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Late Miocene Amphibia from Rudabánya

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KEYWORDS — Amphibia, Caudata, Anura, Miocene, Hungary

*ABSTRACT — Amphibian fauna from the Late Miocene (Vallesian, MN9) locality of Rudabánya (Hungary) consists of five taxa of caudate amphibians (*Mioproteus caucasicus*, two types of *Chelotriton *which might represent two different species, and two types of *Triturus*) and at least nine taxa of anuran amphibians (*Latonia gigantea*, *Bombina *sp., cf. *Discoglossus*, two types of unidentifiable Discoglossidae, *Palaeobatrachus *sp., *Pelodytes *sp., *Hyla *sp., and *Rana *sp.). The most abundant is *Palaeobatrachus *(possibly including more than one species) and *Latonia*. Fossil remnants of *Bombina *and *Hyla *from Rudabánya are among the earliest representatives of their respective genera.*

*RIASSUNTO — Il record degli Anfibi nella associazione faunistica a vertebrati del Miocene superiore (Vallesiano, MN9) di Rudabánya (Ungheria) consiste in sei taxa di caudati (*Mioproteus caucasicus*, due morfotipi di *Chelotriton *che possibilmente rappresentano due specie diverse, e due morfotipi di *Triturus*) ed in almeno nove taxa di anuran (*Latonia gigantea*, *Bombina *sp., cf. *Discoglossus*, due morfotipi di un Discoglossidae non identificabile, *Palaeobatrachus *sp., *Pelodytes *sp., *Hyla *sp., e *Rana *sp.). I taxa più rappresentati sono *Palaeobatrachus *(probabilmente rappresentato da due specie diverse) e *Latonia*. I resti di *Bombina *e *Hyla *di Rudabánya rappresentano il record più antico oggi noto dei due generi.*

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INTRODUCTION

Among Miocene amphibian assemblages of Europe, those from the Vallesian MN9 are comparatively rare, coming mainly from Spanish localities Ampudia 6B, 8 and 9 (*Latonia* sp., cf. *Hyla*), Autilla 1 (*Pelodytes* cf. *arevacus*), Valles de Fuentidueña (*Latonia* sp., *Rana* sp.), Torremormojón 3 and 4 (*Latonia* sp.) (for references see Sanchíz, 1998). Besides these taxonomically rather poor assemblages, the only other ones are from central and eastern Europe, respectively - Suchomasty 3 in the Czech Republic (*Triturus* aff. *montandoni*, *Bombina* cf. *variegata*, *Latonia* sp., *Eopelobates* sp., and *Bufo* cf. *bufo*; Hodrová, 1987), Gritsev (*Mioproteus caucasicus, Chelotriton paradoxus*, *Paleobatracus* sp., *Latonia gigantea, Pelobates* cf. *decheni*, *Pelobates* sp. different from *P. decheni*, and *Rana*), and Rudabánya (present paper). Diversity of fossil amphibian assemblages depends on the extent to which detailed excavations are made. Therefore, it is difficult to decide whether published lists of taxa reflect actual faunal composition. In all three latter localities the results are based on reliable amount of fossil material. Therefore it can be expected that they provide reasonable information.

Latonia, a common discoglossid of the European Neogene is present in all MN9 assemblages with herpetofauna. Although it is often given as *Latonia* sp., most probably it is represented by *L. gigantea*, judging by the type of maxillary sculture (Roček, 1994). Besides, also *Chelotriton* (a salamandrid, preliminarily assigned to *Chelotriton paradoxus*, but recently collected data from various central European localities suggest that there could be some other species in the European Oligocene and Miocene) seems to be a common amphibian in the Neogene of Central and Eastern Europe, though Estes (1981) considered him restricted to Western Europe. In contrast *Mioproteus* (Proteidae), another common tailed amphibian of European Neogene, was considered to be an eastern form because of findings in northern Caucasus and eastern Kazakhstan (Estes, 1981). However, recent findings reveal that it was common also in Central Europe (Estes & Schleich, 1994; Młynarski *et al.*, 1984), and it was even reported from the late Pliocene of France (Bailon, 1995).

In contrast to these common taxa, there were some others whose occurrence vary. The Pelobatidae, although recorded from the early Eocene of Portugal and France by the genus *Eopelobates* (Sanchíz, 1998) and from the Late Oligocene of Germany (Enspel) by the genus *Pelobates*, still remains a minor part of the Miocene assemblages. The problem is to distinguish both genera on the basis of disarticulated bones, especially of the postcranial skeleton. A similar problem occurs with *Palaeobatrachus*: the family was recorded as early as in the Paleocene, and gradually became diversified throughout the Oligocene (as evidenced mainly by findings from Bechlejovice, Czech Republic and Rott, Germany). However, in spite of several attempts to make a taxonomic revision (e.g., Wolterstorff, 1886-7; Špinar, 1972) it is not clear whether morphological variation reflects taxonomic diversity.

It follows from the list of European amphibian assemblages that the peak of taxonomic diversity was reached in early Miocene (Rage & Roček, 2003), when the Proteidae, Salamandridae, Discoglossidae, Pelobatidae and Palaeobatrachidae were joined by the Cryptobranchidae (the earliest occurrence is from the Upper Oligocene of Germany), Bufonidae (MN4 of Spain) and Hylidae (MN6 of Devínska Nová Ves, Slovakia). The Pelodytidae and Ranidae were represented in the European amphibian assemblages since the Eocene (MP16), however, they never became a dominant part of them.

One should also say that although Caudata are well represented in the Tertiary of Europe too, their taxonomic status is much more difficult to clarify because of difficulties with the association of disarticulated elements with findings represented by complete skeletons.

This is the context in which the amphibian fauna of Rudabánya should be assessed. It helps to complete our knowledge on the taxonomic composition of the European east-central MN9 amphibian assemblages and, besides, it can provide important data on the morphological variation which can serve for further taxonomic revisions.

SYSTEMATIC PALAEONTOLOGY

Caudata Scopoli, 1777
Proteidae Hogg, 1838
Mioproteus Estes & Darevsky, 1977

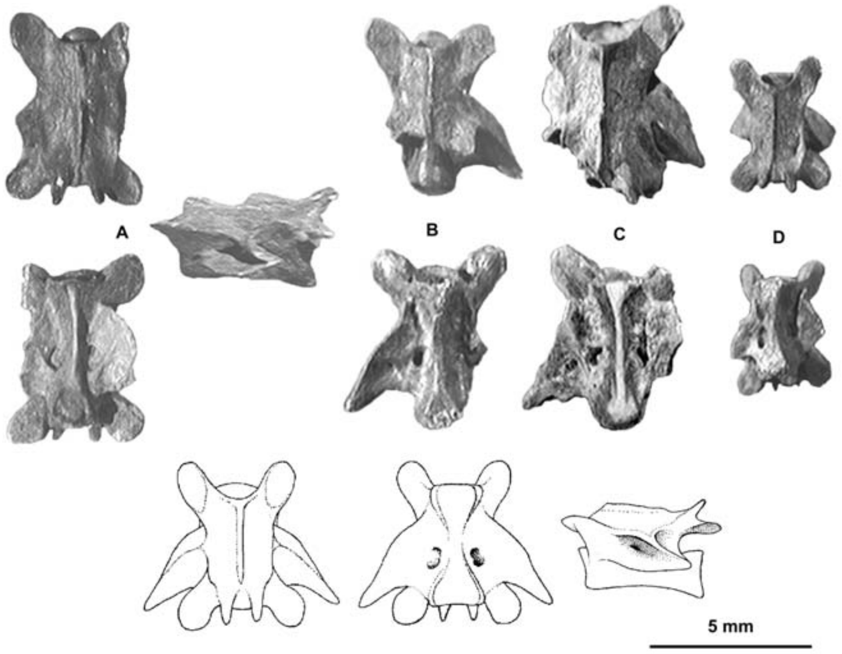
Mioproteus caucasicus Estes & Darevsky, 1977

Material

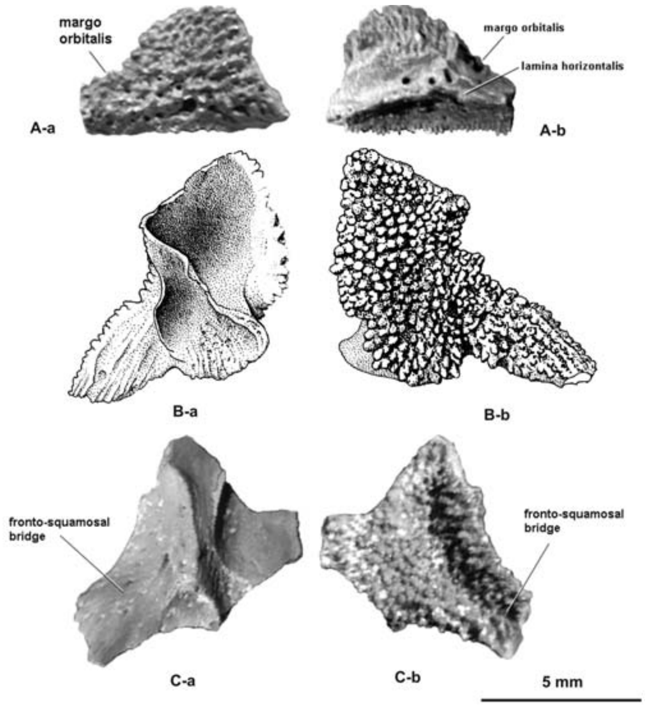
Trunk vertebra (2/35-42; 2/49; 3/2-3; 5/21-25; 6/32-38; 8/12-15; 10/2-7; 11/2-4; 14/18-19; 17/14-15; 19/1-3; 22/10-13; 23/14; 25/3; 27/18-34; 28/21-22; 32/4; 35/14; 37/1-8; 37/10-17; 38/5; 39/5-6; 39/7, Text-fig. 1D; 39/8-13; 39/15; 40/16; 40/17, Text-fig. 1C; 41/34; 41/35; 41/36; 41/37; 41/38; 41/39; 41/40; 41/41; 41/42; 41/43; ?42/48; 46/5; 46/6; 46/9; 49/10; 53/2; 53/3; 53/4, Text-fig. 1B; 54/6, Text-fig. 1A; 54/7).

