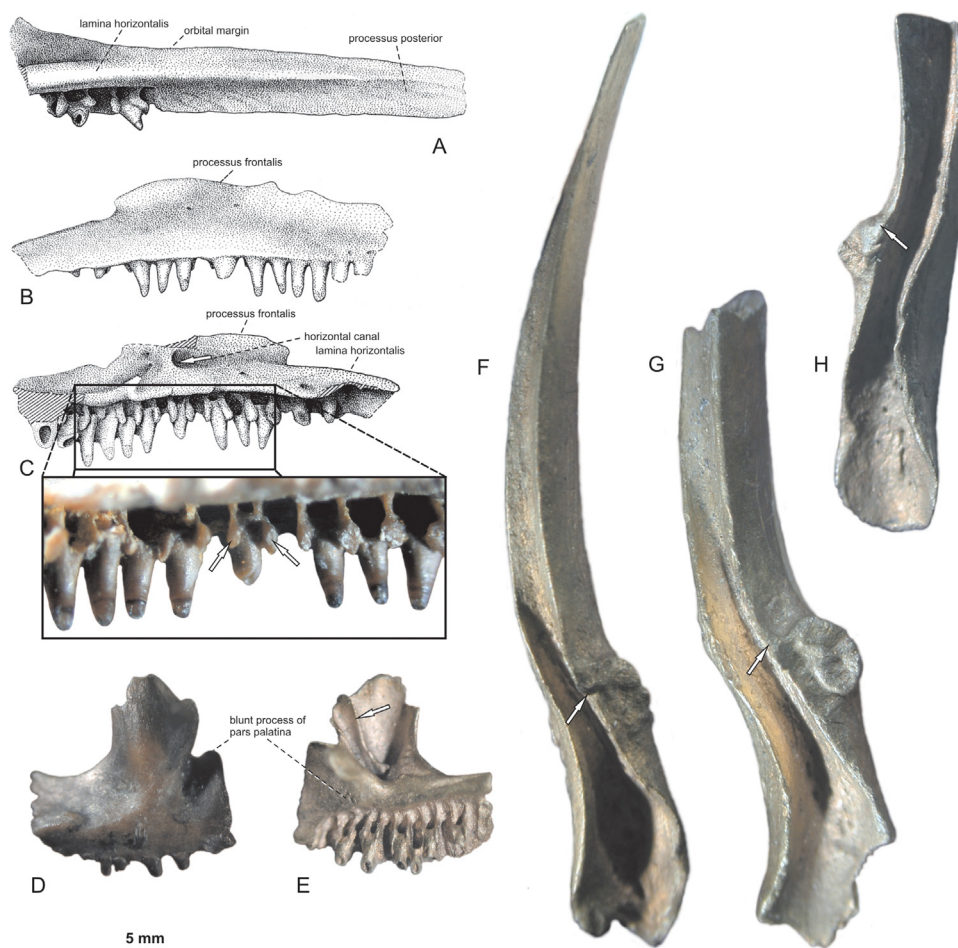


Fig. 7. *Palaeobatrachus* sp. **A.** Posterior part of the right maxilla in medial view (NMNHU-P 2081). **B–C.** Middle section of the right maxilla (NMNHU-P 2080) in lateral (**A**) and medial (**C**) views, with close-up of tooth row. Knob-like thickenings between teeth are marked by arrows. **D–E.** Right premaxilla (NMNHU-P 3300) in labial (**D**) and lingual (**E**) views. The arrow marks the vertical ridge separating concavities on the inner side of the pars palatina. Because important characters are not preserved, the assignment to *Palaeobatrachus* should be only tentative. **F.** Left angular (NMNHU-P 3330) in dorsal view. **G.** Posterior part of the left angular (NMNHU-P 3325) in dorsal view. **H.** Posterior part of the right angular (NMNHU-P 3321) in dorsal view. Tiny processes on medial margins of the sulcus Meckeli are marked by arrows. All specimens are at the same scale.

Fig. 7. *Palaeobatrachus* sp. **A.** Partie postérieure du maxillaire droit en vue médiale (NMNHU-P 2081). **B–C.** Section moyenne du maxillaire droit (NMNHU-P 2080) en vues latérale (**A**) et médiale (**C**), avec fermeture de la rangée dentaire. Des épaissements en forme de bouton (?) entre les dents sont indiqués par des flèches. **D–E.** Maxillaire droit. NMNHU-P 3300 en vues labiale (**D**) et linguale (**E**). Une flèche indique une ride verticale séparant les concavités sur la face interne de la pars palatina. En raison de caractères importants non préservés, l'assignation à *Palaeobatrachus* ne peut être que conjecturale. **F.** Angulaire gauche (NMNHU-P 3330), en vue dorsale. **G.** Partie postérieure de l'angulaire gauche (NMNHU-P 3325), en vue dorsale. **H.** Partie postérieure de l'angulaire droit (NMNHU-P 3321), en vue dorsale. De tout petits processus sur les marges médiales du sulcus Meckeli sont indiqués par des flèches. Tous les éléments sont figurés à la même échelle.

Material. Two frontoparietals (NMNHU-P 3320, NMNHU-P 3338 – Fig. 8A–C); 5 maxillae (NMNHU-P 2089 – Fig. 8F and G; NMNHU-P 2090 – Fig. 8H and I; NMNHU-P 2091 – Fig. 8L and M; NMNHU-P 3302 – Fig. 8J and K; NMNHU-P 3336 – Fig. 8D and E); 1 angular (NMNHU-P 3303 – Fig. 8N); 1 presacral vertebra (NMNHU-P 3540 – Fig. 8L and M); 2 ilia (NMNHU-P 3328 – Fig. 8O; NMNHU-P 3325 – Fig. 8P).

Description. Frontoparietal NMNHU-P 3338 preserves its complete right half, which makes it possible to reconstruct the shape of the bone, as well as the shape of its frontoparietal incassation. Its dorsal surface is covered by a deep pit-and-ridge sculpture, which is slightly less prominent in the anteromedial part of the bone. In NMNHU-P

3320, the sculpture is more reticular (i.e. ridges are of the constant depth, with no tendency to run out in pustules). The processus lateralis superior took part in the formation of a broad postorbital bridge. There is a moderate median convexity on the posterior margin of the bone both on the dorsal and ventral parts (processus posterior dorsalis and ventralis). In ventral aspect, the pars contacta is developed as a ridge that disappears close to the anterior margin of the bone. In NMNHU-P 3338, there are two small foramina for the branches of the arteria orbitonasalis below the margo orbitalis, rather than only one. The foramen for the temporal artery is large and located within the anterior wall of the processus lateralis inferior. There is a short but distinct groove running anteriorly from this foramen towards

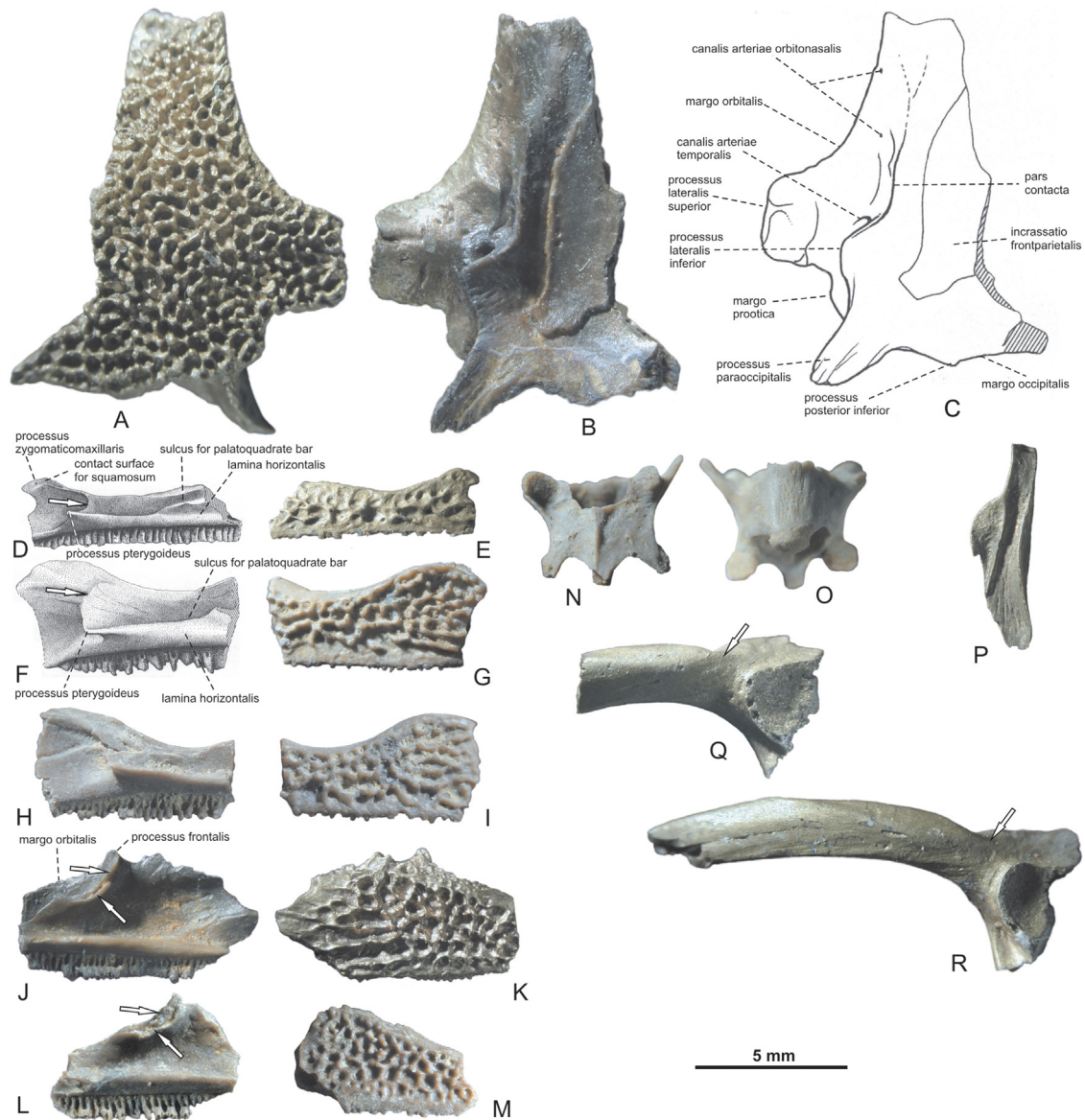


Fig. 8. *Pelobates* sp. **A–C.** Frontoparietal (NMNHU-P 3338) in dorsal (**A**) and ventral (**B**) views; **C** is an interpretative drawing of **B**. **D–E.** Left maxilla of juvenile (NMNHU-P 3336) in inner (**D**) and outer (**E**) views. **F–G.** Left maxilla (NMNHU-P 2089) in inner (**F**) and outer (**G**) views. **H–I.** Left maxilla (NMNHU-P 2090) in inner (**H**) and outer (**I**) views. **J–K.** Anterior part of the right maxilla (NMNHU-P 3302) in inner (**J**) and outer (**K**) views. **L–M.** Anterior part of left maxilla (NMNHU-P 2091) in inner (**L**) and outer (**M**) views (reversed for comparisons). **N–O.** Presacral vertebra (NMNHU-P 3540) in dorsal (**N**) and ventral (**O**) views. **P.** Posterior part of the right angular (NMNHU-P 3303) in dorsal view. **Q.** Left ilium (NMNHU-P 3328) in lateral view. **R.** Left ilium (NMNHU-P 3335) in lateral view. Arrows in **D** and **F** mark the orifice of the canal described in the text, the lower arrows in **J** and **L** mark the broken base of the processus palatinus, the upper arrows mark the crista running onto the processus frontalis, and the arrows in **Q** and **R** mark the oblique groove crossing anteromedially onto the medial surface of the bone. All specimens are at the same scale.

Fig. 8. *Pelobates* sp. **A–C.** Frontopariétal (NMNHU-P 3338), en vues dorsale (**A**) et ventrale (**B**). **C** est un dessin interprétatif de **B**. **D–E.** Maxillaire gauche de juvénile. NMNHU-P 3336 en vues interne (**D**) et externe (**E**). **F–G.** Maxillaire gauche (NMNHU-P 2089), en vues interne (**F**) et externe (**G**). **H–I.** Maxillaire gauche (NMNHU-P 2090), en vues interne (**H**) et externe (**I**). **J–K.** Partie antérieure du maxillaire droit (NMNHU-P 3302), en vues interne (**J**) et externe (**K**). **L–M.** Partie antérieure du maxillaire gauche (NMNHU-P 2091), en vues interne (**L**) et externe (**M**) (retourné pour comparaison). **N–O.** Vertèbre présacrée (NMNHU-P 3540), en vues dorsale (**N**) et ventrale (**O**). **P.** Partie postérieure de l'angulaire droit (NMNHU-P 3303) en vue dorsale. **Q.** Ilium gauche (NMNHU-P 3328) en vue latérale. **R.** Ilium gauche (NMNHU-P 3335) en vue latérale. Les flèches en **D** et **F** indiquent l'orifice du canal décrit dans le texte, les flèches les plus basses en **J** et **L** montrent la base brisée du processus palatinus et les flèches les plus hautes la crista le long du processus frontalis ; en **Q** et **R**, les flèches indiquent le sillon oblique traversant antéromédialement la surface médiale de l'os.

the margo orbitalis. The frontoparietal incassation is well delimited.