Description

The centrum is amphicoelous, reaching up to 6 mm in length. The processus spinosus is thin, reaching nearly or up to the anterior margin of the neural arches. Posteriorly, it terminates in comparatively long distance before the posterior margin of the neural arches, being separated from the processes ("forking process" *sensu* Młynarski *et al.*, 1984) on the posterior margin of the neural arches. In some specimens (e.g., 39/6) these processes take their origin on the dorsal surface of the neural arches, lateral to the posterior section of the median crest. The lateral margins of the neural arches are moderately elevated in their posterior part (i.e., posterior to the base of the processus transversus). The proximal part of the processus transversus is represented by a thin lamina which is declined postero-ventrally. Approximately at the middle of the dorsoventral diameter of the centrum the lamina is joined by similar but horizontal lamina which, in ventral view, terminates arch-like before reaching the margin of the anterior cotyle. The postero-ventrally declined lamina gradually lowers down towards the tip of the transverse process, and the horizontal lamina reaches the tip of the process as well. As evidenced by intact transverse process in 53/4 (Text-fig. 1B), the process is terminated by a tip, without any articular facet for the rib. If Estes (in Młynarski *et al.*, 1984: 212) was right in stating that anterior vertebrae could bear ribs, those with the pointed transverse processes should be from the more posterior section of the vertebral column. The horizontal lamina is pierced medially by a foramen which is connected with the anterior of the two foramina entering the single "subcentral foramen" well seen in ventral aspect. However, the mentioned two foramina may be entirely separate, so that this character is a matter of considerable variation. The ventral surface of the centrum is laterally compressed in its middle part so that it is prominent ventrally as a more or less sharp crista (termed the "subcentral keel" by Młynarski *et al.*, 1984). In general, the vertebrae correspond to that described by Bailon (1995) from the Upper



Text-fig. 1 - *Mioproteus caucasicus*. A - Trunk vertebra, 54/6. B – Trunk vertebra, 53/4. C - Trunk vertebra, 40/17. D - Trunk vertebra, 39/7. A in dorsal (above), ventral (below) and sinistral (right) views, B-D in dorsal (above) and ventral (below) views. Line drawings are the composite reconstruction of the trunk vertebra in dorsal, ventral and sinistral views. All in the same scale.



Text-fig. 2 - *Chelotriton* sp. A - Postorbital section of the left maxilla in outer (a) and inner (b) view, 37/38. B - Right frontal in ventral (a) and dorsal (b) view, 39/31. C - Right frontal in ventral (a) and dorsal (b) view, 54/2. All in the same scale.

Pliocene of Balaruc II, France.

Besides larger vertebrae, there are also small vertebrae in the material from Rudabánya, characteristic in that the dorsal margin of their transverse processes is much lower than the lateral margins of their neural arches. Consequently, the margins of the neural arches are represented by a continuous horizontal edge which is not confluent with the dorsal ridge of the transverse process. It is possible that this type of vertebrae represents anterior caudals. This seems to be supported by relatively short transverse processes, only moderately extending beyond the level of the postzygapophyses.

Remarks

Whereas *Mioproteus caucasicus* Estes & Darevsky, 1977 can be easily distinguished from contemporary *Proteus anguinus* (see also Haller-Probst & Schleich, 1994), specific separation of *Mioproteus wazei* Młynarski, Szyndlar, Estes et Sanchíz rests only on minor differences in variable character states, such as shape of forking process and of the subcentral keel. Since variation of all these characters fits into the variation range of *Mioproteus caucasicus* (compare Młynarski *et al.*, 1984: fig. 1 with Estes & Darevsky, 1977: figs. 2 and 3), and because it is reasonable to admit that certain variation exists also within a single vertebral column, it seems that specific separation of both forms is not well supported. This is also confirmed by the material described from other Miocene and Pliocene localities (Estes & Schleich, 1994; Bailon, 1995), although Bailon (1995: 6) tried to find more reliable diagnostic characters than those given in the original diagnosis of *Mioproteus wazei* by Estes (in Młynarski *et al.*, 1984).

Salamandridae Gray, 1825
Chelotriton Pomel, 1853

Chelotriton sp., type I

Material

Left frontale (8/18; 36/13-14), right frontale (8/21; 23/10; 36/15; 38/15; 54/2, Text-fig. 2C), parietale (44/19), ? right praemaxilla (14/6), left maxilla (6/39; 8/19; 37/38, Text-fig. 2A), quadratojugale (2/46), left dentary (14/5; 15/5); right lower jaw (8/20; 19/43; 26/7), unidentified sculptured cranial elements (4/18; 6/40; 8/17; 9/19; 14/7-8; 15/1; 23/11; 38/13; 38/14; 38/16; 38/17; 38/18; 43/20; 45/13; 53/7), trunk vertebra (8/16; 39/18).

Description

The dorsal surface of the dermal cranial bones is covered by deep, dense pustular sculpture, with bottom of grooves between single pustules pierced by small pores (53/7). However, sculpture on the frontal is not too dense, and more robust along the elevated margins of the fronto-squamosal bridge (Text-fig. 2C-b) and on the orbital margin. Pustules on the fronto-squamosal bridge tend to fuse in parallel ridges. The ventral surface of the frontal is smooth, convex along the axis of the fronto-squamosal bridge where it is pierced by several tiny foramina (Text-fig. 2C-a), and concave in the medial part of the bone so the roof of the braincase is a thin layer of dermal (i.e. frontal) bone. Only the parts of the frontal filling fenestrae in the roof of the endocranial braincase (called incrassations by Jarošová & Roček, 1982) are prominent from this surface and well delimited. Both the ventral surface of the bridge and the roof of the braincase are separated by a strip of bone defined laterally and medially by well developed cristae. Margins of the sculptured surface may be bordered by an elevated narrow crest consisting of variously sized tubercles, separating the sculptured surface from smooth bone (e.g., between the parietal and the otic capsule; 44/19). Similar crests are developed in contemporary *Tylototriton* and *Echinotriton*.

The dentary has markedly extended lamina horizontalis in its symphysial part, so that the lamina diverges to the level of the tooth bases dorsally and to the lower margin of the bone ventrally. Its contact surface is nearly straight, situated in the midline. In outer view, the crista dentalis is devoid of sculpture so that there is a smooth strip along the upper edge of the bone. The ventral edge of the bone is irregular due to a variously prominent sculpture. The upper surface of the lamina horizontalis, below the tooth bases, is pierced by comparatively large foramina. As can be judged by specimen 8/20 which is the posterior part of the lower jaw, the lamina horizontalis is thin in its section posterior to the tooth row, extending medially from the vertical part of the bone along its lower margin. It terminates abruptly so the posterior part of the bone bears no lamina on its inner surface. The outer surface is covered by sculpture which, however, does not reach its upper edge; the sculpture comes onto the ventral surface of the bone from which individual pustules are well prominent (especially if seen from medial side).

Chelotriton sp., type II

Material

Left frontal (44/17), right frontal (36/17; 39/31, Text-fig. 2B), ? squamosal (26/6), unidentified dermal bone (14/20; 15/45; 37/39; 41/45).

Description

This form is different from *Chelotriton* sp. type I in that its sculpture consists of tiny dense pustules, which only on the fronto-squamosal bridge tend to fuse in ridges. Narrow grooves between pustules are pierced by small foramina, as it is characteristic for the genus. The bridge, which forms the posterior margin of the orbit, makes nearly the right angle with the lateral (orbital) margin of the frontal. Marginal fragment of a dermal bone (? frontale, 41/45) shows that the scultured surface is elevated and free vertical margins of the bone are smooth.

Remarks

Disarticulated bones of *Chelotriton* are common in the European Neogene deposits but their dermal sculpture obscures determination of cranial bones and, as a result, interspecific variation. Recently, complete skeletons were found in the late Oligocene locality of Enspel, Germany which, together with earlier findings of articulated but mostly poorly preserved skeletons from the late Oligocene locality Rott, Germany, can help to understand the skeletal structure of the genus. Distinguishing two morphotypes in the Rudabánya material may reflect taxonomic, individual or developmental variation.

Triturus sp., type I

Material

Trunk vertebra (2/34; 3/4; 19/4; 35/15; 39/16; 40/18, Text-fig. 3A), humerus (36/23, Text-fig. 3B).

Description

Opisthocoelous vertebra corresponding in size to contemporary *Triturus vulgaris* or *Triturus alpestris*, i.e., much smaller than in the type II (46/4, Text-fig. 3C). The anterior surface of the cotyle is nearly vertical, not typically convex. The articular surface of the cotyle is separated from the centrum by a narrow, groove-like constriction. In anterior aspect, the cotyle is only moderately compressed dorso-ventrally. The diameter of the centrum is distinctly shorter than that of the neural canal. If seen from above, both anterior margins of the neural canal meet in a broad V-shaped incisure; consequently, the most anterior part of the neural canal remains uncovered dorsally. Both praezygapophyses slightly exceed the level of the cotyle, and their articular surface is ellipsoid in shape. The transverse process is declined posteriorly, consisting of the dorsal and ventral branches. The postero-lateral margin of the praezygapophysis is connected with the anterior margin of the proximal part of the dorsal branch by a thin horizontal lamina, and a similar horizontal lamina connects the ventro-lateral surface of the centrum, below the basis of the praezygamopohysis, with the proximal part of the ventral branch of the transverse process. The lateral wall of the vertebra between both laminae is moderately concave, pierced by several small foramina. There is a large foramen between the basis of the praezygapophysis and the anterior end of the lower lamina. The dorsal median crest does not reach the anterior margin of the neural canal. The posterior margin of the neural canal is slightly elevated, projecting in a bifurcated spinal process. The dorsal margins of this bifurcation are not continuous with the dorsal median crest. The basis of the postzygapophysis is separated from the basis of the dorsal branch of the transverse process by a wide incisure. In ventral aspect, the anterior horizontal cristae joining the proximal part of the transverse process on either side, together with similar cristae which run posteriorly from the transverse processes, form a typical rhomboid pattern, though less extensive if compared with specimen 46/4 (see below). In contrast, the pattern is better developed than in contemporary *Triturus*, where it is reduced to the anterior and posterior peduncles separated by a single and large subcentral foramen. In Rudabánya specimen 40/18 there are several small subcentral foramina an either side of the centrum; the centrum is only slightly elevated beyond the level of the rhomboid lamellae.

The preserved proximal part of the humerus cannot be distinguished from that in contemporary medium-sized *Triturus*.

Remarks

This is clearly a *Triturus* vertebra, however, differing from the contemporary species in more extensive rhomboid laminae.

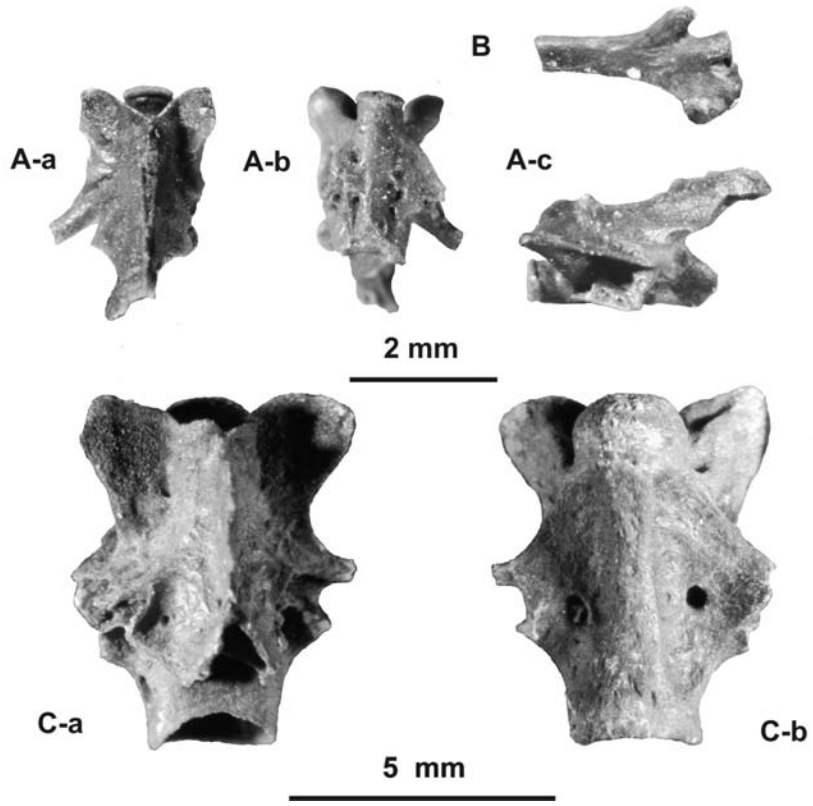
Triturus sp. type II

Material

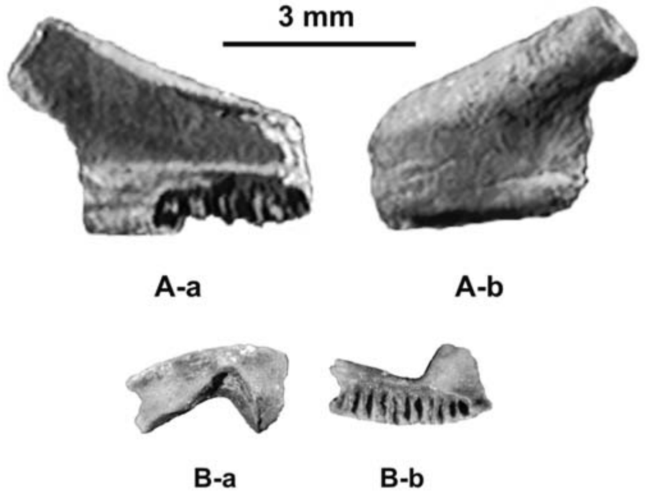
Trunk vertebra (35/16-17; 46/4, Text-fig. 3C)

Description

The vertebrae are opisthocoelous, much larger than in the type I (e.g., 40/18), with the condyle only slightly extending beyond the level of the dorsal margin of the neural canal. In dorsal aspect, the horizontal diameter of the neural arches approximately equals to the diameter of one praezygapophysis. The spinal process is thin but deep vertical lamina which is bifurcated posteriorly, anteriorly extending almost to the margin of the neural arches. A small foramen is piercing transversally the basis of the spinal process close anteriorly to its bifurcation. Laterally, two canals entering horizontally the basis of the praezygapophysis may be seen, some others, smaller, enter the bone in the area between the praezygapophysis and the transverse process. There is a crista running from the posterior margin of the praezygapophysis toward the transverse process, and another one which connects the basis of the praezygapophysis and the transverse process. The latter crista continues posteriorly from the transverse process to the lateral margin of the cotyle. If seen ventrally, both cristae form together with their counterparts from the



Text-fig. 3 - *Triturus* sp. A - Trunk vertebra in dorsal (a), ventral (b) and sinistral (c) views, 40/18. B - Humerus, 36/23. C - Trunk vertebra in dorsal (a) and ventral (b) views, 46/4. A and B in the same scale, different from C.



Text-fig. 4 - Salamandridae indet. A - Left maxilla in inner (a) and outer (b) view, 23/13. B - Left praemaxilla in dorsal (a) and posterior (b) view, 45/11. Both in the same scale.

opposite side a typical rhomboid pattern. There are two large foramina (besides one or more smaller ones) entering the vertebral centrum on its lateral surface but facing posteriorly; one is on the lateral side of the cotyle, the other is adjacent to the vertical wall of the transverse process. The subcentral ridge on the ventral surface of the centrum is widely rounded, moderately constricted both in ventral and lateral views. Two large subcentral foramina pierce the ventral surface of the vertebra, on either side of the subcentral ridge.

Remark

The vertebrae are intermediate in structure between those in *Chelotriton* (the processus spinosus deep and bifurcated posteriorly, though not terminated dorsally by a horizontal, sculptured plate) and *Triturus* (large foramina on the ventral side).

Salamandridae indet.

Material

Left praemaxilla (45/11, Text-fig. 4B), left maxilla (23/13, Text-fig. 4A).

Description

The processus frontalis of the praemaxilla is short, attaining approximately the level of the dorsal margin of the praemaxillo-maxillary suture. There is a triangular area on the antero-dorsal surface of the bone, delimited by two low cristae. One is coming from the area of the frontal process, the other from the area of the dorsal end of the praemaxillo-maxillary suture. Both meet in approximately right angle above the tooth row. Although the lateral portion of the bone is broken away, it is obvious that the praemaxilla bore at least 13 tooth positions. The lamina horizontalis in the posterior part of the maxilla is narrow, with a sharp medial edge. There is a horizontal depression above the lamina which continues onto the basis of the postorbital process where it is seemingly deeper because the orbital margin is markedly bent medially. The teeth are separated from each other by narrow spaces and the last tooth position is covered by a thin vertical lamina on its labial side. The lateral surface of the bone is smooth, with the shallow but distinct concavity between the orbital margin of the postorbital process and lower margin of the bone.

Anura Giebel, 1847
Discoglossidae Günther, 1854

Latonia gigantea (Lartet, 1851)

Material

Frontoparietale (1/6; 2/45; 5/1-2, Text-fig. 5E; 6/30; 14/14; 15/46; 19/50; 27/1; 36/16; 37/64, Text-fig. 5D), right praemaxilla (5/26), left maxilla (5/13; 15/32; 19/40; 30/1, Text-fig. 5F; 32/21; 37/63; 47/11), right maxilla (15/33-36; 19/37; 19/39; 20/1; 23/12, Text-fig. 5G; 26/15), left praearticulare (2/24; 5/15; 10/13-14; 15/24-25; 20/4, Text-fig. 5B; 23/5, Text-fig. 5A; 25/7; 32/12, Text-fig. 5C; 33/1; 42/5; 47/1), right praearticulare (6/21; 9/7; 14/22-23; 16/2; 17/21; 25/6), atlas (12/9; 17/18; 32/19, Text-fig. 5M; 42/47; 49/3), vertebra (4/17; 43/10), vertebrae - V4 (20/5, Text-fig. 5L), sacral vertebra (35/30), urostyle (17/5; 37/34-35; 38/9; 43/8), right scapula (15/40); left humerus (2/13; 25/24; 27/7; 36/7; 37/50, Text-fig. 5H; 37/51; 42/17; 42/32), right humerus (36/2), left ilium (1/7, Text-fig. 5J; 2/51; 5/9; 10/23-24; 12/5-6; 14/12; 15/22; 16/5; 20/2, Text-fig. 5K; 32/17-18; 37/24; 37/27; 42/40-41; 43/3, Text-fig. 6I; 45/1; 45/3), right ilium (15/10; 35/2; 37/20; 43/6), tibiofibula (5/12).

Description

Both extremely large (30/1; 37/50, Text-fig. 5H) and small individuals were recorded (23/12; 32/12, Text-fig. 5C; 32/18). Only fragments of the anterior portion of the frontoparietal is available. However, typical morphology of its ventral surface (pars contacta, wrinkled articulation area for the sphenethmoid; see Roček, 1994: fig. 7E) and sculpture on its dorsal surface suggest that it no doubt belongs to *Latonia gigantea*. In contrast to other specimens (even from other localities; see Roček, 1994), 5/1 is unique in preservation of its tectum supraorbitale which diverges posteriorly suggesting that both orbits were separated from the vertical walls of the braincase, similar to the condition in the holotype of *Latonia seyfriedi* (Roček, 1994: fig. 2).

General morphology of the maxilla does not differ from that in other species of *Latonia* (see, e.g., Roček, 1994: fig. 9D), except for *L. ragei* (Hossini, 1993). On its outer surface there is a typical patch of sculpture adjoining the posterior part of the orbital margin and the processus zygomaticomaxillaris. This pattern of sculpturing is typical for *L. gigantea*. In 32/21 the dense sculpture is extending anteriorly to the lateral margin of the orbit, anterior to the bifurcated imprint of vessels running from the posterior part of the orbit to the outer surface of the bone, better developed than in *Latonia gigantea* from the Late Miocene of Polgárdi 2, Hungary (identified as "*Pelobates robustus*" by Bolkay, 1913: pl. XI, fig. 1). In the largest specimen (30/1) the sculpture is densely pustular, similar to the lectotype of *Latonia gigantea* illustrated in Roček (1994: fig. 7F).

The praearticular (Figs 5A, B, C) bears two characteristic medial tubercles, the processus coronoideus directed dorsally, and processus paracoronoideus directed medioventrally. The groove for Meckel's cartilage is deep, with sharp margins within a short section at the level of the coronoid process nearly closing the groove dorsally. On the lateral surface of the posterior part of the bone, there is a deep and comparatively well delimited depression. Although anteriorly the groove turns onto the lateral side of the bone, it is ventrally delimited by a vertical low edge. The overall morphology of the bone closely recalls that of the praearticular from the Middle Miocene locality of Sansan, France illustrated in Roček (1994: fig. 12G). All charactersitic features are developed as early as in very small individuals (Text-fig. 5C).

The fragmentary atlas 49/3 bears distinctly developed median crista on its ventral surface (see Roček, 1994: fig. 13C), with both condyloid fossae well separated from one another (see Roček, 1994: fig. 14G). Neural arches of the praesacral vertebrae are imbricate, and bear a thin median crista extending up to the tip of the spinal process (43/10). Fragmentary V4 (Text-fig. 5L) indicates that ribs could be co-ossified with the transverse processes in large individuals.