All maxillae are fragmentary, but some important features are observable. The sculpture in the largest individual (NMNHU-P 3302, Fig. 8K) is the same as in the frontoparietal NMNHU-P 3338, i.e. transitional between pitted and pustular, but differs from that in NMNHU-P 2091, which is uniformly pitted (without signs of pustules). Differences are also in that NMNHU-P 3302 is ornamented up to the lower margin of the bone, whereas NMNHU-P 2091, even if it is from the same level of the bone, has the lower margin smooth. However, NMNHU-P 2090 (Fig. 8I), which is a fragment of the posterior part of the bone, combines smooth margin with a pitted and pustular sculpture, so it is difficult to decide whether the type of sculpture and the smooth or ornamented margin of the maxilla represent some morphological types.

Rather distinct is a small left maxilla (NMNHU-P 3336 – Fig. 8D and E), the estimated length of which is about 10 mm. Its outer surface is heavily sculptured, but the pits along the margo orbitalis are shallower than those in the lower part of the bone. In inner view, the lamina horizontalis runs out posteriorly in a prominent processus pterygoideus. This process is connected with the margo orbitalis by a sharp edge, posterior to which there is a deep depression. The anterior wall of this depression is pierced by the orifice of a large canal for the ramus maxillaris superior (marked by arrows in Fig. 8D and F). Dorsally, the depression is roofed by another sharp edge, which, together with the dorsal outer margin of the bone, delimits the triangular indentation, which is obviously the contact area for the squamosal. The groove for the palatoquadrate bar is deep, wide, pierced by several small foramina, and delimited dorsally by a well-pronounced edge. Between the latter and the outer margin of the bone, the margo orbitalis is broad and only moderately concave. This maxilla is about less than half size of the other pelobatid maxillae from Gritsev, but it is difficult to decide whether it belonged to a juvenile or fully-grown adult.

The vertebra NMNHU-P 3540 (Fig. 8N and O) bears general pelobatid features and probably may be V_7 or V_8 . The right angular NMNHU-P 3303 (Fig. 8P) has a typically elongated, widely rounded, and dorsoventrally compressed coronoid process, which is markedly concave in its posterior half. The sulcus for Meckel's cartilage is broad, rather dorsal in the preserved part of the bone.

Both ilia (Fig. 8Q and R) display typical pelobatid morphology; namely, the pars ascendens is separated from the dorsal margin of the ala ossis ilii by a groove (marked by arrows in Fig. 8Q and R) passing from the outer surface of the bone anteromedially onto the inner side, where the groove may continue for a short distance. Anteriorly, there is a distinct albeit shallow groove along the dorsal margin of the ala, slightly deeper laterally than medially. This is the contact surface for the dilated transverse process of the sacral vertebra. The posterior part of the ala up to the groove is simply rounded on its dorsal side.

Comparisons: The sculpture of the frontoparietal NMNHU-P 3338 is intermediate between the regular pitted type of *Eopelobates* and *Pelobates decheni* from the

Oligocene, and pustular type of recent *Pelobates* (Roček et al., 2014). If this evolutionary trend were to be recapitulated in the ontogeny of *Pelobates* from Gritsev, as it seems to be supported by regular, pitted sculpture in the fragment of small frontoparietal NMNHU-P 3320 and in the small maxilla NMNHU-P 3336 (Fig. 8D and E), then all the frontoparietals and maxillae of *Pelobates* from Gritsev would belong to a single species, different from both *Pelobates decheni* and all Recent species of *Pelobates*. However, it is also possible that the mentioned small frontoparietal and maxilla indicate the occurrence of another, smaller form of *Pelobates* in Gritsev. This seems to be evidenced by a thick layer of bone above the lateral orifice of the canalis arteriae temporalis, which suggests that the processus lateralis superior was well developed and that the individual was a fully-grown adult. Thus both possibilities are equally possible.

Bufonidae Gray, 1825.

Bufo Garsault de, 1764.

Bufo sp.

Material. 1 V_1 (NMNHU-P 3542 – Fig. 9A–C); 1 sacral vertebra (NMNHU-P 3304 – Fig. 9D–F).

Description. The atlas (Fig. 9A–C) is comparatively large (compared with the sacral vertebra), its neural arches are not preserved. Remarkable is its centrum, which is strongly dorsoventrally compressed. The sacral vertebra is smaller and its cotylus is only moderately ellipsoid, with a tiny foramen in its center. This is the orifice of the canal for the notochord that pierces the centrum and opens posteriorly between both condyles (marked by arrow in Fig. 9E). The sacral wings (although broken away close to their bases) suggest that they were inclined posterolaterally and only moderately extended.

Comparisons. Both vertebrae have a procoelous, dorsoventrally compressed centrum, which is, however, not semilunar as is the case with *Palaeobatrachus* (Vergnaud-Grazzini and Młynarski, 1969; Vergnaud-Grazzini and Hoffstetter, 1972). Besides, in *Palaeobatrachus*, both V_1 and V_9 are fused in adult individuals with adjacent vertebra (with V_2 and V_8 , respectively).

Remarks. Differences in the size and shape of the intervertebral joints may suggest that these vertebrae do not represent the same species.

Ranidae Gray, 1825.

Rana Linnaeus, 1758.

Rana sp.

Material. 1 ilium (NMNHU-P 3312 – Fig. 9G and H).

Description. The tuber superius is thin, as is the crista ilii, and prominent laterally, with faint ridges on its lateral surface. The ventral part of the iliac shaft is cylindrical so that its lower margin is widely rounded. In contrast, the upper part of the shaft is a thin lamina, with its dorsal margin as an acute edge termed the crista ilii. The lateral surface of the shaft is smooth, with a deep and well delimited depression between the cylindrical ventral part and the tuber superius. On the inner surface of the shaft there is a distinct horizontal groove parallel to its dorsal margin. The dorsal margin of the pars ascendens is broad and rounded, inclined medially. There is a circular pit between the tuber superius and the pars ascendens, close to the dorsal margin of the acetabulum. The anterior margin of

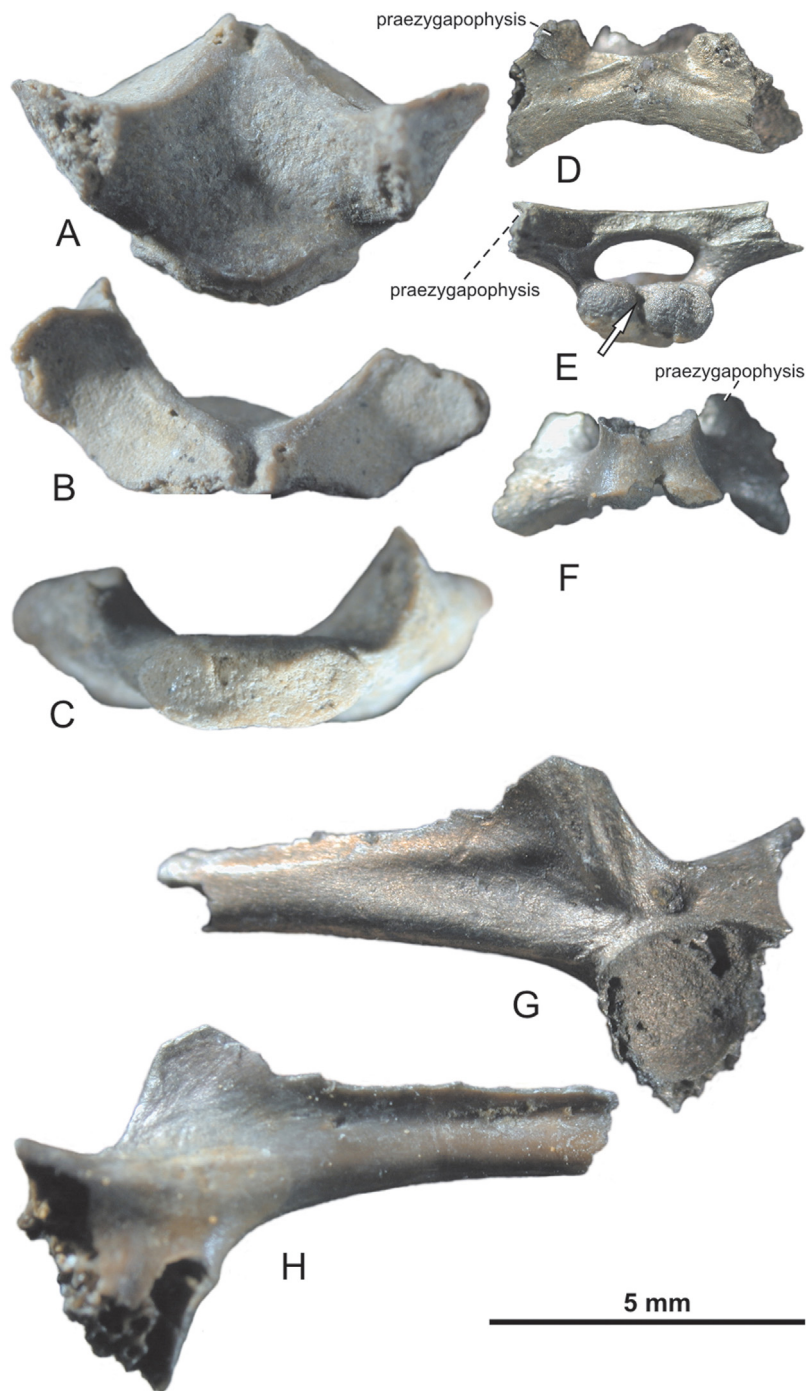


Fig. 9. *Bufo* sp. and *Rana* sp. **A–C** V_1 (NMNHU-P 3542) with neural arches broken away in dorsal (**A**), anterior (**B**), and posterior (**C**) views. **D–F** Sacral vertebra (NMNHU-P 3304) in dorsal (**D**), posterior (**E**), and ventral (**F**) views. The arrow marks the foramen for the notochord that passes through the centrum. **G–H.** *Rana* sp. (NMNHU-P 3312) in lateral (**G**) and medial (**H**) views. All specimens are at the same scale.

Fig. 9. *Bufo* sp. et *Rana* sp. **A–C.** V_1 (NMNHU-P 3542) avec les arcs neuraux brisés ôtés, en vues dorsale (**A**), antérieure (**B**), postérieure (**C**). **D–F.** Vertèbre sacrée (NMNHU-P 3304), en vues dorsale (**D**), postérieure (**E**) et ventrale (**F**). La flèche indique le foramen pour le notochorde qui traverse le centre. **G–H** *Rana* sp. (NMNHU-P 3312), avec vues latérale (**G**) et médiale (**H**). Tous les éléments sont figurés à la même échelle.

the acetabulum extends beyond the level of the anterior margin of the pars descendens.

Reptilia Linnaeus, 1758.

Gekkota Camp, 1923

Gekkota indet.

Material. 1 dentary (NMNHU-P 2018 – Fig. 10A).

Description. The dentary is tiny and slender (length of the fragment is about 3.5 mm). The teeth are blunt cones,

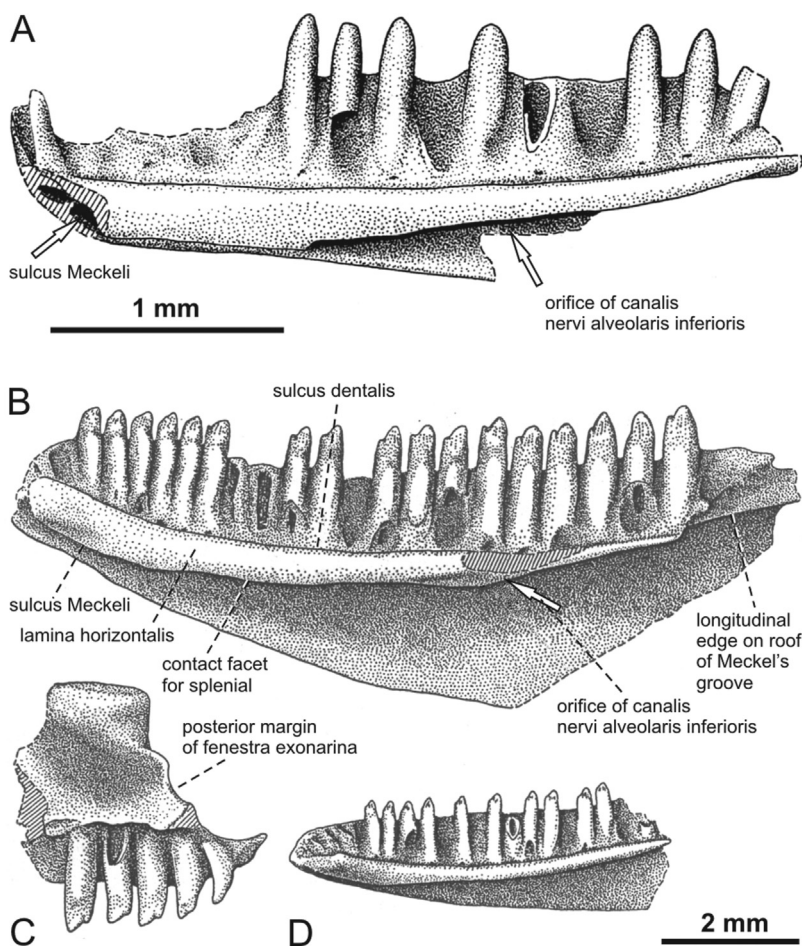


Fig. 10. **A.** Gekkonidae indet., juv. (NMNHU-P 2018), right dentale in inner aspect. **B.** *Lacerta* sp., type I (NMNHU-P 1964), right dentale in inner aspect. **C.** *Lacerta* sp. (NMNHU-P 2034), left maxilla in inner view. **D.** *Lacerta* sp., type II (NMNHU-P 1984), right dentale in inner aspect. The Lacertidae are at the same scale.