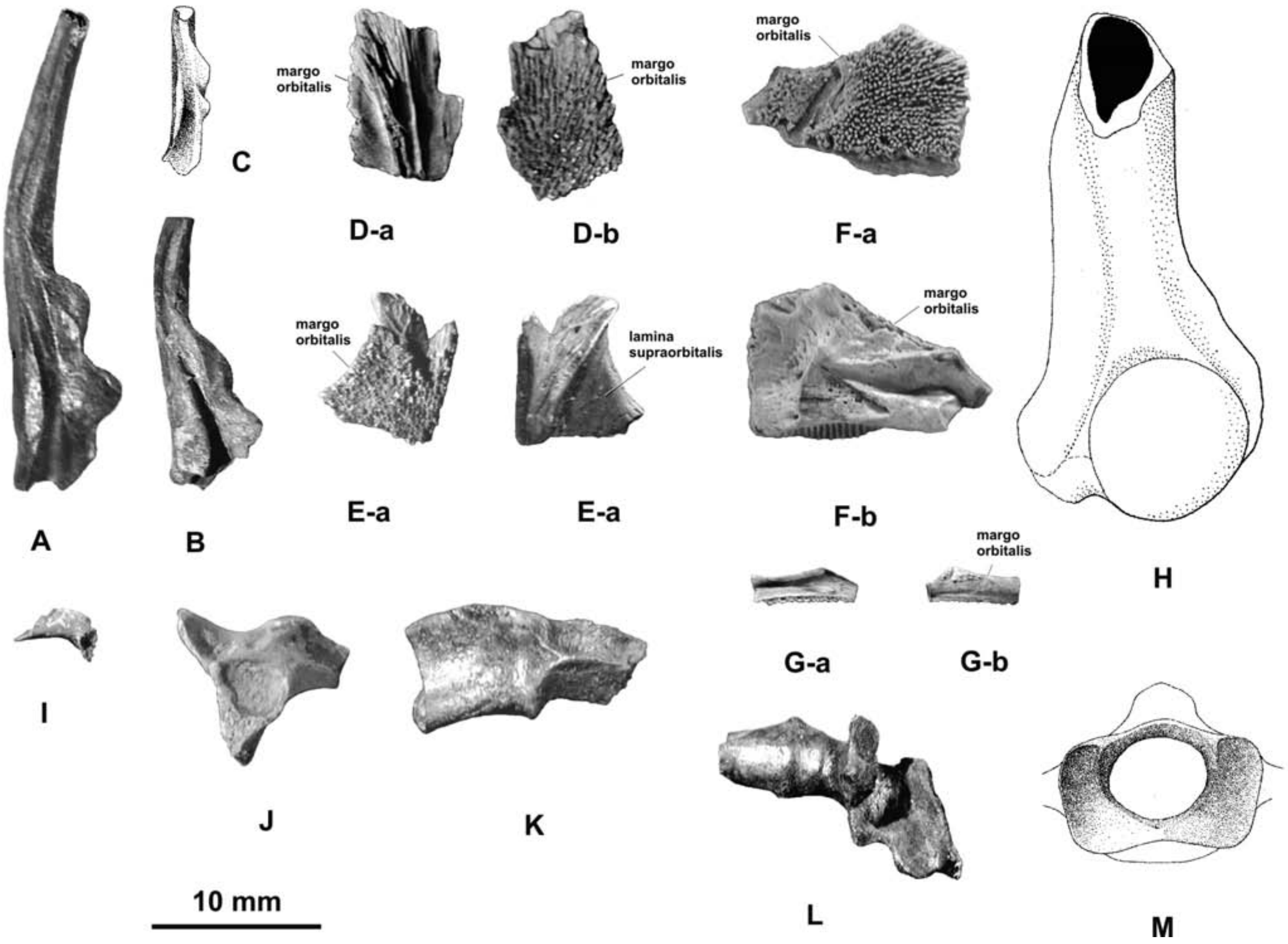
The urostyle displays all typical features of *Latonia*, such as the transverse processes declined posteriorly and connected postero-medially with the lateral surface of the neural canal by a horizontal lamina, and the intervertebral canal underneath the proximal part of the transverse process (see also Roček, 1994: fig. 15).

The humerus is characteristized by its fossa cubitalis ventralis, though indistinct, which is represented by a shallow groove along the dorsal margin of the caput. The medial epicondyle is large, whereas the lateral one is just a dorsal part of the lateral crista joining the lateral surface of the caput (as in the specimen illustrated in Roček, 1994: fig. 17F). Judging by the humeri, some individuals could reach a considerable size (in 36/2, the diameter of the caput humeri is about 7 mm).

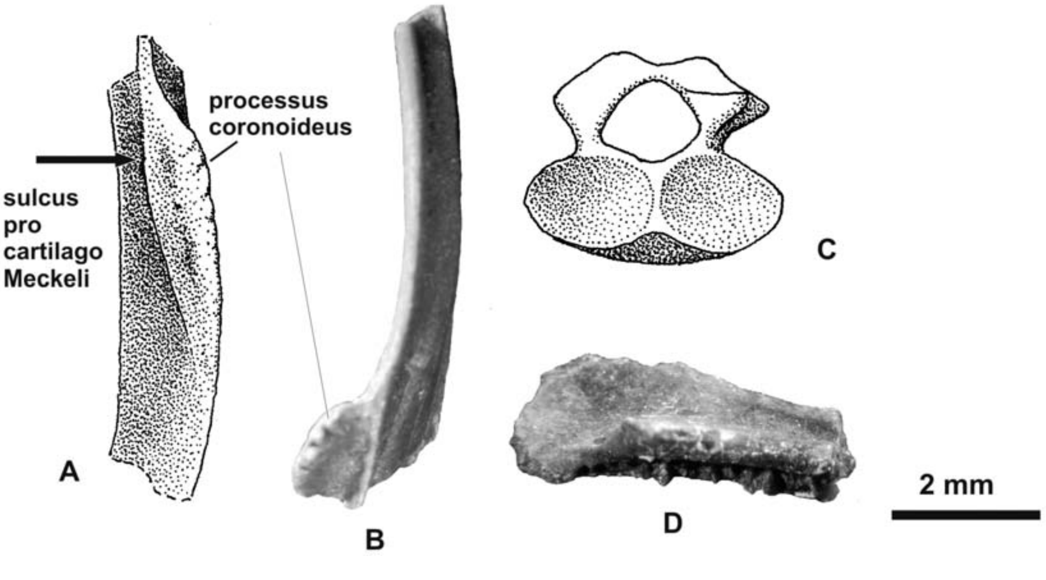
The ilium is large, with the anterior margin of the acetabulum extending beyond the antero-ventral outline of the bone and elevated laterally, whereas its dorsal margin is slanting down to the level of the surrounding bone. There is a foramen entering the bone postero-dorsally to the acetabulum, at the basis of the pars ascendens. Two other foramina are located anterodorsally to the acetabulum. The dorsal margin of the bone, as well as other features, correspond to those in the specimen from the Middle Miocene of La Grive St. Alban, France illustrated in Roček (1994: fig. 18G).

Remarks

Since the postcranial skeleton of *Latonia* is virtually uniform, assignment of its elements to *Latonia gigantea* can be based only on indirect evidence (simultaneous occurrence of cranial elements). It should also be noted that in early metamorphosed *Latonia* (43/3) the general morphology of the bone is essentially the same as in fully grown adults; however, since the postcranial skeleton of young *Latonia* does not differ from that in contemporary *Discoglossus*, one should also admit that the ilium 43/3 could belong to the latter genus. Same holds for urostyles identified below as cf. Discoglossidae. One of few characters different in *Latonia* and *Discoglossus* is that the carina neuralis (dorsal median crista extending up to the spinal process) is developed as a distinct vertical lamina



Text-fig. 5 - *Latonia gigantea*. A - Left praearticular, 23/5. B - Left praearticular, 20/4. C - Left praearticular, 32/12. D - Anterior part of the frontoparietal in ventral (a) and dorsal (b) view, 37/64. E - Anterior part of the frontoparietal in dorsal (a) and ventral (b) view, to show extent of the lamina supraorbitalis, 5/1. F - Left maxilla in outer (a) and inner (b) view, 30/1. G - Right maxilla of the juvenile in inner (a) and outer (b) view, 23/12. H - Left humerus, 37/50. I - Left ilium of the juvenile, 43/3. J - Right ilium, 1/7. K - Left ilium, 20/2. L - Vertebra 4 in dorsal view, with proximal part of the left rib ankylosed, 20/5. M - Atlas in anterior view, 32/19. All in the same scale.



Text-fig. 6 - A - *Bombina* sp. Posterior section of the left praearticular in dorsal view, 46/7. B - *Bombina* sp. Right praearticular, 31/10. C - Discoglossidae inc. sedis. Urostyle in anterior view, 25/2. D - cf. *Discoglossus*. Left maxilla in lingual view, 3/21. E - Discoglossidae inc. sedis. Urostyle, 3/8. All in the same scale.

in the former, whereas it is absent in the latter.

Bombina sp.

Material

Left praearticulare (46/7, Text-fig. 6A), right praearticulare (31/10, Text-fig. 6B), left humerus (46/13).

Description

The posterior part of the praearticular is characterized by a vertical and dorsally prominent sharp lamina, the lateral surface of which is wrinkled. The groove for Meckel's cartilage is rather shallow but delimited both medially and laterally by sharp cristae. The medial crista is not antero-posteriorly continuous; rather, the medial margin of the groove is formed by dorsally prominent margin of the bone and the groove runs on the lateral surface of the bone in its anterior section. There is a deep elongated depression between the lamina and the medial margin of the groove.

The humerus is small, with its fossa cubitalis ventralis restricted to an indistinct groove along the dorsal margin of the caput. The crista lateralis is sharp, slightly lifted ventrally, joining the lateral surface of the caput without producing the lateral epicondyle. Although the distal surface of the caput is worn out it is obvious that the latter was large, with its transverse diameter equal to nearly half of that of the caput.

Remarks

The morphology of the posterior part of the praearticular (especially of the coronoid process) is one of few characters clearly distinguishing *Bombina* from *Discoglossus*. This is especially important in context of the view (Smirnov, 1989, 1990) that *Bombina* is a paedomorphic *Discoglossus*.

cf. *Discoglossus*

Material

Left maxilla (3/21, Text-fig. 6D), right maxilla (19/38), urostyle (15/41).

Description

The outer surface of the maxilla is smooth. The lamina horizontalis was terminated by the processus pterygoideus which is, however, broken off. There is a distinct groove for the palatoquadrate bar above the lamina horizontalis. The tooth row reaches posteriorly the level of the base of the processus pterygoideus.

Remarks

This maxilla corresponds in its size to the postcranial elements described below as Discoglossidae incertae sedis. Since corresponding in size maxillae of *Latonia* already bear sculpture on their external surface (see Roček, 1993: fig. 11A), it seems more probable that this element belongs to *Discoglossus*.

Discoglossidae incertae sedis type I

Material

Right maxilla (15/37), praesacral vertebra (probably V5) (48/3), sacral vertebra (19/5), urostyle (3/8, Text-fig. 6E), right humerus (42/28), left humerus (2/12).

Description

Praesacral vertebrae opisthocoelous, with imbricate neural arches meeting each other posteriorly in a prominent spinal process (only slightly lifted postero-dorsally). The dorsal surface is nearly flat, horizontal, extending to the proximal part of the posterior margin of the transverse process by a horizontal lamina. A median ridge is developed indistinctly only on the spinal process posteriorly, and on somewhat lifted anterior margin of the neural arches anteriorly (there is a deep groove between this lifted margin and the praezygapophysial articular area). There is also a deep incisure on the dorsal margin of the cotyle.

The urostyle is not different from that in *Latonia* and *Discoglossus*, however, its small size does not allow one to determine to which of these two genera it may be referred.

The medial epicondyle of the humerus is markedly large, whereas the lateral is substituted by the distal end of the crista lateralis joining the lateral surface of the caput humeri. The fossa cubitalis ventralis is present, but limited to a shallow groove along the dorsal margin of the caput. Both medial and lateral cristae are comparatively short, modified in rounded ridges proximally, toward the middle part of the bone.

Remarks

General morphology of the praesacral vertebra is in agreement both with that of contemporary *Discoglossus* and of small individuals of *Latonia*. This is why assignment to either of both genera is difficult, though occurrence of cranial bones can be taken as an indirect evidence for *Latonia*.

Discoglossidae incertae sedis type II

Material

Urostyle (25/2, Text-fig. 6C; 43/7; 45/9).

Description

The urostyle 25/2 is small, similar to that of *Discoglossus* or *Latonia*, but different in that it has a lateral process protruding anteriorly from the lateral wall of the neural canal (Text-fig. 6C). Since the opposite side of the bone is broken off it is not possible to decide if this is a vestigial praezygapophysis or not. Two other urostyles also bear two condyloid fossae suggesting the presence of a bicondylar sacro-urostylar articulation. Since the dorsal part of the neural canal is broken off it is difficult to decide whether the bone belongs to the Ranidae or Discoglossidae. A moderately developed horizontal crista on both sides of the bone, which is well developed in some specimens of *Latonia* (Roček 1994: fig. 15), suggests referral to the Discoglossidae.

Palaeobatrachidae Cope, 1865

Palaeobatrachus sp.

Material

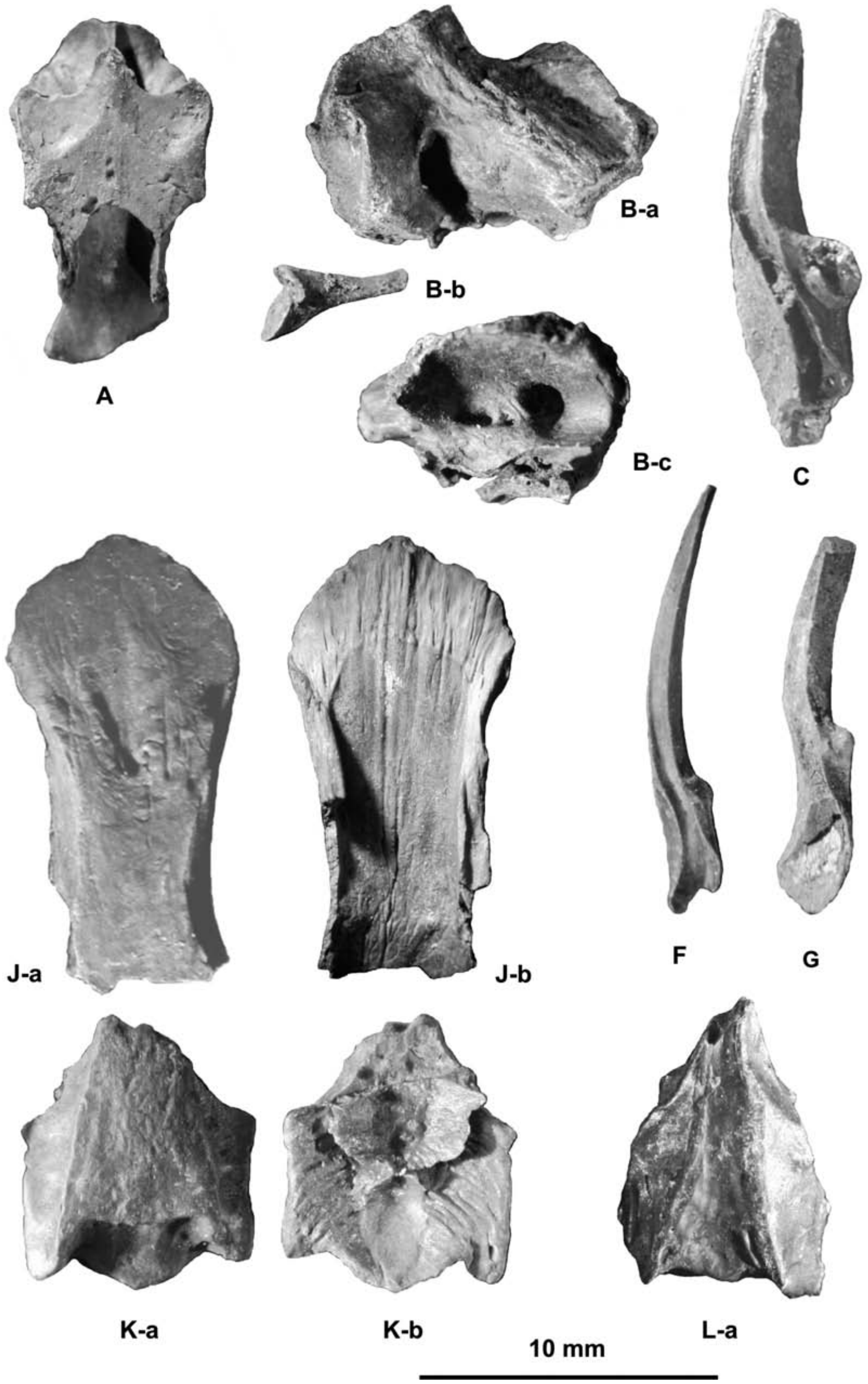
Sphenethmoid (3/20; 6/41; 8/22-23; 10/8; 12/10; 17/1-4; 19/30; 22/6-7; 30/2; 37/36-37; 39/2-4; 40/13; 41/1; 41/2, Text-fig. 7A; 41/3; 42/12-15; 43/16-17; 45/8; 53/9), oticooccipitale and columella (42/50, Text-fig. 7B), frontoparietale (5/3; 23/4; 26/4-5; 31/7; 37/62; 38/12; 41/26-27; 42/42, Text-fig. 7K;

42/43; 42/51; 43/19, Text-fig. 7L; 48/1, Text-fig. 7J; 48/2; possibly also juvenile 17/11), right praemaxilla (5/28; 44/14, Text-fig. 8D), left maxilla (2/49; 3/1; Text-fig. 8A; 22/16-19; 26/10; 26/13; 38/20; 38/21; 44/15; 49/11, Text-fig. 8C), right maxilla (5/29; 26/9; 26/11-12; 26/14; 36/11; 36/21; 36/24; 37/65; 38/19; 39/35; 40/14; 54/10, Text-fig. 8B), left squamosum (10/1; 44/11, Text-fig. 14/D); left praearticulare (1/3-5; 2/16-17; 2/20; 2/23; 3/5-7; 4/6; 5/14; 6/17-20; 6/22; 8/25; 9/5; 9/10; 9/11; 10/11-12; 10/16; 11/6; 11/8; 12/2; 13/5; 15/27-29; 16/1; 16/3; 17/22; 19/7; 19/14; 22/2; 25/9-11; 25/16; 27/10-13; 28/10; 28/12; 29/2; 31/3-4; 32/5; 32/7-10; 35/24; 35/25, Text-fig. 7E; 35/26; 37/41; 37/46, Text-fig. 8-D; 37-47; 37/49; 40/2; ?40/4; 40/5; 41/16-17; 41/20-21; 41/24; 42/6, Text-fig. 7F; 42/7-8; 42/10-11; 42/16; 44/1; 44/2; 45/6; 45/7; 47/2; 47/3, Text-fig. 7G; 49/4; 52/1, Text-fig. 7C; 53/1; 54/5), right praearticulare (1/1-2; 2/19; 2/21-22; 6/16; 9/4; 10/10; 10/15; 11/5; 11/7; 12/1; 12/3-4; 14/25; 15/26; 15/30-31; 16/4; 17/19-20; 17/23-24; 19/6; 19/8; 19/10-13; 24/1; 25/8; 25/12; 25/14; 27/8-9; 27/14; 28/9; 28/11; 28/13; 32/6; 32/11; 33/2; 35/22-23; 35/28; 37/40; 37/42-45; 37/48; 40/3; 41/18-19; 41/22-23; 41/25; 42/9; 47/4, Text-fig. 7H; 49/6, Text-fig. 7I), atlas (9/15; 14/11; 32/19), presacral vertebra (17/16; 26/1-3; 41/13-14), synsacrum (35/19; 41/15; 52/1), urostyle (25/1; 27/16), right coracoid (5/18; 8/24; 10/17; 14/28; 17/13; 22/8, Text-fig. 9-I), left scapula (13/6; 27/5; 37/60-61, Text-fig. 9-A; 41/29; 42/49; 50/1, Text-fig. 9-B), right scapula (28/7; 40/24; 41/28; 43/14; 43/15, Text-fig. 9-C; 46/3), left humerus (2/8; 2/14; 3/9-10; 3/12; 4/7; 5/5-6; 5/8; 6/10; 6/12; 8/5; 8/9; 9/3; 11/9-10; 11/12-13; 13/1; 14/2-3; 15/12-13; 15/15; 15/18; 15/51; 19/15; 19/17; 19/19-22; 19/25-28; 22/5; 23/3; 25/26-28; 25/32; 27/2-2; 27/5-6; 32/2-3; 34/2; 36/1; 36/4; 37/52; 37/54; 37/57; 41/6; 41/9; 42/20; 42/21; 42/23; 42/24; 42/27; 42/29; 44/7; 45/10; 46/12; 49/1; 49/2; 51/1; 53/5), right humerus (2/9-11; 3/11; 3/14; 4/8-11; 5/4; 5/7; 6/11; 7/1; 8/1; 8/3; 9/1-2; 10/19-20; 13/3; 14/1; 15/14; 15/16-17; 15/19-20; 16/7; 19/16; 19/24; 20/3, Text-fig. 9-D; 22/3-4; 28/15-17; 29/1; 32/1, Text-fig. 9-E; 36/3; 37/53; 37/55; 37/58; 40/23; 41/5, Text-fig. 9-F; 41/7; 42/18; 42/19; 42/22; 42/26; 42/30; 44/3; 44/4; 44/5; 44/6; 46/10; 47/8; 50/2; 53/6; 54/1), left ilium (1/8; 2/3; 2/5; 4/1; 4/3; 6/14; 8/11; 11/14; 15/2; 15/6; 16/6; 18/1; 28/23; 42/36; 43/5; 43/9; 44/10; 46/1, Text-fig. 9-H; 47/7; 47/10; 49/8; 49/9), right ilium (2/7; 5/10-11; 6/13; 15/7; 15/9; 19/31; 19/35-36; 23/7; 25/23; 28/24; 32/16; 35/3; 37/19; 37/25; 37/29-30; 39/32; 41/10; 41/11; 41/12, Text-fig. 9-G; 42/35; 42/38-39; 44/9; 45/2).