Fig. 10. **A.** Gekkonidae indet., juv. (NMNHU-P 2018), dentaire droit dans son aspect interne. **B.** *Lacerta* sp., type I (NMNHU-P 1964), dentaire droit dans son aspect interne. **C.** *Lacerta* sp. (NMNHU-P 2034), maxillaire gauche en vue interne. **D.** *Lacerta* sp., type II NMNHU-P 1984, Dentaire droit dans son aspect interne. Les Lacertidae sont à la même échelle.

dark pigmented in their upper parts. Meckel's groove is closed in its anterior part, but the suture running on the ventral edge of the bone is still discernible. There is a low vertical longitudinal crista separating Meckel's groove from the orifice of the canalis nervi alveolaris inferioris (marked by an arrow in Fig. 10A). It is obvious that originally the bone was slender and long.

Remark. It can be determined, although with some doubts, as a juvenile gekkotan.

Lacertidae Bonaparte, 1831.

Lacerta sp., type I.

Material. 28 dentaries (NMNHU-P 1962; 1963; 1964 – Fig. 10B; 1965; 1966; 1968; 1969; 1970; 1972; 1973; 1978; 1982; 1983; 1985; 1988; 1991; 1992; 1994; 1995; 1997; 2002; 2009; 2010; 2017; 2021; 2022; 2027; 2035); 9 maxillae (NMNHU-P 2123; 2025; 2030; 2031; 2034 – Fig. 10C; 2042; 2049; 2132; 2138).

Description. The dentary is comparatively deep; the orifice of the canalis alveolaris inferioris in the roof of the sulcus Meckeli (Fig. 10B) is at the level of about 17th tooth

position (counted from the anterior; Edmund, 1960). The teeth in the posterior and middle sections of the bone are bicuspid, those in the anterior section are monocuspid, the tip being shifted posteriorly. Only in some specimens the most posterior teeth are three cuspid. The upper lingual part of each tooth is slightly striated. The outer surface of the bone is pierced by four to five foramina pro rami nervorum alveolarium inferiorum. In general, the bone does not differ from the generalized lacertid dentary described by Roček (1984, figure 1, plates IV, V) from the lower Miocene of Dolnice. The uniformity of lacertid dentaries was also confirmed by Čerňanský (2016) and Čerňanský et al. (2016).

The maxillae were associated with type-I dentaries based on the size and morphology of the teeth. The smooth part of the outer surface of the bone is pierced by a row of the foramina pro rami nervorum alveolarium superiorum, which are located at half distance between the lower margin of scutes and the crista dentalis. Posterior foramina in this row are in shallow but distinct horizontal depression. The scutes coalesced to the bone are only moderately

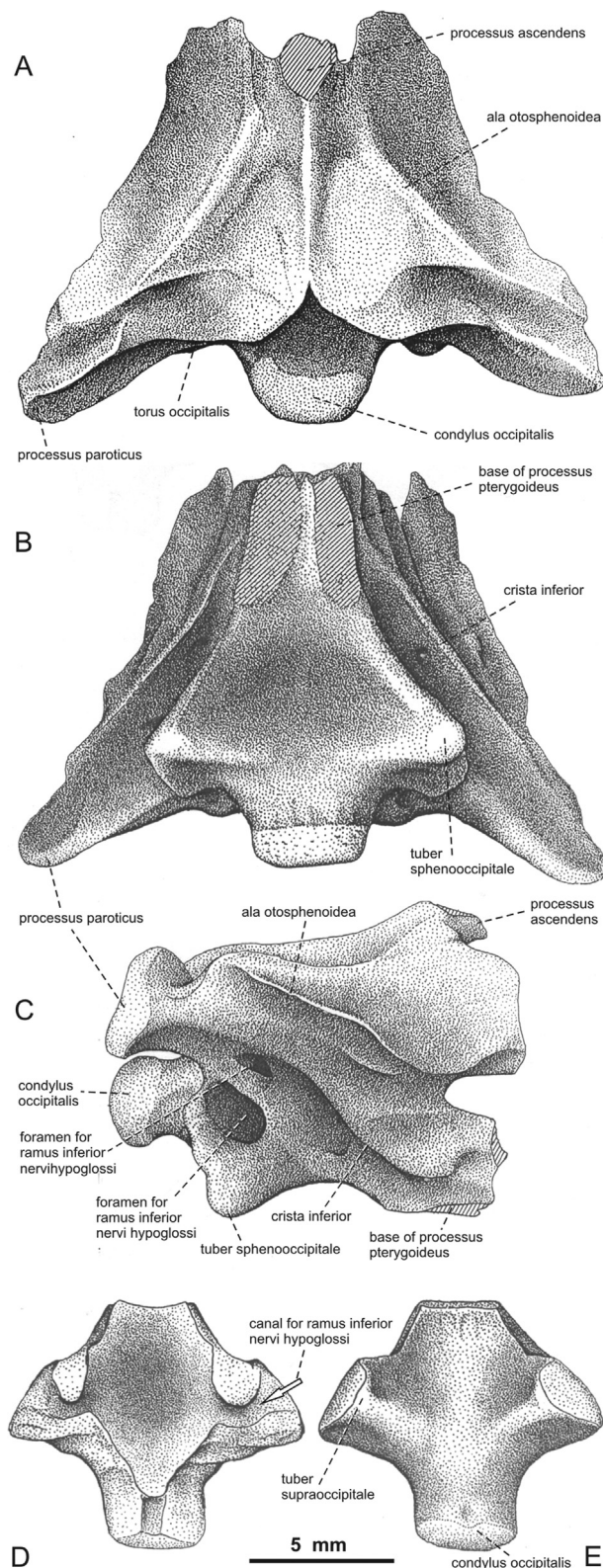


Fig. 11. *Pseudopus pannonicus* (Kormos, 1911). A–C. Occipital element (NMNHU-P 3390) in dorsal (A), ventral (B), and dextral (C) views. D–E. Isolated basioccipital (NMNHU-P 3453) in dorsal (D) and ventral (E) views. All specimens are at the same scale.

wrinkled. The posterior margin of the fenestra exonarina is rather prominent but rounded; that on the outer side of the bone is protruding in a tip that represents the most anterior part of the bone (Fig. 10C). The vertical part of the posterior wall of the fenestra exonarina is pierced by the anterior orifice of the canalis nervi alveolaris superioris. The margo orbitalis is rounded. In inner aspect, the inner margin of the wall of the fenestra exonarina does not join the anterior margin of the vertical wall of the bone but instead, it runs out in a blunt process and then it turns posteriorly and joins the inner surface of the vertical wall. The lamina horizontalis is thin, with irregular (not straight) margin. There is a deep smooth depression between the margin of the fenestra exonarina and an oblique crista running posterodorsally from the margin of the lamina horizontalis. The posterior orifice of the canalis nervi alveolaris superioris is large, communicating directly with the most posterior foramen pro ramus nervi alveolaris superioris, which is located at the same level as the former (at the level of the 5th tooth position from behind).

Lacerta sp., type II.

Material. 9 dentaries (NMNHU-P 1976; 1980; 1984 – Fig. 10D; 2007; 2010; 2012; 2014; 2016; 2020).

Description. These dentaries are morphologically the same as type-I ones, but they differ by their small size. Intermediate forms are lacking. This might suggest that both types represent different species.

Remark. Some specimens of both types (e.g., NMNHU-P 1967, 2040) have bicuspid teeth constricted below their tips, so that the small cusp is seemingly directed anteriorly. However, closer examination revealed that the enamel of those teeth is worn out, so that the upper part of the crown is thinner than its upper end. Hence, this is an artefact, not a taxonomic feature.

Lacertidae indet.

Material. One dentary (NMNHU-P 1979).

Description. Small lacertid dentary, different from those described above as *Lacerta* sp. in having three cuspid teeth in the middle of the bone (16th tooth position).

Remark. The teeth are reminiscent of those in *Miolacerta* (Roček, 1984, pl. VI, Figs. 6 and 7, pl. VII, Figs. 1 and 2), but more precise comparison is not possible due to the fragmentary nature of the specimen. It is difficult to decide whether this feature is only due to intraspecific variation or if it is of taxonomic importance.

Lacertidae indet.

Material. One dentary (NMNHU-P 2019); 5 maxillae (NMNHU-P 2028, 2029, 2052, 2053, perhaps also 2043).

Description. The teeth on the dentary are low (only 1/3 of their depth exceeds over the level of the crista dentalis) and blunt. The labial surface of some of them can continue without any distinct border into the outer surface of the bone. In lingual aspect, the tooth crowns are convex, but they may be moderately compressed from the lingual side

Fig. 11. *Pseudopus pannonicus* (Kormos, 1911). A–C. Élément occipital (NMNHU-P, 3390), en vues dorsale (A), ventrale (B), dextrale (C). D–E. Basioccipital isolé (NMNHU-P 3453), en vues dorsale (D) et ventrale (E).

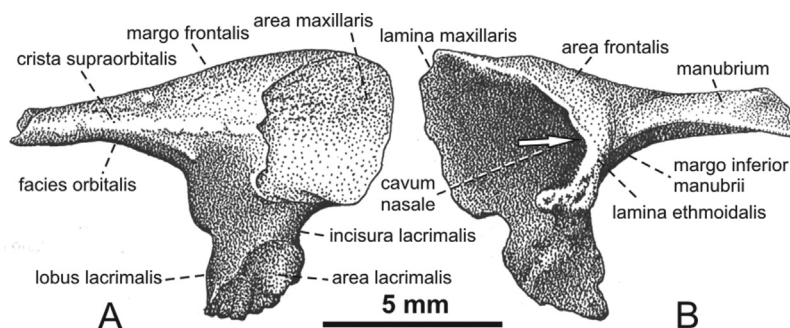


Fig. 12. *Pseudopus pannonicus* (Kormos, 1911). **A–B.** Right praefrontal (NMNHU-P 3378) in outer (A) and inner (B) views. Cavum nasale marked by an arrow.
Fig. 12. *Pseudopus pannonicus* (Kormos, 1911). **A–B.** Préfrontal droit (NMNHU-P 3378), en vues externe (A) et interne (B). La cavité nasale est indiquée par une flèche.

below their upper ends. The lamina horizontalis is straight, with a rounded margin, and with distinct contact facet for the splenial in its posterior part. The sulcus dentalis is deep. The anterior section of Meckel's groove is facing medially rather than ventromedially.

As in the genus *Lacerta*, the margo orbitalis of the maxilla is low and rounded. On the outer surface of the bone, the most posterior of the foramina pro rami nervi alveolaris superioris is the largest. At about the level of this most posterior foramen, or slightly anterior to it, is the posterior orifice of the canalis nervi alveolaris superioris. In contrast to *Lacerta*, the anterior margin of this orifice is not lifted so that the orifice is facing from the dorsal surface of the lamina horizontalis dorsally, not posteriorly. The lamina horizontalis, if viewed from the inner side, is convex medially, slanting down both anteriorly and posteriorly. In some specimens it may be quite broad in its medial part, exceeding considerably the level of the tooth row. The edge of the crista that runs posterodorsally from the margin of the lamina horizontalis onto the inner surface of the vertical wall of the bone is directed posteriorly. There are moderately wrinkled scutes coalesced to the outer surface of the bone.

Remark. The elements of this fragmented material have been associated with each other based on their teeth, but it is not granted that it belongs to a single taxon. On the other hand, their assignment to Lacertidae is very probable, and differences from the genus *Lacerta* suggest that there was another lacertid lizard in Gritsev.

Anguidae Gray, 1825.

Anguinae Gray, 1825.

Ophisaurus Daudin, 1803.

Ophisaurus sp.

Material. Four dentaries (NMNHU-P 1971, 1974, 2107, 2116).

Description. The teeth are blunt cones not compressed latero-medially, hence without anterior and posterior vertical ridges. The number of the tooth positions in complete dentaries is 17. The crista splenialis at the level of 6–7th tooth position is the lowermost part of the bone; due to this, Meckel's groove opens ventrolaterally. The spina splenialis is at the level of 10th tooth position (in contrast to *Ophisaurus spinari* from Dolnice (MN 4) where it is at the level of the 4–5th tooth position) and in no specimen from Gritsev it is inclined posteriorly. On the outer surface, the number of the foramina nervi alveolaris inferioris

ranges from 4 to 6. The processus supraangularis is reaching approximately the same level as the processus coronoideus. The incisura coronoidea represents the posterior margin of the contact facet for attachment of the coronoid. A similar facet (for attachment of the angular and supraangular) is close to the lower margin of the bone, within the extent of the sinus supraangularis and processus angularis. The orifice of the canalis nervi alveolaris inferioris is situated at the level of the 4–6th tooth positions from behind. This feature may, however, be dependent on individual age.

Remark. It should be noted that *O. spinari* was established by Klembara (1979) based on the parietal, and the association of the dentaries from the same locality and horizon with this species was based mainly on morphometric data (Roček, 1984: 39). Klembara (1981) assigned these dentaries (illustrated in his pl. III, Figs. 1–3) only to the genus *Ophisaurus*.

Pseudopus Merrem, 1820.

Pseudopus pannonicus (Kormos, 1911).

1911 *Ophisaurus pannonicus* – Kormos, p. 17, figure 19.

1912 *Ophisaurus novorossicus* – Alekseyev, p. 15.

1913 *Ophisaurus intermedius* – Bolokay, p. 221.

1913 *Varanus deserticolus* (partim) – Bolokay, p. 222.

1913 *Anguis polgardensis* – Bolokay, p. 222, pl. XII, figure 1.

1923 *Ophisaurus pannonicus* (ex err.) – Fejérváry-Lángh, p. 178.

1981 *Pseudopus pannonicus* – Klembara, p. 136.

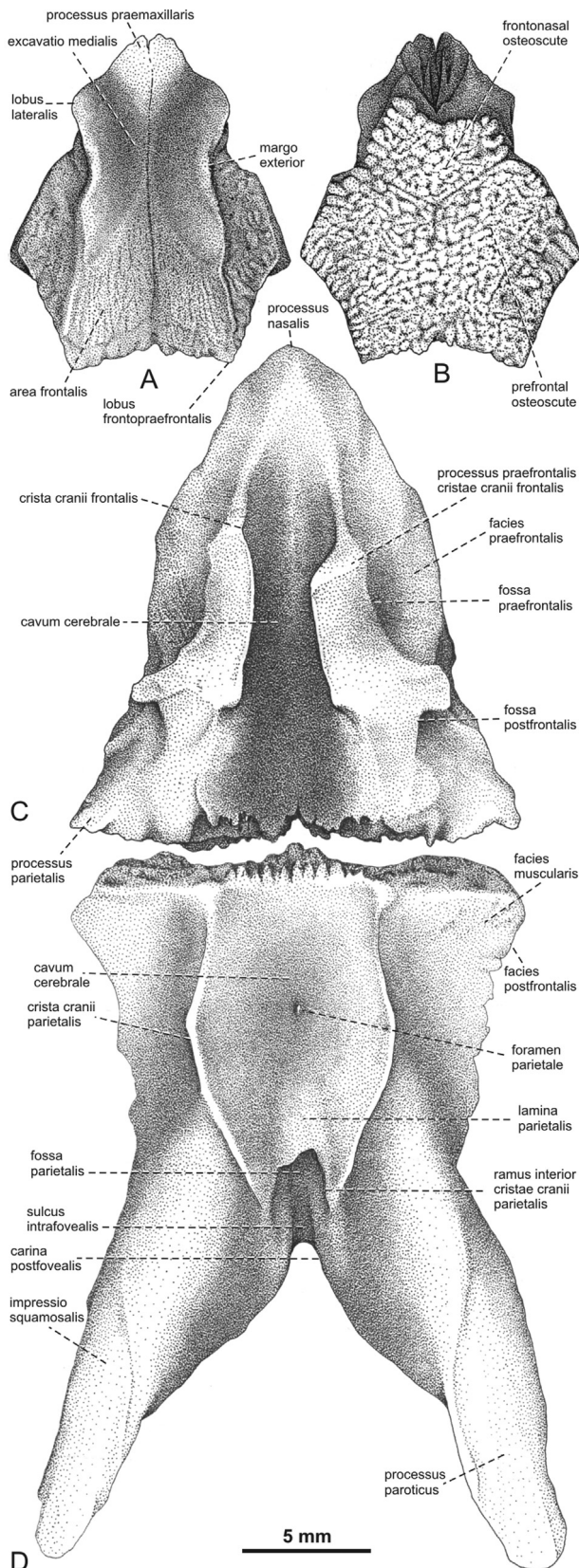
Holotype. Not stated.

Neotype. Left dentary; Hungarian Geological Institute (Magyar Állami Földtani Intézet, Budapest), Coll. No. MÁFI Ob 5058. Illustrated in Kormos (1911, figure 19/1).

Type locality. Polgárdi (West Hungary); now Polgárdi 2 (Venczel, 2006).

Stratum typicum. Late Miocene (MN 13).

Diagnosis (amended on the basis of material from Gritsev). Similar to *Pseudopus apodus* (see Klembara et al., 2014, 2017 and Čerňanský et al., 2019 for comparisons), but larger (estimated body length ca. 200 cm, max. skull length ca. 9–10 cm); higher number of maxillary teeth and of foramina maxillaria; greater development of muscle crests and tubercles (e.g., proc. zygomaticus jugalis, which is prominent posteriorly; Fig. 16C); thicker osteoscutes; parietal broader, with the axes separating interparietal, parietal and occipital scutes being nearly



perpendicular, this being apparent even in very young specimens (Bachmayer and Mlynarski, 1977: 292; Estes, 1983: 142). Frontonasal scutes fused into a single median and unpaired one, prefrontal scutes incompletely separated; however, young individuals may be closer to the pattern of *P. apodus* in this respect. Posterior teeth on jaws never fused and permanent as in old individuals of *P. apodus* (cf. Roček, 1980: 25, figure 3). Lymphapophysis of the first sacral vertebra without additional processes.

Material. 14 nasals, some of them fused in pairs (NMNHU-P 2075, 2076, 2876, 2877 – Fig. 13A, B, 3342–3344, 3347–3354); 6 frontals, some of them fused in pairs (NMNHU-P 2859 – Fig. 13C, 2871, 2872, 2875, 2880, 2881); 17 parietals (NMNHU-P 2857 – Fig. 14B, 2858 – Fig. 14D, 2860 – Fig. 14C), 2861, 2862, 2863 – Fig. 14F, 2864 – Fig. 13D and 14E, 2865 – Fig. 14G, 2866, 2867 – Fig. 14H, 2868 – Fig. 14K, 2869, 2870, 2873 – Fig. 14I, 2874 – Fig. 14J, 2878 – Fig. 14A, 2882; 44 maxillae (NMNHU-P 2642, 2653–2681, 2683–2686, 2711–2713, 2849 – Fig. 15C, 2850–2856, 3159); 5 intermaxillae (NMNHU-P 2648–2651, 2652 – Fig. 15A); 50 dentaries (NMNHU-P 2602–2641, 2643–2645, 2646 – Fig. 15E, 2647–2648, 2682, 2687, 2689, 2708–2710, 2716); 18 supraangulals (NMNHU-P 2714–2715, 2718, 2721–2726, 2729, 2731–2733, 2845, 2846 – Fig. 15F, 2847, 2848, 2879).

Description. The occipital segment represents the posterior part of the neural endocranium and includes both otic capsules. In posterior view, there is a big, crescent-shaped condyle called the pars condyloidea ossis basioccipitalis by Fejérváry-Lángh (1923, figure 1); its upper lateral margin exceeds the level of the bottom of the foramen magnum. The otic capsule is prominent into the braincase (bulla vestibulocochlearis sensu Fejérváry-Lángh, 1923, figure 1). In ventral aspect (Fig. 11B), two prominent tubera sphenoccipitalia with their tips devoid of periost are located posteriorly, and two ventrolaterally and slightly anteriorly directed outgrowths with their distal ends dilated (for the attachment to the pterygoid), called the processus pterygoidei, are below the anterior end of the segment. In all available specimens, these processes are broken off at their bases, except in NMNHU-P 3393, where it is present on one side, though without the tip. In comparison with *P. apodus*, the cristae on the dorsal surface are well developed. If viewed anteriorly, there is a pit in the bottom of the braincase. The walls of the braincase are thin and often broken off (except for the margins of the fontanella prootica) in this anterior part of the bone.

The basioccipitale can be incompletely coalesced with the rest of the complex in younger individuals (as it is in adults of *Pseudopus apodus*), so it may be found isolated in the fossil material (Fig. 11D and E). If viewed from its

Fig. 13. *Pseudopus pannonicus* (Kormos, 1911). A–B. Nasals (NMNHU-P 2877) in ventral (A) and dorsal views (B). C. Frontal (NMNHU-P 2859) in ventral view. D. Parietals (NMNHU-P 2864) in ventral view. All specimens are at the same scale.

Fig. 13. *Pseudopus pannonicus* (Kormos, 1911). A–B. Os nasaux (NMNHU-P 2877), en vues ventrale (A) et dorsale (B). C. Os frontal (NMNHU-P 2859) en vue ventrale. D. Os pariétaux (NMNHU-P 2864) en vue ventrale. Tous les éléments sont figurés à la même échelle.

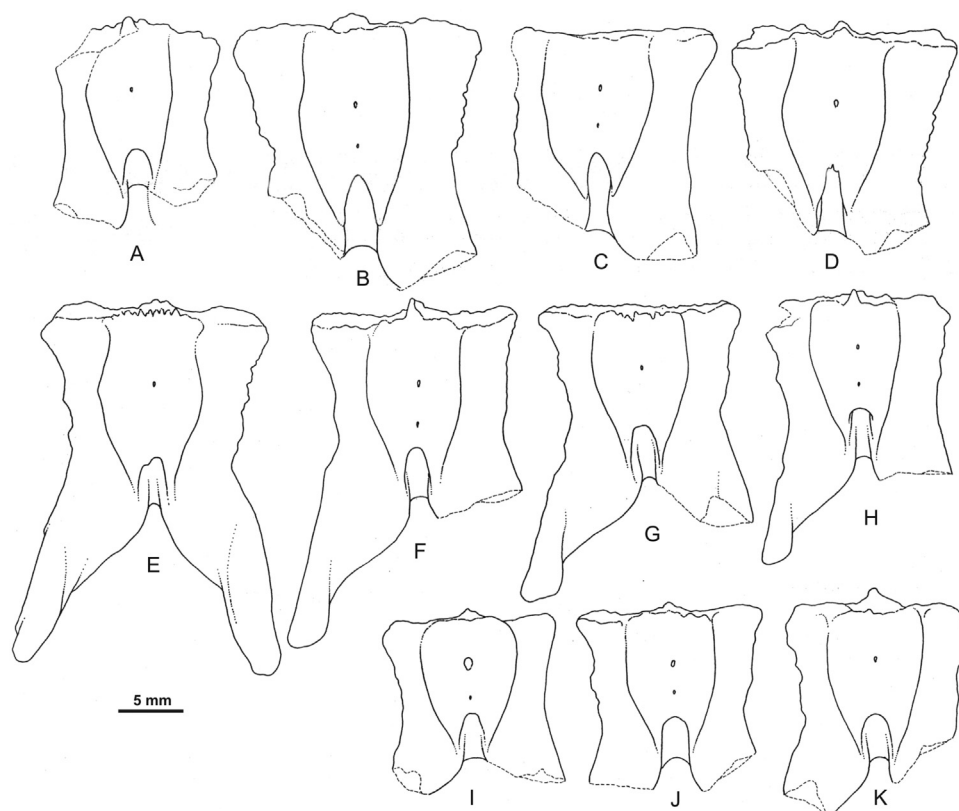


Fig. 14. *Pseudopus pannonicus* (Kormos, 1911). Variation in shape of the parietals (ventral view). **A** – NMNHU-P 2878. **B** – NMNHU-P 2857. **C** – NMNHU-P 2860. **D** – NMNHU-P 2858. **E** – NMNHU-P 2864. **F** – NMNHU-P 2863. **G** – NMNHU-P 2865. **H** – NMNHU-P 2867. **I** – NMNHU-P 2873. **J** – NMNHU-P 2874. **K** – NMNHU-P 2868.

Fig. 14. *Pseudopus pannonicus* (Kormos, 1911). Variations dans la forme des os pariétaux, en vue ventrale. **A** – NMNHU-P 2878. **B** – NMNHU-P 2857. **C** – NMNHU-P 2860. **D** – NMNHU-P 2858. **E** – NMNHU-P 2864. **F** – NMNHU-P 2863. **G** – NMNHU-P 2865. **H** – NMNHU-P 2867. **I** – NMNHU-P 2873. **J** – NMNHU-P 2874. **K** – NMNHU-P 2868.

inner (dorsal) side (Fig. 11D), one can trace the course of the canalis pro rami inferioris nervi hypoglossi (see also Fig. 11C).

As regards the quadratum (Fig. 12), there are no obvious morphological differences between these bones in *P. apodus* and *P. pannonicus*. In older individuals, the incisura postfrontalo-squamosalis may be nearly closed by distal parts of the condylus cephalicus and epiphysis columnaris. In *P. apodus*, Fejérváry-Lágh (1923: 148) found in the same place a sesamoid ossification called by her the “sesamum columnarium ossis quadrati.” The margin of the sharp vertical crista running on the inner surface of the bone (called the crista pterygoidea) may be irregularly serrated and thickened in older individuals, which obviously reflects insertion of strong muscles.

The antero-posterior diameter of the nasals (Fig. 13A and B), measured between the processus praemaxillaris and lobus frontoparietalis, ranges between 10 and 15 mm. Those nasals, in which the maximum value of this diameter is less than 13 mm, are separated in the midline, whereas those that are larger are coalesced in the median suture. Apparently, the fusion proceeded towards the anterior, which is suggested by a not yet fully closed suture between both processus praemaxillares. Only in the largest specimen, the suture was completely closed. The

dorsal surface of the bones is covered by secondary dermal ossifications called by Fejérváry-Lágh (1923: 191) the ossicula dermalia (osteoscutes or osteodermal shields of other authors). They have vermiform ornamentation and are coalesced with underlying nasals. In living animals, the osteoscutes were covered with epidermal scutes; however, their shape and size did not necessarily correspond (Meszoely, 1970, figure 1). The anterior part of the nasals is adjoined by an unpaired, median osteoscuta termed the ossiculum dermale frontonasale (Fejérváry-Lágh) or the frontonasal osteoscuta (Fig. 13B). There is no trace of the median division of this element in large specimens, but in smaller individuals where both nasals are separated, it is broken in two symmetrical parts, which suggests its paired origin (median subdivision marked by groove may be found in some specimens of *P. apodus*; Klembara et al., 2017). The posterior elements are usually termed the prefrontal osteoscutes (ossicula dermalia praefrontalia of Fejérváry-Lágh) and may be separated by a more or less complete line of division. In ventral view (Fig. 13A), both nasals are distinctly narrower than the prefrontal osteoscutes. The median suture between both nasals depends on the degree of individual development. Both processus praemaxillares are blunt, but they meet in the midline in a prominent and sharp ridge. Farther posteriorly, this median ridge is less

prominent and rounded. There is a deep, posteriorly facing concavity between the dorsal surface of the processus praemaxillares and ventral surface of the frontonasal osteoscut. The anterior inner surface of the nasals is smooth and arch-like depressed (excavatio medialis; Fejérváry-Lángh); it is separated from the posterior part of the surface, which is antero-posteriorly striated and called the area frontalis (Fejérváry-Lángh), by a distinct border diverging from the midline. The lateral margin of both nasals (margo exterior) is prominent and, in the middle of its length, it forms together with the ventral surface of the prefrontal osteoscut a deep groove-like concavity. The exposed ventral surface of the osteoscut is moderately sculptured and pierced by several small foramina in the bottom of irregular grooves. Except for the age-dependent degree of fusion of both nasals, some variation seems to exist in the size and proportions the osteoscutes.