Description

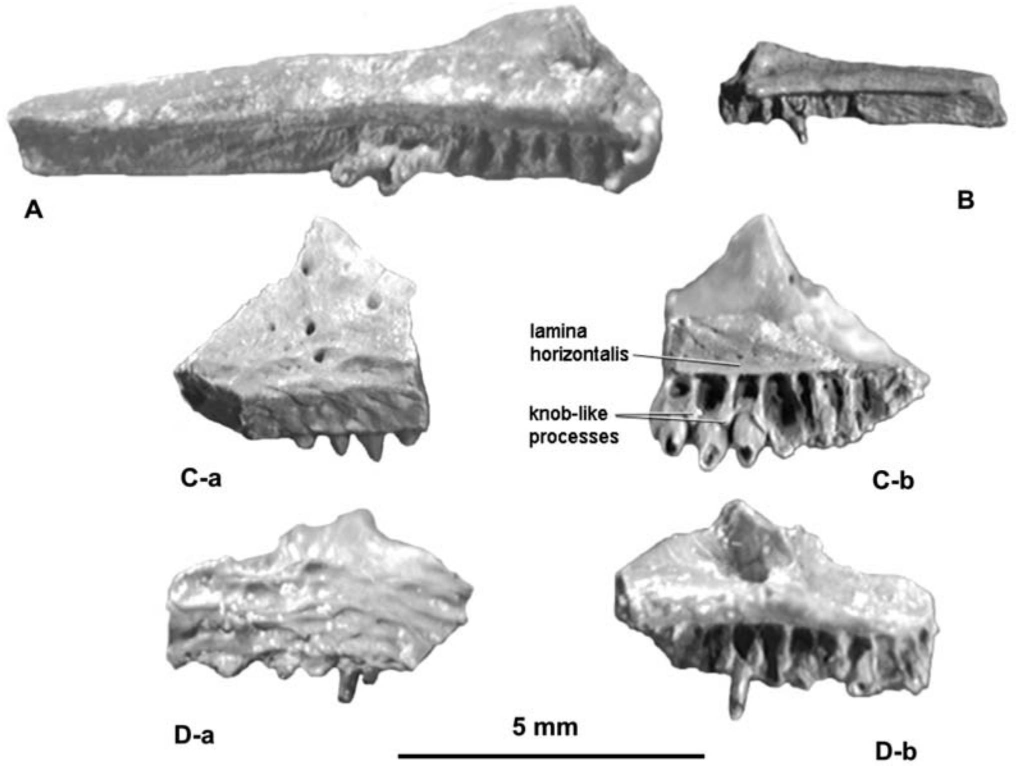
The sphenethmoid is long, with its bottom part below the foramen opticum slightly divergent posteriorly. There are two depressions on its dorsal surface along the anterior margin of the osseous tectum synoticum, which meet one another in a rounded median crista. They served as articulation areas for the nasals (see Špinar, 1972: pl. 9, fig. 1). The remaining elevated portion of the bone's dorsal surface (contact area for the frontoparietal) is triangular in shape, covered by antero-posteriorly oriented grooves. The osseous postnasal wall extends only moderately beyond the lateral outline of the bone. Similarly, the septum nasi is also ossified in a lesser extent than in other anurans; the most anteriorly prominent part is its ventral part which is confluent with the bases of the ethmoidal capsules (solum nasi). In older individuals it is terminated by a rounded tip (41/1), but less extensive in younger ones (40/13, 42/2). On the ventral surface of the bone, there is a deep median groove reaching the anterior margin of the bone (i.e., the basis of the septum nasi). The groove served for insertion of the anterior section of the parasphenoid which, according to Špinar (1972: pl. 9, fig. 2), reached up to the praemaxillary symphysis. Towards the posterior, the groove becomes shallower, and near the posterior border of the bone the contact area for the parasphenoid is flat, with tiny cristae on both sides. The canal for the medial branch of the ophthalmicus nerve (ramus medialis nervi ophthalmici), seen from the nasal cavity, is situated close dorso-ventrally to the olfactory canal, separated from the latter only by a thin partition and reaching about half of its diameter, or even joining the olfactory canal before entering the nasal cavity (45/8). In juvenile individuals (40/13), in which most of the nasal capsule is still cartilaginous, the olfactory canal is comparatively broad, nearly equal to the diameter of the osseous part of the capsule. The medial branch of the ophthalmicus nerve enters the postnasal wall from the orbit underneath comparatively large orbitonasal lamina. In the largest sphenethmoids (30/2) the diameter of the bone between lateral tips of the osseous postnasal walls can reach up to 12 mm.

The oticooccipitale is shallow, and although its lateral part is broken off, it probably extended far laterally. It is attributed to *Palaeobatrachus* on the basis of its parallel grooves on the ventral surface of the otic capsule which served as an articular surface for the lateral wings of the parasphenoid. The same type of grooves occur on the dorsal surface of the sphenethmoid of *Palaeobatrachus* (contact area for the frontoparietale). Moreover, the posterior surface of the prominentia canalis semicircularis posterioris runs out in a sharp vertical ridge, which is in agreement with morphology of the posterior surface of the frontoparietale (see below). The dorsal surface of the otic capsule is flat, delimited posteriorly and postero-laterally by a rounded horizontal ridge. The occipital condyle is elongated, only moderately broader in its dorsal part, and slightly exceeding the level of the dorsal margin of the foramen magnum. The condyle markedly exceeds the level of the posterior wall of the capsule. The jugular canal is broad, its outer orifice is roofed by a thin horizontal lamina. Its anterior wall is pierced by two foramina, the foramen perilymphaticus superius and inferius, respectively; both are, however, horizontally coplanar. Two other foramina, the foramen acusticum anterior and posterior, connect the cavity of the capsule with the braincase (Text-fig. 8B-c). The foramen endolymphaticum is absent. The most anterior part of the capsule is its prominent ventral part, triangular in shape, terminated in a broad rounded point. It is separated medially from the braincase wall (below the fissura prootica) by a deep concavity, whereas laterally there is a broad horizontal groove (probably the sulcus venae jugularis) running postero-laterally.

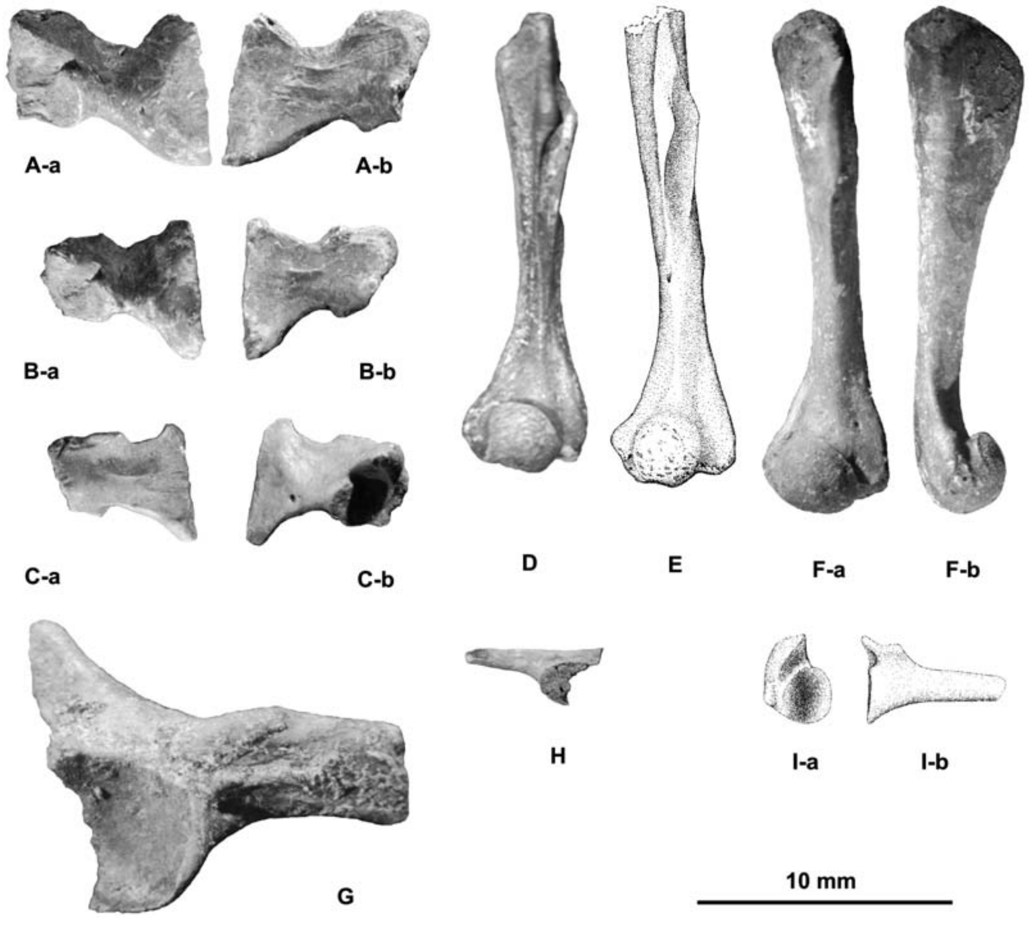


Text-fig. 7 - Cranial bones of *Palaeobatrachus* sp. A - Sphenethmoid in dorsal view, 41/2. B - Right prooticooccipital in posterodorsal (a) and inner (c) view, with the columella (b) found *in situ*, 42/50. C - Left praearticulare, 52/1. D - Left praearticulare, 37/46. E - Left praearticulare, 35/25. F - Left praearticular, 42/6. G - Left praearticular, 47/3. H - Right praearticular, 47/4. I - Right praearticular, 49/6. J - Anterior part of the frontoparietal in dorsal (a) and ventral (b) view, 48/1. K - Posterior part of the frontoparietal in dorsal (a) and ventral (b) view, 42/42. L - Posterior part of the frontoparietal in dorsal (a) and ventral (b) view, 43/19. All in the same scale.