The length of the frontals ranges between 15.0 and 19.5 mm. Both are firmly coalesced, but suture may be apparent in some specimens on the dorsal surface of the bone not covered by the frontonasal and prefrontal scutes (NMNHU-P 2872, 2859, 2881), and rarely also on the ventral surface between both cristae frontales (NMNHU-P 2872, 2881). The presence of vestigial suture is not correlated with size (i.e. it may occur also in the largest individuals). The frontal epidermal scale is unpaired, either well separated from the frontoparietal scale and from the most anterior part of the interparietal and supraorbital scales (NMNHU-P 2875, 2859, 2880) or the grooves between the scales are obliterated. This feature is also not correlated with age. In NMNHU-P 2859, the right frontoparietal scale is divided into two parts. If the supraorbital scale is broken off on both sides (NMNHU-P 2871), the frontal scale is seemingly narrow and constricted in the middle of its length. That this is due to lack of the supraorbital scutes is evidenced by the fact that the epidermal cover of the frontal is narrower than the width of the bone. In ventral view, some variation exists in the extent of the contact area for the palatine and in the morphology of the bone between both cristae cranii frontales, namely, in some specimens, there are two longitudinal depressions separated by a median rounded ridge within the extent of the anterior half of the cristae; in other specimens, such depressions are poorly developed or entirely absent. The presence or absence of the median suture between both bones and of the sutures between epidermal scutes (see also Bailon, 1991, figure 45D; Klembara, 1986: 95), as well as the morphology of the ventral surface of the bone, seem to depend on individual, not developmental variation. The frontal assigned to *Pseudopus* cf. *P. pannonicus* by Bailon (1991, fig. 45D) differs in having short, stout, posterolateral process exceeding posteriorly the level of the median part of the bone, whereas in the material from Gritsev as well as that from Ivanovce and Tardosbanya (Klembara, 1986, pl. III, figures 5–7), the posterior margin of the bone is nearly straight.

The largest complete parietals from Gritsev reached 28 mm (NMNHU-P 2864) though, according to the proportions, there were also larger specimens that supposedly reached about 30 mm. The epidermal scales may be either well delimited or entirely fused. As is the case with

frontals, this feature is not correlated with size because sutures between scales are obliterated both in the smallest (NMNHU-P 2882) and the largest (NMNHU-P 2857) specimens. The scales may reach up to the lateral margin of the bone or this part of the bone may be exposed. The foramen parietale is always apparent on the ventral surface of the bone; however, its dorsal orifice is obliterated in those individuals in which also sutures between the epidermal scales are obliterated. In some specimens (e.g., NMNHU-P 2857, 2863, 2867, 2874), there is a similar opening on a low convexity in the midline that reflects the anterior part of the fossa parietalis. It is, however, a mere pit that does not communicate with the fossa. A similar condition was found by Bachmayer and Młynarski (1977: 293) in a large individual from Deutsch Altenburg. The material from Gritsev indicates that the presence or the absence of this pit is not related to developmental variation, but is just an individual variation. As it is obvious from Fig. 14, there is some variation in the morphology of the fossa parietalis. This set of characters was used by Klembara (1979: 167) for distinction between the genera *Ophisaurus* and *Pseudopus*; however, *Pseudopus pannonicus* from Gritsev displays both conditions. In contrast to this, the bone always exceeds laterally both cristae parietales and consequently the facies muscularis is well developed in all specimens. Considerable variation may be observed in the length and proportions of the posterolateral processes (processus parotici sensu Bachmayer and Młynarski, 1977: 293, processus supratemporales sensu Klembara, 1979, Fig. 2). This is obvious also from comparisons of the specimens illustrated in Fig. 14E–H.

The largest complete maxilla (NMNHU-P 2849, Fig. 15C) is 24 mm long. In this specimen, the number of teeth is 11 (Bachmayer and Młynarski, 1977: 293 and Klembara, 1986 give the maximum 12). The smallest maxilla NMNHU-P 2713 is almost complete and its estimated length is about 10 mm. Its tooth row is comprised of 9 teeth. The 7th tooth is the largest in all specimens. The teeth, except the most anterior ones, are close to one another, blunt, with an obtuse point that is slightly striated. In some specimens, the striated part of the teeth is black, as it is the case with some intermaxillae. One cannot say whether blunt teeth are also in younger specimens. In *P. apodus* blunt teeth are characteristic of older individuals, and those in the posterior section of the tooth row become even permanent and consequently worn off (Roček, 1980, Fig. 3). Anteriorly, the lamina horizontalis is bifurcated into two processes, the anterior one being adjoined to the processus maxillaris of the praemaxilla, and the anteromedial one being directed towards the anterior part of the vomer. The anterior and posterior margins of the latter process continue onto the dorsal surface of the lamina horizontalis as two cristae. The anterior one is higher, joining the narial margin of the maxilla; the posterior one is lower and continues posterodorsally onto the inner surface of the lamina horizontalis. At the level between the 6th and 7th teeth, there is an orifice of the canalis nervi alveolaris superioris. On the outer surface are 6–7 foramina for branches of the rami nervorum alveolarium superiorum, the anterior of them being sometimes accompanied by small additional ones. Close dorsal to these foramina is the margin of the area covered

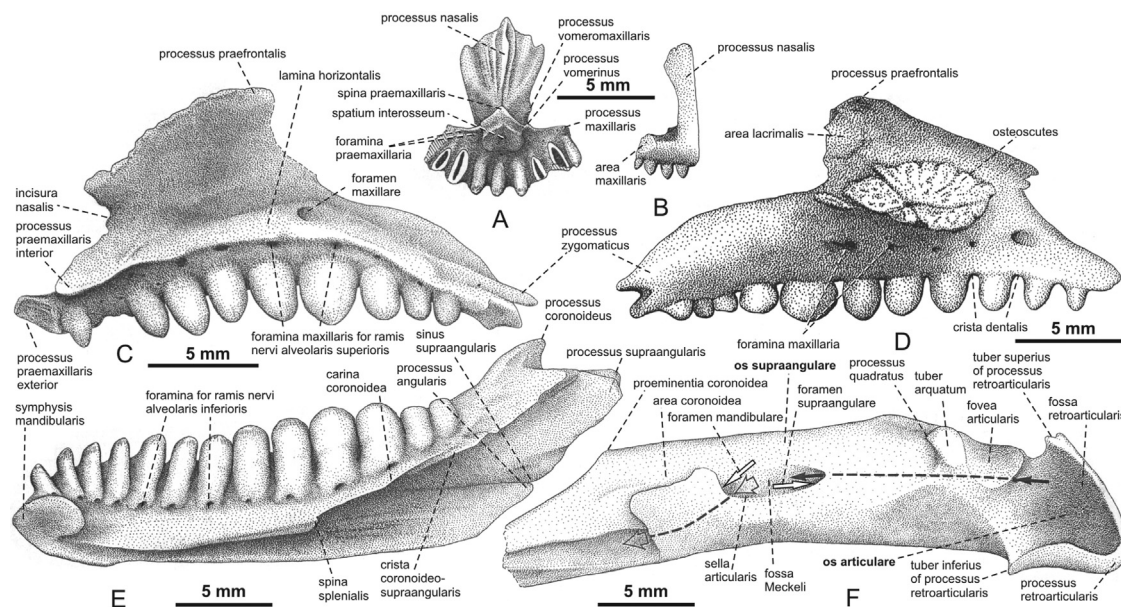


Fig. 15. *Pseudopus pannonicus* (Kormos, 1911). **A.** Intermaxilla (NMNHU-P 2652) in inner view. **B.** Right praemaxilla in anterior view (NMNHU-P 3104). **C.** Right maxilla (NMNHU-P 2849) in inner view. **D.** Right maxilla in outer view (NMNHU-P 3159). **E.** Right dentale (NMNHU-P 2646) in inner view. **F.** Left articulare + supraangulare complex (NMNHU-P 2846) in inner view. The black arrows mark the canal connecting the fossa retroarticularis and the fossa Meckeli; the empty arrows mark course of sulcus pro cartilago Meckeli.

Fig. 15. *Pseudopus pannonicus* (Kormos, 1911). **A.** Intermaxillaire (NMNHU-P 2652) en vue interne. **B.** Vue antérieure du prémaxillaire droit (NMNHU-P 3104). **C.** Maxillaire droit (NMNHU-P 2849) en vue interne. **D.** Maxillaire droit (NMNHU-P 3159) en vue externe. **E.** Dentaire droit (NMNHU-P 2646) en vue interne. **F.** Complexe articulaire + supraangulaire gauche (NMNHU-P 2846) en vue interne. Les flèches noires indiquent le canal reliant les fossa retroarticularis et fossa Meckeli ; les flèches blanches indiquent le chemin du sulcus pro cartilago Meckeli.

by a row of the epidermal scales (see also Bachmayer and Mlynarski, 1977, pl. II, Figs. 9 and 16; Klembara, 1986, pl. III, Fig. 4A). More dorsally, the epidermal scales are detached in disarticulated maxillae. In *P. apodus*, these scales are located higher up and are much thinner. Therefore, this character may be useful for distinguishing between the two species.

The intermaxilla (Fig. 15A) is a compound bone that takes its origin from a pair of premaxillae (Fig. 15B). The tooth number in the intermaxilla is 7–9 (cf. Bachmayer and Mlynarski, 1977, pl. I, Fig. 7), the odd tooth being located in the midline. Teeth are blunt, with their upper part striated and, in some individuals (e.g., NMNHU-P 2652), distinctly black. The articular facet on the processus maxillares (Klembara et al., 2010, figure 3) is clearly delimited by more or less pronounced crista on the dorsal surface of the lamina horizontalis, which runs out in a point on the margin of the lamina above the most lateral tooth. Besides, the horizontal lamina also runs out in much more prominent median point. In some specimens (e.g., NMNHU-P 2650), another spine occurs between the median and lateral ones, continued as a sharp and rather high crista towards the base of the nasal process. Such additional spina and associated crista are developed to a lesser degree also in some other specimens and their presence cannot be taken as a species-differentiating character. On the dorsal surface of the lamina horizontalis, there is a vestige of the median suture that continues onto the inner surface of the nasal process. On the ventral surface of the lamina, in the midline, there is a characteristic infundibular structure.

The processus nasalis is pointed in NMNHU-P 2652, but such point probably may be also lacking (Bachmayer and Mlynarski, 1977: 294). NMNHU-P 3104 (Fig. 15B) is one single praemaxilla, not yet coalesced to its counterpart.

The prefrontal (Fig. 12) is a robust bone located within the anterior margin of the orbit and taking part in the formation of the nasal capsule. In inner aspect, one can see the cavity (cavum nasale), the outer wall of which is thin, but on its surface with well delimited contact area for the maxilla (area maxillaris). Medially, the cavum is delimited by a thin margo inferior, which is terminated ventrally by rather a thickened horizontal section that is called the lamina ethmoidalis by Fejérváry-Lágh (1923) (Fig. 12). However, she extended this designation also to a short convex section on the sharp lower margin of the manubrium. The lower part of the bone is a vertical lamina (lobus lacrimalis) delimited dorsally by the deep incisura lacrimalis. In outer view, one can see a smooth surface that takes part in the formation of the orbit, and two well delimited contact areas, the upper one for the maxilla and the lower one for the lacrimale. Both are separated from one another by a smooth surface that is delimited anteriorly by the margin of the incisura lacrimalis. This surface forms the medial wall of the canalis nasolacrimalis. The dorsal surface of the manubrium may be moderately wrinkled in older individuals, because in living animals it was adjoined by osteoscutes. What is called (and illustrated as a sharp edge) the crista supraorbitalis by Fejérváry-Lágh (1923, Fig. 12) is in *P. pannonicus* from Gritsev an only moderately prominent and rounded ridge. It seems that the manubrium is shorter in *P. apodus* than in

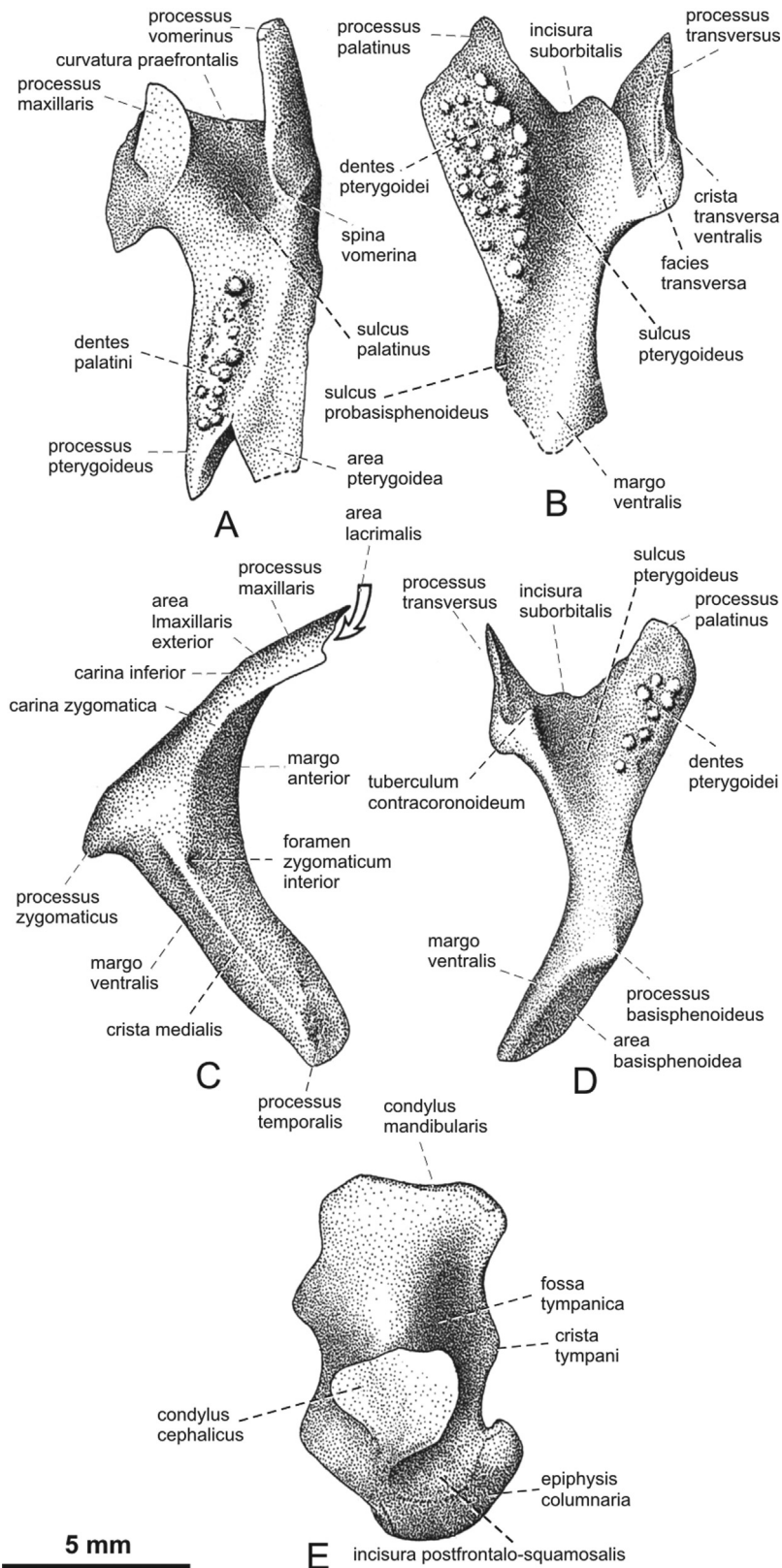


Fig. 16. *Pseudopus pannonicus* (Kormos, 1911). **A.** Right palatinus (NMNHU-P 2770) in ventral view. **B.** Left pterygoid (NMNHU-P 2830) in ventral view. **C.** Left jugale (NMNHU-P 2823) in ventral view. **D.** Right pterygoid (NMNHU-P 2835) in ventral view. **E.** Left quadratum (NMNHU-P 2781) in posterior view. All specimens are at the same scale.

P. panonicus, but whether this may serve as the diagnostic character can only be decided on an investigation of larger series.

The jugale (Fig. 16) is similar both in proportions and morphology to that in *Pseudopus apodus*, but differs in that the processus zygomaticus (tuberculum zygomaticum sensu Fejérváry-Lángh, 1923: 184) is developed as a well-defined outgrowth (Fejérváry-Lángh, 1923, plate 1, figure 6), sometimes even prominent posteriorly. Its basis is pierced by a canal that opens on the inner surface of the bone by the foramen zygomaticum interior (located close to the crista medialis, rarely on its edge), on the outer surface by one or two foramina zygomatica exteriora (which may be fused to various extent). Rarely (found in NMNHU-P 3287), the canal and thus also foramina were not developed at all. The outer surface is moderately wrinkled in older individuals.

The palatine (Fig. 16A) bears teeth that vary in number and location and in no case can be taken as a diagnostic character. In dorsal view, there is a foramen entering posteriorly the processus jugalo-maxillaris, called by Fejérváry-Lángh (1923, figure 17) the foramen posterior canalis palatini pro nervo supraorbitali. The canal is piercing the bone postero-anteriorly and opens at the basis of the processus maxillaris. The number of the foramina medialis ossis palatini (sensu Fejérváry-Lángh, 1923, Fig. 17) varies in number, position, and size. The outgrowth called the spina vomerina (Fejérváry-Lángh, 1923, Fig. 17) is mostly low and rounded.

The pterygoid is a long and fragile bone so that it is only rarely found complete (Fig. 16B, D; see also Klembara et al., 2010, figure 12). The teeth are dispersed on the surface of a well-defined and lifted field (NMNHU-P 3401, 3417). Apparently, the number of teeth, even if it varies in number, is not an age-dependent character. However, it seems that in younger individuals (represented for instance by specimens NMNHU-P 3404 and 3405) the processus transversus may be comparatively short and the tuberculum contracornoideum is only moderately prominent. In contrast, the processus basisphenoideus is well prominent in all specimens, in some cases even provided with a sharp crista running from its tip towards the tuberculum contracornoideum. In these cases, the lateral margin of the bone is thickened and the sulcus pterygoideus is deep. Since the posterior tip of the bone was broken off in all available specimens, the proportions of the bone cannot be estimated.

On the dorsal surface of the bone there is a conspicuous fossa columellae (Fejérváry-Lángh, 1923, Fig. 19). Anterior to it, the bone may be (but not necessarily is) pierced by foramina for undetermined nerves (in Fejérváry-Lángh, 1923, figure 17, designated as “Nervenlöcher”). The tip of the processus palatinus is usually broken off, but it is obvious that the contact area for the palatinum is distinct. The crista transversa dorsalis (sensu Fejérváry-Lángh, 1923, figure 19) is sharp, delimiting laterally the contact area for the transversum. However, the medial margin of

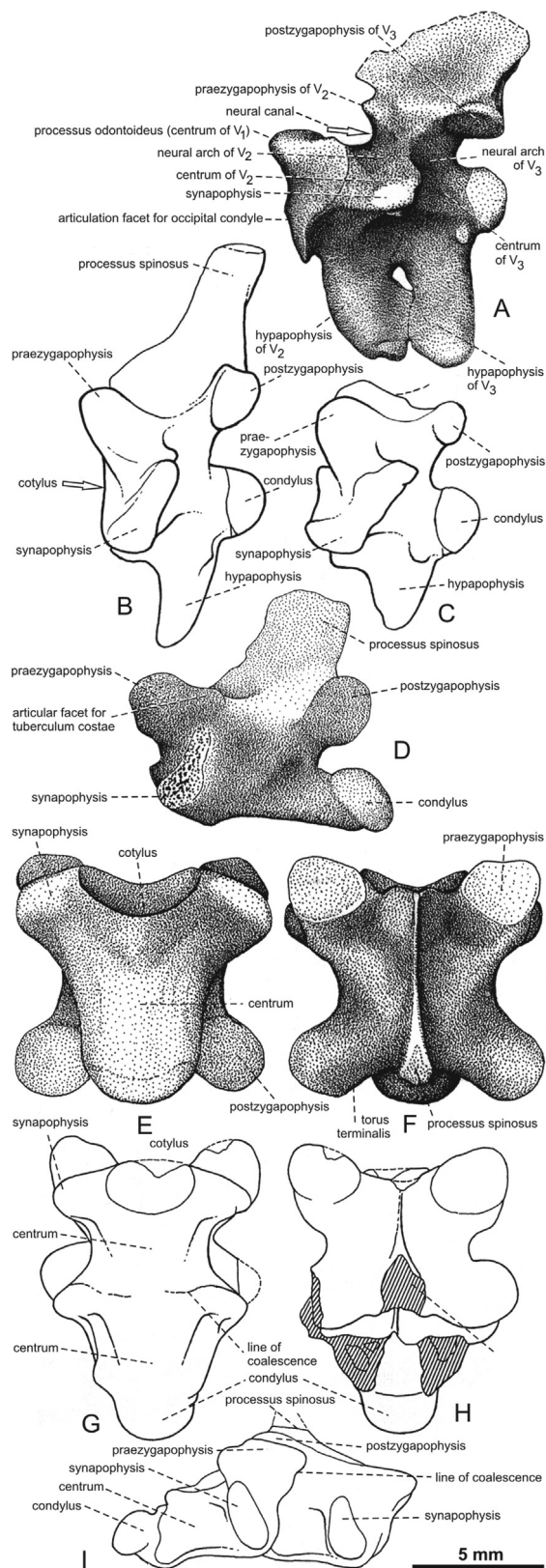
this contact area is indistinct. This area, together with that on the ventral side of the processus transversus (Fig. 16B) fix the pterygoid and transversum together.

The antero-posterior length of the dentale (Fig. 15E) ranges between 17 (NMNHU-P 2618) and 33 mm (NMNHU-P 2646, Fig. 15E). The number of tooth positions in the smallest specimen is 12, in the largest one 13; however, NMNHU-P 2645 has 14 teeth in the tooth row (total length 26.5 mm), whereas NMNHU-P 2611 has 11 teeth (total length 29 mm). The 9th or the 10th tooth (counted from the symphysis) is the largest. The anterior teeth are terminated by an obtuse point slightly declined posteriorly, and their upper part is moderately striated. They are not close to one another, whereas the posterior teeth are widely blunt, not striated in large specimens, located close to one another, and slightly constricted in the middle of their depth. The teeth that are posterior to the largest one either gradually decrease in size or the last two or three in the tooth row are distinctly smaller (Fig. 15E). Black upper parts of teeth were observed only in one specimen (NMNHU-P 2637). The symphyseal articular surface encloses the anterior termination of the sulcus Meckeli and this surface continues for a short distance below the anterior section of Meckel's groove. The dorsal and ventral margins of Meckel's groove bear distinctly flat contact facets for the splenial. Only the dorsal facet is interrupted by a rounded section that in complete mandible takes part in the formation of a foramen called by Meszoely (1970, figure 4) the “anterior inferior alveolar foramen.” The orifice of the canalis nervi alveolaris inferioris is at the level of the 8th to 11th tooth, according to the number of tooth positions. On the outer surface of the bone, there are two articular facets (for the coronoid and supraangular) accompanied by the corresponding incisura coronoidea and sinus supraangularis (see Roček, 1984, Fig. 4). The number of foramina for the rami nervorum alveolarium inferiorum is 4–6 (this number is not correlated with size), and 1 (sometimes 2) similar foramina are at the posterior margin of the bone, below the processus supraangularis.

Fused posterior teeth on the dentaries, as it is sometimes the case with the oldest individuals of *P. apodus* (Roček, 1980: 25, figure 3), were never observed, even in the oldest individuals of *P. panonicus* from Gritsev (the relative individual age is estimated both by size and number of tooth positions).

The largest supraangular (NMNHU-P 2879) reached the length of 35 mm, which approximately corresponds to the material from Ivanovce (Klembara, 1986: 96). The basic morphology is similar to that in *Pseudopus apodus*. Some variation exists concerning the morphology of the anterior margin of the articular surface for the quadratum because it is rimmed by cartilage in living animals. This cartilage may ossify to various extents. It should be noted that Klembara (op. cit.) interpreted the foramen located immediately posterior to the articular facet for the quadratum as the foramen for the chorda tympani (cf. figure 15F).

Fig. 16. *Pseudopus panonicus* (Kormos, 1911). **A.** Palatinum droit (NMNHU-P 2770) en vue ventrale. **B.** Ptérigoïde gauche (NMNHU-P 2830) en vue ventrale. **C.** Jugal gauche (NMNHU-P 2823) en vue ventrale. **D.** Ptérigoïde droit (NMNHU-P 2835) en vue ventrale. **E.** Quadratum gauche (NMNHU-P 2781) en vue postérieure. Tous les éléments sont figurés à la même échelle.



The atlas is obviously too fragile to be preserved. However, several more or less complete specimens were found, which represent a composite bone consisting of a fused centrum of atlas, together with complete axis and V_3 (Fig. 17A). The dorsal part of this element consists of neural arches of V_{2+3} , but its distal margin is broken off in nearly all specimens. However, the shape of the remaining part suggests that it was fan-like in lateral view, with its anterior and posterior margins divergent dorsally. NMNHU-P 2748 is complete and its spinal process extends anteriorly over the anterior entrance of the neural canal up to the level of the processus odontoides; the dorsal median ridge of the process is moderately convex. There is no line of coalescence neither between the two neural arches nor between the centra of $V_1 + V_2 + V_3$. In contrast, a slight line of coalescence may be traced between the hypapophyses, sometimes (but not always) even with a foramen (Fig. 17A). According to Hoffstetter and Gasc (1969: 273, fig. 59), the hypapophyses are fused second and third intercentra. Their distal ends are distinctly swollen. Anteriorly, there is a large, saddle-like articular facet for articulation with the occipital condyle. Its dorsal part (the odontoid process that was originally the centrum of the atlas) is moderately extending beyond its lower part (Fig. 17A). The praezygapophysis of V_2 is vestigial, whereas the postzygapophysis of V_3 is developed in a normal functional shape. The distal part of the synapophysis was obviously covered with cartilage. There is a small outgrowth on either side at the transition between the condyle and the hypapophysis of V_3 .