The dorsal surface of this most anterior part of the capsule is horizontal and flat. The dorsal portion of the anterior part of the capsule is declined posteriorly. There is a horizontal groove on the horizontal surface of the lower part of the capsule where it meets the anterior vertical wall of the upper part of the capsule, most probably for the nerves running through the prootic fissure. In addition, there is a small canal entering this vertical wall posteromedially. It probably enters the cavity of the capsule. The lateral part of the capsule in the area of the foramen ovale and crista parotica was crushed and the fragments, including the proximal part of the columella, were pushed inside the capsule. Although the distal part of the columella is thin and probably not complete, the proximal section (the "footplate") is markedly extended and asymmetrical (Text-fig. 8B-b). Thus, it can be taken



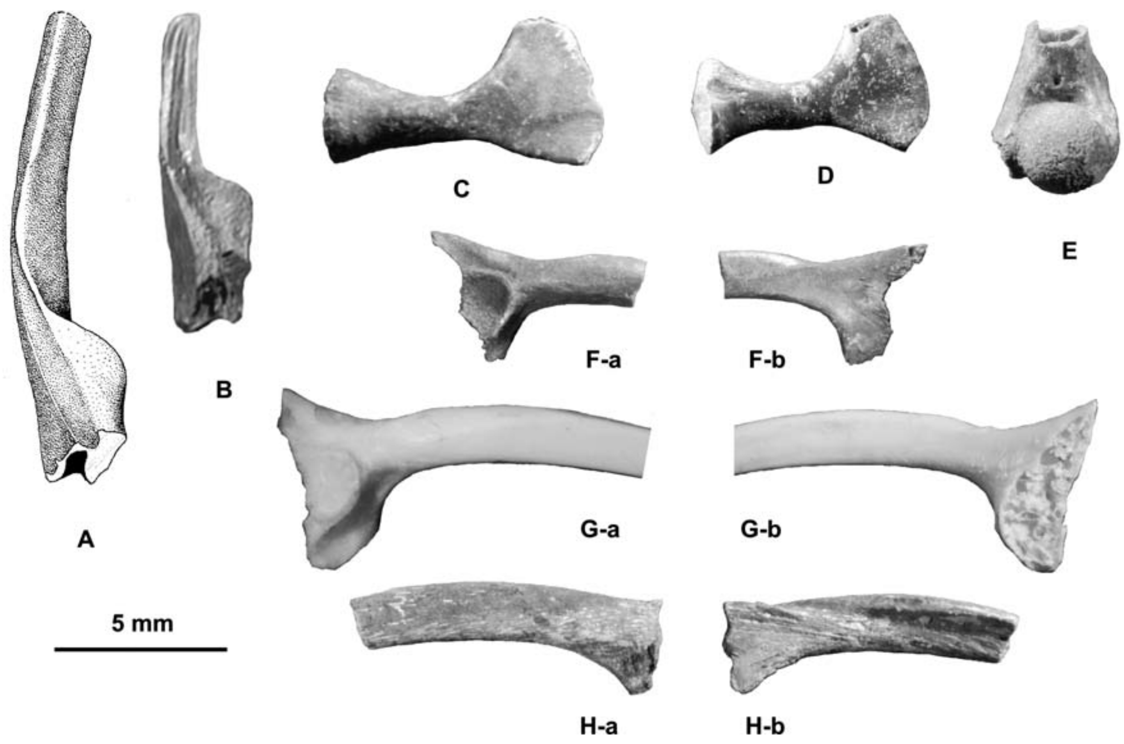
Text-fig. 8 - Upper jaw bones of *Palaeobatrachus* sp. A - Posterior part of the left maxilla in inner view, 3/1. B - Posterior part of the right maxilla in inner view, 54/10. C - Middle section of the left maxilla in outer (a) and inner (b) view, 49/11. D - Left praemaxilla in outer (a) and inner (b) view, 44/14. All in the same scale.



Text-fig. 9 - Postcranial bones of *Palaeobatrachus* sp. A - Left scapula in dorsal (a) and ventral (b) view, 37/61. B - Left scapula in dorsal (a) and ventral (b) view, 50/1. C - Right scapula in ventral (a) and dorsal (b) view, 43/15. D – Right humerus, 20/3. E - Right humerus, 32/1. F - Right humerus in ventral (a) and lateral (b) views, 41/5. G - Right ilium, 41/12. H - Left ilium, 46/1. I - Left coracoid in internal (= dorsal, b) and lateral (a) view, 22/8. All in the same scale.

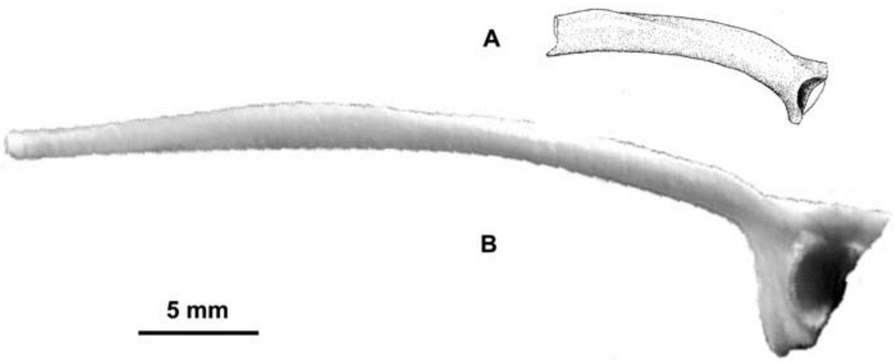
granted that there was a well developed sound-conducting apparatus in *Palaeobatrachus* (see also Špinar, 1972: text-figs 11B, 12J-M).

The frontoparietal consists of a spatulate anterior horizontal part, the margin of which is moderately pointed in the midline. Whereas in some specimens (48/1) the dorsal surface is horizontal and smooth, in others (48/2) its anterior part is moderately indented. The middle part of the bone is distinctly narrower; the dorsal surface breaks here into the lat-

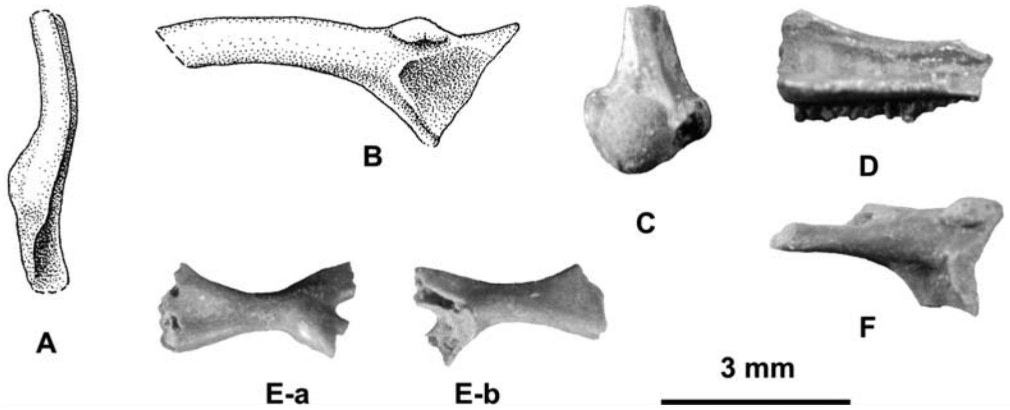


Text-fig. 10 - Pelobatidae. A - Left praearticulare, 38/4. B - Left praearticulare, 23/6. C - Right coracoid in ventral view, 5/16. D - Right coracoid in ventral view, 5/17. E - Humerus, 46/11. F - Right ilum in lateral (a) and medial (b) view, 10/21. G - Right ilium of *Pelobates fuscus*, recent, Czech Republic. H - Right iliac shaft in lateral (a) and medial (b) view, 15/4. All in the same scale.

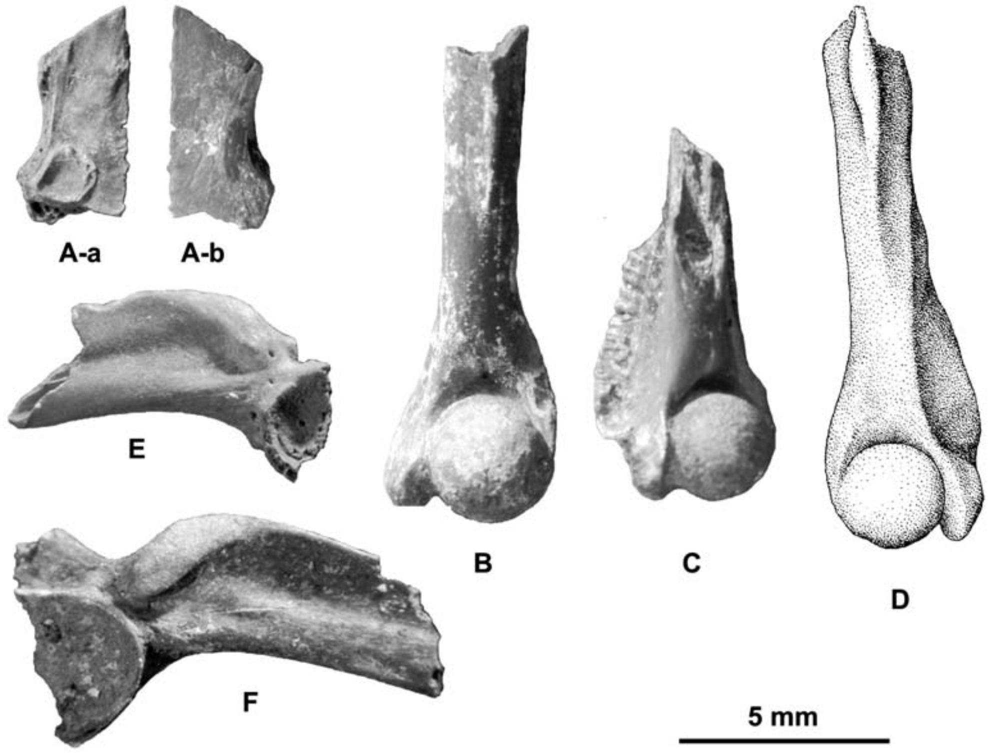
eral, nearly vertical walls in a sharp ridge which can even extend laterally as a narrow crista (in some, presumably younger specimens like e.g. 31/7, however, the ridge is rounded, not too sharp). The pineal foramen is directed anteriorly, and is located approximately at the posterior border of the anterior third of the bone. In ventral aspect, the anterior margin of the bone is paralleled by comparatively broad strip which bears antero-posteriorly oriented striation. This is the contact area for the sphenethmoid. It is clearly separated from that part of the bone which covers the dorsal fenestra in the endocranial braincase (functionally substituting elevated frontoparietal incrassation as in other anurans). A network of grooves representing imprints of vessels covers this part of the surface. Some of these grooves are connected through foramina in their bottom with the pineal foramen on the dorsal surface, or there is a single large foramen entering the bone (48/2). The posterior half of the bone (43/19) bears a deep depression with irregular, lifted margins, and with few small holes and tubercles on its bottom. This is the posterior part covering the frontoparietal fenestra and substituting thus the frontoparietal incrassation (*sensu* Jarošová & Roček 1982). The adjacent area of the ventral surface is covered by irregular, more of less parallel grooves oriented perpendicular to the margin of the bone. In large individuals (42/42, but also in much smaller ones 38/12) this part is delimited by a sharp crista extending over the grooved marginal surface of the bone. The depression covering the frontoparietal fenestra extends posteriorly, along the midline, as a shallower, smooth and ovoid depression, well separated by an elevated transverse ridge. In supposedly younger individuals (42/43) this part of the "incrassation" is still continuous with the main, anterior part, and separated by only small lateral incisures; this difference seems to depend on individual age as evidenced by juvenile individual 42/51. The dorsal surface of the bone is smooth, like in the anterior section of the bone, with the median part elevated and delimited laterally by a rounded ridge on each side. This elevated median part is clearly constricted in the middle of the antero-posterior diameter of the bone, and terminated posteriorly by a vertical wall, more or less convex in the midline. In larger, and supposedly older individuals (42/42, but also in smaller 38/12), the posterior surface is not vertical but slanting down from the transverse crista delimiting posteriorly the elevated horizontal flat area