In general, the cervical vertebrae bear the hypapophysis that may be more or less inclined anteriorly. The synapophysis is robust, slightly compressed in its mid-length; its distal surface is devoid of periost and obviously was covered with cartilage. The upper part of the synapophysis provides the support for the praezygapophysis. The centrum, compared with those of the trunk vertebrae, is short so that the most anterior part of the cotylar margin does not extend over the lower portion of the synapophysis. The antero-posterior extent of the neural arches is even shorter. In the anterior cervical vertebrae, the neural arches on either side meet to form only indistinct ridge anteriorly, whereas posteriorly they run out in prominent spinal process declined posteriorly. In posterior cervical vertebrae, the spinal process continues anteriorly as a distinct, sharp

Fig. 17. *Pseudopus pannonicus* (Kormos, 1911). **A.** Complex of axis and V_3 in sinistral view (NMNHU-P 3424). **B.** Anterior cervical vertebra in sinistral view (NMNHU-P 3465). **C.** Posterior cervical vertebra in sinistral view (NMNHU-P 3466; originally dextral aspect but reversed for comparison). **D–F.** Trunk vertebra (NMNHU-P 2900) in sinistral (**D**), ventral (**E**), and dorsal (**F**) views. **G–I.** Two coalesced trunk vertebrae (NMNHU-P 2902) in ventral (**G**), dorsal (**H**), and dextral (**I**) views. All specimens are at the same scale.

Fig. 17. *Pseudopus pannonicus* (Kormos, 1911) **A.** Complexe d'axe et de V_3 en vue sinistrale (NMNHU-P 3424). **B.** Vertèbre cervicale antérieure en vue sinistrale (NMNHU-P 3465). **C.** Vertèbre cervicale postérieure en vue sinistrale (NMNHU-P 3466 ; aspect dextre à l'origine, mais retournée pour comparaison). **D–F.** Vertèbre de tronc (NMNHU-P 2900) en vues sinistrale (**D**), ventrale (**E**) et dorsale (**F**). **G–I.** Deux vertèbres de tronc coalescentes (NMNHU-P 2902) en vues ventrale (**G**), dorsale (**H**) et dextre (**I**). Tous les éléments sont figurés à la même échelle.

ridge up to the anterior margin of the neural arches, similar to the condition in the trunk vertebrae.

In the trunk vertebrae (Fig. 17D–F), the ventral surface of the centrum is nearly flat (only the cotylar margin is slightly elevated) and, because its lateral margins diverge anteriorly towards the synapophyses, it is rather triangular in shape. In its anterior part, the ventral surface of the centrum is pierced by a pair of small foramina. There is a distinct groove between the ventral surface of the centrum and the condylus (well observable in lateral view). The spinal process is broken off in nearly all specimens and judging by the condition in contemporary representatives of the genus *Pseudopus*, it can vary in shape according to its position in the vertebral column. The spinal process continues anteriorly as a ridge up to the anterior margin of the neural arches. This margin is markedly lifted medially, but slants down on either side towards the praezygapophysial articular facet. The dorsal surface of the praezygapophyses slants down into a deep depression, even beyond their articular facets. The dorsal surface of the neural arches do not display any ridges. The lateral margin of the praezygapophyses run out in a slight convexity corresponding to the articular facet of the tuberculum costae. This facet is an indistinct oval depression immediately dorsal to the synapophysis. Posterior to the latter are two depressions: the one which is less distinct is immediately posterior to the dorsal part of the synapophysis, the other one is deeper and beneath the postzygapophysis. The bottom of the neural canal is subdivided by a median ridge into two parallel grooves.

As can be judged from specimen NMNHU-P 2902 (Fig. 17G–I), the trunk vertebrae could coalesce with each other to such a degree that the line of coalescence on the ventral side is nearly impossible to discern.

The first sacral vertebra (Fig. 18 A and B) is provided on each side with strong, flat, lateroventrally directed process, called “lymphapophysis” by Hoffstetter and Gasc (1969, figure 51). They are broken off close to their basis in most specimens, but as suggested by NMNHU-P 2912 (Fig. 18B), one can easily distinguish a proximal, compressed part, as well as a slender distal section; the transition between both is abrupt, so the flat proximal section is terminated by two indistinct outgrowths, the spina posterior and spina anterior (*sensu* Fejérváry-Lángh, 1923: 207, fig. 35). In contrast to *Pseudopus apodus*, these spines are not developed in a form of additional processes (Hoffstetter and Gasc, 1969, Fig. 51). Hence, the shape of the lymphapophysis may be considered a diagnostic character, and presumably reflects different biomechanical conditions for locomotion. There is a pair of antero-posteriorly elongated and asymmetrical foramina on the ventral surface of the centrum, but the lymphapophyses are not pierced by any of them (compare the second sacral vertebra).

The second sacral vertebra (Fig. 18C and D) is less robust than the first one. Although it bears the chevron bone (haemapophysis), it is not considered the first caudal (Hoffstetter and Gasc, 1969: 266, 267). The condyle is compressed dorsoventrally, but the cotyle corresponds to the more oval shape of the condyle of the first sacral. Rather characteristic is that, like in more posterior caudals, the cotyle is facing antero-ventrally and, correspondingly,

the large condyle posterodorsally. If observed from the ventral side, the lymphapophyses are pierced at their proximal section by a medium-sized foramen, which is an orifice corresponding to a laterally directed canal passing through the lymphapophysis. It opens again at its lateral end, between the spina anterior and the protrusio iliaca. This is the transverse canal that, in the limbless Anguidae, connects the posterior lymphatic hearts and the median perivascular lymphatic space (Hoffstetter and Gasc, 1969: 265). Besides these lateral foramina, there is a pair of small medial ones piercing the ventral surface of the centrum. These foramina are homologues of those on the centrum of the first sacral. The spinal process is comparatively long, dilated antero-posteriorly, and extending over the condyle.

The caudal vertebrae bear long, slender and posteriorly declined chevron bone. The position of the autotomic septum is indicated by a small median spine, called the dorsal paraseptal apophysis by Hoffstetter and Gasc (1969: 271) on the dorsal side of the vertebra, and by the proximal bifurcation of the transverse process resulting in an elongated foramen (Fig. 18G). However, in more anterior caudals, the pleurapophyses are simple and the course of the septum is indicated only by a small posteriorly directed process (Fig. 18F). In Anguidae, the transverse autotomic split begins at the 5th to 7th caudal (in *Anguis* and *Ophisaurus* even more posteriorly); consequently, all caudals present in our material are supposedly more posterior than the 4th caudal.

Remarks. All skeletal elements of *P. pannonicus* from the type locality Polgárdi are illustrated in Fejérváry-Lángh (1923, pls. 1–3).

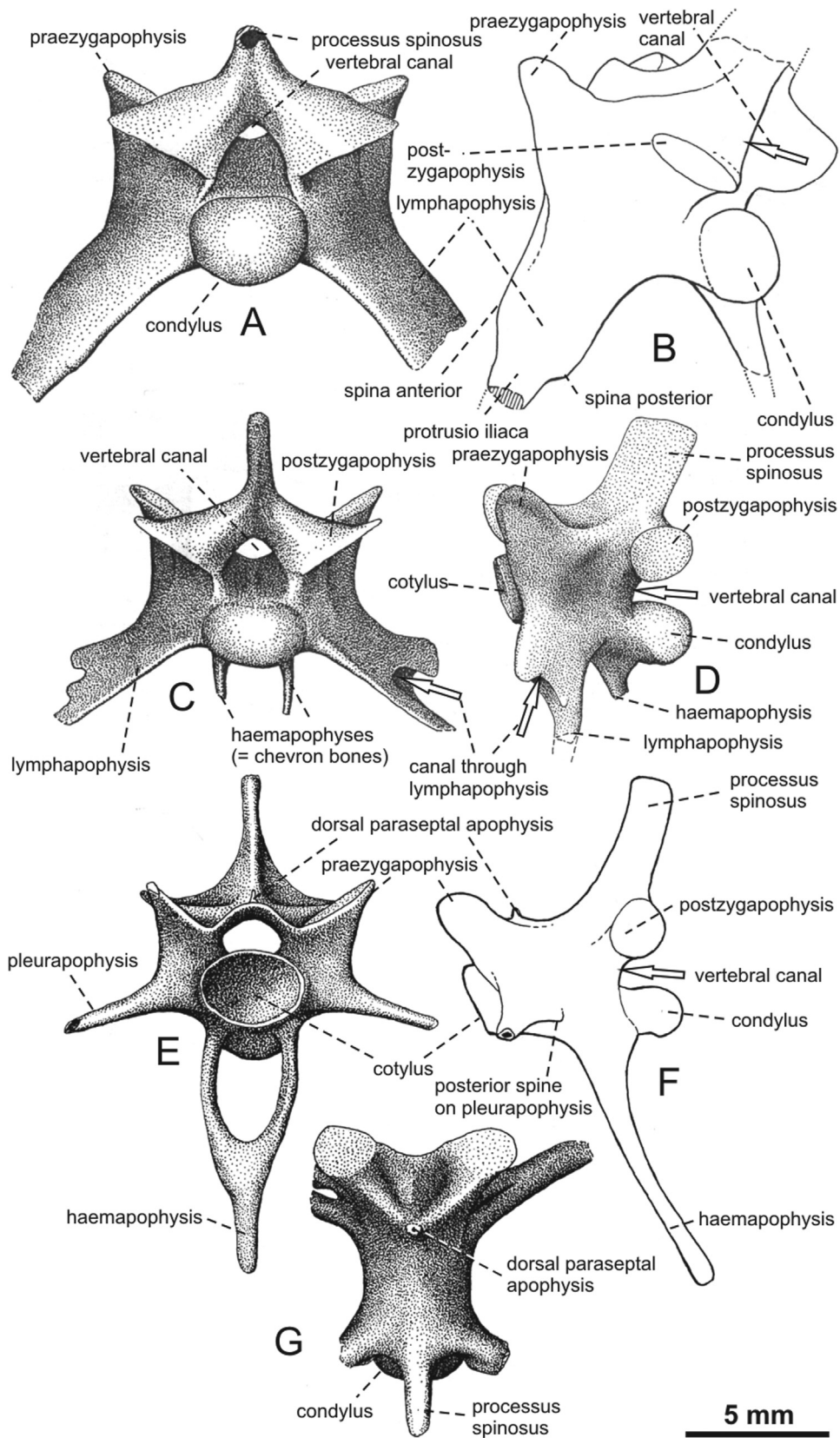
Stratigraphic occurrence. Possibly middle Miocene, MN 7 (Opole, Wegner, 1913) or upper Miocene, Pannonian “F” (Gotzendorf, Kohfidish; Bachmayer and Mlynarski, 1977: 289) to lower Pleistocene, Biharian (Deutsch Altenburg; Bachmayer and Mlynarski, 1977: 288).

Geographic distribution. Canal Negre 1 – Spain (Blain et al., 2016); Montousse 5 – France (Bailon, 1991); Hamblech 11 and 13, Hammerschmiede – Germany (Böhme in Klembara et al., 2010; Čerňanský et al., 2017); Deutsch Altenburg, Eichkogel bei Modling, Kohfidish, Gotzendorf – Austria (Bachmayer and Mlynarski, 1977; Papp and Thenius, 1954; Thenius, 1952); Banyahegy, Beremend, Csarnota, Kopecz, Polgárdi, Tardosbánya, Urkút-Újhuta, Osztramos – Hungary (Bolkay, 1913: 222; Estes, 1983: 142; Fejérváry-Lángh, 1923: 139; Klembara, 1986: 92; Kormos, 1911; Kretzoi, 1956; Venczel, 2001, 2006); Hajnáčka, Ivanovce, Včeláre – Slovakia (Fejfar, 1961; Klembara, 1986: 92, 93); Częstochowa, Kadzielnia, Opole – see note in Stratigraphic occurrence, Rębielice Królewskie I, Węże – Poland (Bachmayer and Mlynarski, 1977; Mlynarski, 1960, 1962, 1964; Wegner, 1913); Betfia (= Püspökfürdő) – Romania (Fejérváry-Lángh, 1923: 139); Novo Elisavetovka (now Novoelisavetovka, Ukraine), Savitskoye – Russia (Alekseyev, 1912, 1916).

Pseudopus cf. *pannonicus*.

Material. Three nasals (NMNHU-P 2077, 3345, 3346).

Description. These nasals are all within the variation range of *Pseudopus pannonicus*; the only difference is their small size.



Anguidae indet.

Material. Three dentaries (NMNHU-P 2081 – Fig. 19A–C; NMNHU-P 2109 – Fig. 19F–G; NMNHU-P 2117 – Fig. 19D–E).

Description. Dentary NMNHU-P 2081 is similar to that of *Anguis* (also in number of tooth positions), but differs in the position of Meckel's groove, which opens ventrally rather than ventrolaterally, and in the fact that the medial contact facet of the coronoid is anteriorly delimited by an indistinct outgrowth on the horizontal lamina, which is connected with the margin of the canalis nervi alveolaris inferioris by a crista. The total number of tooth positions is 11. The spina splenialis is at the level of the 3rd–4th tooth positions from behind. Dentary NMNHU-P 2117 differs from NMNHU-P 2081 by longer teeth that exceed the level of the crista dentalis by more than one-half of their length. NMNHU-P 2109 is larger than the two previous ones (its anterior end is broken off), but the teeth are short, blunt, and not so prominent above the crista dentalis. The orifice of the canalis nervi alveolaris inferioris is directed posteriorly (marked by arrows in Fig. 19).

4. Discussion and conclusions

The fossil material from Gritsev used in this study suggests that at least 16 taxa occurred in this locality:

- *Mioproteus caucasicus* Estes and Darevsky, 1977;
- *Chelotriton paradoxus* Pomel, 1853;
- *Latonia* sp.;
- *Palaeobatrachus* sp.;
- *Pelobates* sp.;
- *Bufo* sp.;
- *Rana* sp.;
- Gekkonidae indet.;
- *Lacerta* sp. type I;
- *Lacerta* sp. type II;
- Lacertidae indet.;
- Lacertidae indet.;
- *Ophisaurus* sp.;
- Anguidae indet.;
- *Pseudopus pannonicus* (Kormos, 1911);
- *Pseudopus* cf. *pannonicus*.

Only three of them could be determined at the species level. The reason is not only the preservation of the fossils (in great part just fragments of bones), but also the definition of fossil taxa. For instance, the majority of the currently recognized species of *Palaeobatrachus* were established based on articulated skeletons. This can

provide information on whole skeletal units such as the skull, the vertebral column including the shape of ribs and the sacral diapophyses, the morphometric proportions of the skeleton, and also on the ontogenetic age of an individual (judged by epiphyses of the long bones or presence/absence of tiny carpals). In contrast, disarticulated bones can provide precise information on individual bones, but their preservation is selective – prevailing are those of lesser taxonomic importance, such as the ilia, whereas cranial bones, such as the frontoparietals or maxillae, are usually absent. Their association with other bones in the sample is mostly speculative. This is why using criteria gained from articulated skeletons for the determination of disarticulated and fragmentary bones is somewhat risky, and the same holds for taxonomic determination of articulated skeletons after the criteria gained from disarticulated bones. This situation improved only recently when micro CT scanning of articulated skeletons provides information on individual, virtually disarticulated bones.

Another but equally annoying fact is that the reliability of fossil species is closely associated with the knowledge of their individual and developmental variation. It is often difficult to decide whether some deviation from the morphological status of a species indicates a new taxon or just a case (or even malformation) within its normal variation range.

This is why only three taxa are presented here at the species level. *Mioproteus caucasicus* was established by Estes and Darevsky (1977) based on several tens of vertebrae from different parts of the vertebral column. The main features distinguishing *Mioproteus* from Recent *Proteus anguinus* are robust, well-ossified vertebrae. This, together with similar stratigraphic ages of Gritsev and the type locality Belaya River (middle Sarmatian), strongly supports the view that the fossil from Gritsev is conspecific with that from the Caucasus.

As regards *Chelotriton paradoxus*, the situation is not so unequivocal. All disarticulated cranial elements from Gritsev bear the same type of sculpture, which consists of irregular tubercles, whereas the best preserved *Chelotriton* from the late Oligocene of Enspel (Roček and Wuttke, 2010; Schoch et al., 2015) has the sculpture not so dense, more uniform, with a tendency to be vermicular. It is logical that *Chelotriton* from the late Oligocene (MP 29–30) of Enspel is stratigraphically closer to that from the type localities of *Chelotriton* – Chaffours (MP 27) and Langy (MN 30 or MN 2a), than that from the middle Sarmatian (MN9a) of Gritsev. Thus, if only sculpture itself would be taken for the determination of *Chelotriton* from Gritsev, then its different type (irregular tubercles) would suggest that it may be

Fig. 18. *Pseudopus pannonicus* (Kormos, 1911). **A.** First sacral vertebra (NMNHU-P 2912) in posterior view. **B.** Same specimen in posterolateral view, to show the shape of the lymphapophysis. The vertebral canal is marked by an arrow. **C.** Second sacral vertebra (NMNHU-P 3421) in posterior view. **D.** Same specimen in sinistral view. **E.** Caudal vertebra (NMNHU-P 3422) in posterior view. **F.** Same specimen in sinistral view. **G.** Caudal vertebra (NMNHU-P 3423) in dorsal view. All specimens are at the same scale.

Fig. 18. *Pseudopus pannonicus* (Kormos, 1911). **A.** Première vertèbre sacrée (NMNHU-P 2912) en vue postérieure. **B.** Même spécimen en vue postérolatérale, pour montrer la forme de la lymphapophyse. Le canal vertébral est indiqué par une flèche. **C.** Seconde vertèbre sacrée (NMNHU-P 3421) en vue postérieure. **D.** Même spécimen en vue sinistrale. **E.** Vertèbre caudale (NMNHU-P 3422) en vue postérieure. **F.** Même spécimen en vue sinistrale. **G.** Vertèbre caudale (NMNHU-P 3423) en vue dorsale. Tous les éléments sont figurés à la même échelle.

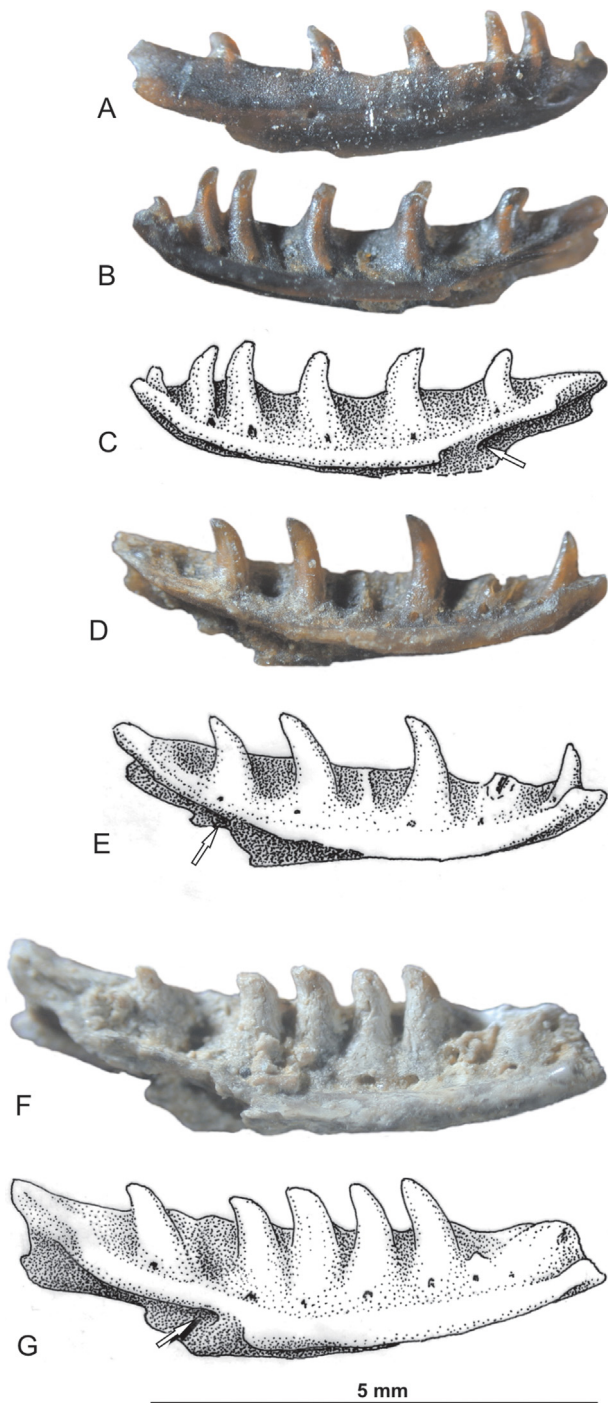


Fig. 19. Variation in dentition of Anguillidae from Gritsev. **A–C.** Right dentary (NMNHU-P 2081) in labial (**A**) and lingual (**B, C**) views. **D–E.** Left dentary (NMNHU-P 2117) in lingual view. **F–G.** Left dentary (NMNHU-P 2109) in lingual view. All specimens are at the same scale.

Fig. 19. Variation dans la dentition des Anguillidae de Gritsev. **A–C.** Dentaire droit (NMNHU-P 2081) en vues labiale (**A**) et linguale (**B, C**). **D–E.** Dentaire gauche (NMNHU-P 2117) en vue linguale. **F–G.** Dentaire gauche (NMNHU-P 2109) en vue linguale. Tous les éléments sont figurés à la même échelle.

taxonomically different from *Chelotriton* from Enspel. However, the problem would then be how (and whether it would be reasonable) to compare the cranial sculpture of *Chelotriton* from Enspel with the sculpture on vertebral horizontal plates of the vertebrae from Chauffours and Langy (which are now lost) or with the sculpture on the neotype vertebra from Coderet. [Estes and Hoffstetter \(1976\)](#) only write “*épine neurale très haute, surmontée par une plaque d’os dermique, en général pustuleuse, cette dernière variant d’une forme arrondie à celle d’un chevron.*” The only way would be to find a sculptured cranial bone from Coderet, which would provide information on the cranial sculpture of *Chelotriton*, which would be the closest to *C. paradoxus*, but this is beyond the scope of this paper. Comparisons could be then extended to other middle Miocene *Chelotriton*, preferably that represented by articulated skeletons (e.g., from Öhningen; [Westphal, 1978](#)), which would provide information about the variation of sculpture in Miocene forms. Thus, assignment of *Chelotriton* from Gritsev to *C. paradoxus* should only be taken as temporary.

Pseudopus pannonicus is the taxon that may be considered as well-defined thanks to a recent differential diagnosis between *Pseudopus laurillardi*, on the one hand, and *P. pannonicus* and *P. apodus*, on the other hand ([Klembara et al., 2010](#)). However, some doubts concerning the discrimination between *P. pannonicus* and recent *P. apodus* still exist. The earliest record of *P. pannonicus* is from the late Miocene, MN 9 of Hammerschmiede, Germany (M. Böhme in [Klembara et al., 2010](#)), which is of the same age as that of Gritsev, and continued to exist till the middle Pleistocene ([Blain and Bailon, 2006](#)). However, already [Fejérváry-Láng \(1923: 190\)](#) recognized that *P. apodus* corresponds by the majority of its characters to not fully-grown *P. pannonicus*. Thus, *P. pannonicus* was considered by most paleontologists to be just a robust form of *P. apodus*. [Młynarski \(1962, 1964\)](#) suggested that *P. pannonicus* may have been no more than a very large northern race of *P. apodus*, and [Estes \(1983: 142\)](#) stressed a continuous morphological transition between the middle Pleistocene *P. pannonicus* and Holocene *P. apodus*. In contrast, [Klembara \(1986\)](#) claimed that he was able to recognize both species in the early Pliocene (MN 15) of Ivanovce, Slovakia, based on other features than only their different size, which also meant that both species stratigraphically overlapped in the Pliocene and Pleistocene. Besides, it may be inferred from the description of *Pseudopus* from Gritsev and from the revised diagnosis of *P. pannonicus* given above that old individuals of *P. apodus* already developed their own specializations that were not present in *P. pannonicus* and, consequently, that it is reasonable to maintain a separate status for both forms. This is why the assignment of the material of *Pseudopus* from Gritsev to *P. pannonicus* seems to be granted. At the same time, *Pseudopus pannonicus* from Gritsev provides, besides the above-mentioned record from Hammerschmiede, another piece of evidence for the lower boundary of its stratigraphic range.

The material of *Latonia* was not determined to the species level because of the current discussion on the taxonomic identity of *L. seyfriedi* and *L. gigantea*. The latter species is well documented by isolated bones from the middle Miocene of Sansan, France, but it was described later than *L. seyfriedi* from the middle Miocene of Öhningen, Germany. Because *L. seyfriedi* is documented exclusively by articulated skeletons embedded in the matrix by their dorsal side, it is not known whether their dermal bones of the skull roof were covered by sculpture. Current investigations by micro CT scan should clarify this question. If the dermal bones of *L. seyfriedi* will be sculptured in the same way as in *L. gigantea*, then the latter species will be the junior synonym of *L. seyfriedi* and the material from Gritsev could be most conveniently ascribed to it.

A slightly different problem is with *Palaeobatrachus*, although it also caused that the fossils cannot be determined to the species level. The genus *Palaeobatrachus* involves permanent water-dwellers, which resulted in their morphological uniformity. Moreover, a majority of species were based on articulated skeletons. This is why it would be too risky to try to determine the fragmentary material from Gritsev to any of the currently recognized species, especially because the sample of available bones does not include frontoparietals and sacralis, considered the most distinctive for determination.

The same holds true, although to a lesser degree, for *Pelobates*. The only available frontoparietal indicates rather robust postorbital bridge connecting the lamella alaris of the squamosal with the frontoparietal. This is a strong evidence that this frontoparietal does not belong to *Eopelobates*. The sculpture, which is intermediate between pitted and pustular, indicates that this cannot be *Pelobates decheni*, whose sculpture is still similar to *Eopelobates* (Roček et al., 2014). Because sculpture of this frontoparietal (and also of the large maxilla) differs from the pustular type of all recent *Pelobates* with postorbital bridge, the pelobatid material from Gritsev most probably belongs to a distinct but not yet described species; nevertheless, the available material is not sufficient for its formal description.

In conclusion, it can be noted that there is some additional material not included in the paper. Therefore, it is not excluded that the list of taxa from Gritsev may be extended, and that excavations may continue in the locality, so that knowledge of their characteristics will be improved.

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