Text-fig. 11 - *Pelodytes* sp. A - Left ilium, 2/2. B - Left ilium of contemporary *Pelodytes punctatus*, loc. Banyuls, southern France. All in the same scale.



Text-fig. 12 *Hyla* sp. A - Right praearticular, 35/29. B - Left ilium, 40/20. C - Right humerus, 36/22. D - Middle section of the right maxilla, 4/19. E - Left scapula in ventral (a) and dorsal (b) view, 14/17. F - Left ilium, 8/10. All in the same scale.



Text-fig. 13 - *Rana* sp. A - Right frontoparietale in ventral (a) and dorsal (b) view, 36/12. B - Left humerus, 42/31. C - Left humerus, 25/25. D - Right humerus, 37/56. E - Left ilium, 46/2. F - Right ilium, 45/4. All in the same scale.

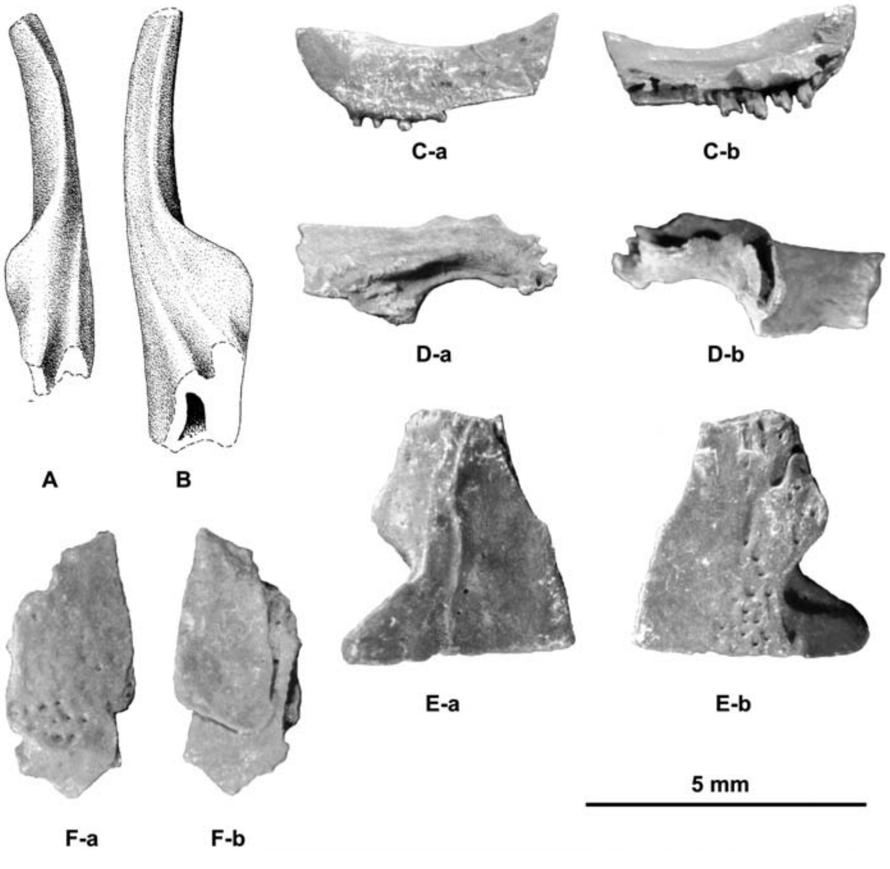
towards the posterior margin of the bone. Both lateral ridges are terminated in projecting points from which they continue as vertical diverging cristae towards the postero-lateral margins of the bone, or producing posterolateral processes which, however, do not extend posteriorly beyond the level of the median convexity. In juvenile specimens (42/51), the ridges on the dorsal side are less developed, and the "incrassation" on the ventral surface is delimited by less prominent cristae. The frontoparietal may be comparatively shallow and flat in these supposedly juvenile individuals (e.g., 26/5).

The processus frontalis of the praemaxilla (Text-fig. 8D) is strongly declined posteriorly. The outer surface of the bone bears irregular horizontal ridges. The tooth morphology and lower surface of the lamina dentalis correspond to those in the maxillae. The maxilla is robust, well ossified, with indistinct and not too dense sculpture on its outer surface which is pierced by comparatively large and variously oriented foramina. These foramina may possibly be connected with a large canal entering the inner surface of the bone above the lamina horizontalis. The lamina is deep, rounded on its margin, and producing a sharp ridge on its lower surface, covering tooth bases. This is the maxilla's typical character. Another typical feature of the maxilla is the presence of partitions separating the bases of the teeth; these partitions run out in rounded processes (pedicels) protruding between the bases of the tooth crowns. Teeth are conical with blunt tips; the latter are black and this dark portion is separated from the rest of the tooth crown by a sharp straight border. The posterior part of the maxilla is extended in a relatively slender posterior process. The lamina horizontalis extends onto the dorsal margin of the posterior process, exceeding the posterior termination of the tooth row. The dorsomedial surface of the lamina is convex; its medial, and at the same time lower margin, is formed by a sharp ridge. The lower part of the inner surface of the posterior process, below the lamina and posterior to the termination of the tooth row, is moderately wrinkled. The vertical wall of the maxilla terminates posteriorly with a ridge which, if viewed in dorsal view, has a sigmoid shape.

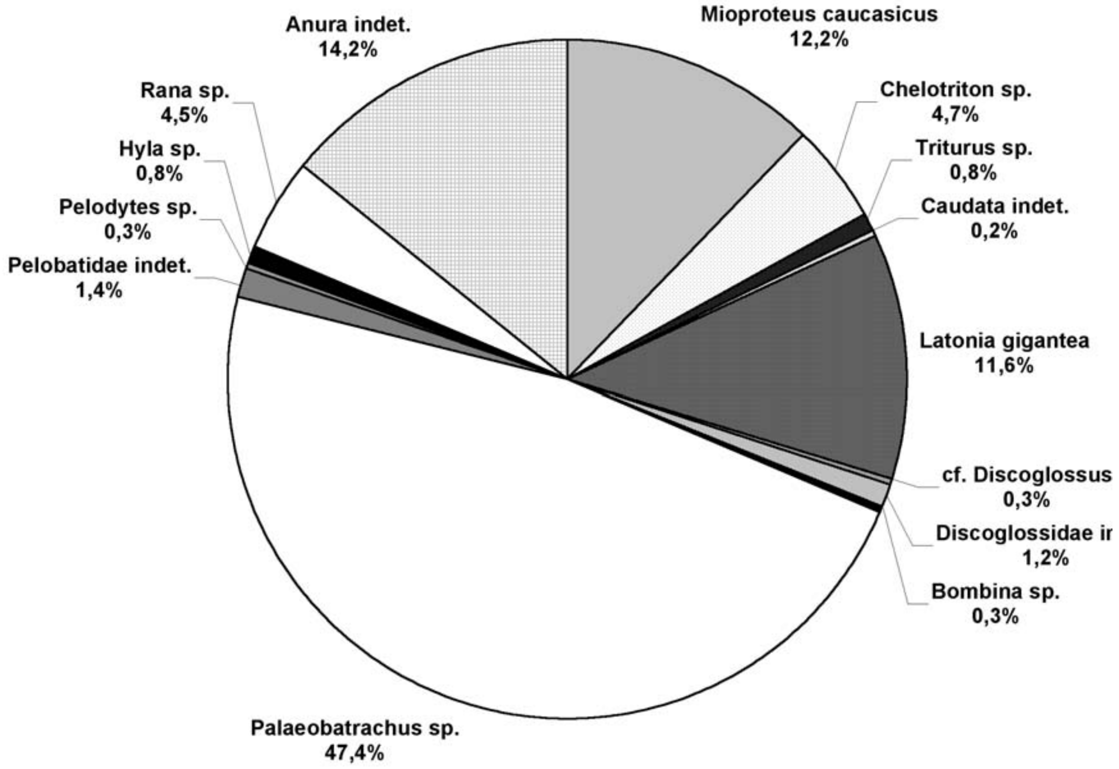
Judging by the general shape (see Špinar, 1972: pl. 12/1), the squamosals 10/1 and 44/11 (Text-fig. 14D) may be tentatively assigned to *Palaeobatrachus* also. The lamella alaris squamosi is elongated horizontally, with its posterior part shallow, rounded and moderately declined ventrally; this posterior margin is rather irregular, bearing tubercles and incisures in the largest specimens. In contrast, the dorsal margin of the anterior portion is nearly straight. At the level of the processus posterolateralis, there is a pointed outgrowth on the dorsal margin of the lamella. The outer surface of the lamella is smooth in juveniles (10/1), whereas it bears indistinct horizontal rounded ridges in adults (44/11), the lower-most of them being well distinguished and probably homologous with the single ridge in juveniles. The dorsal surface of the ramus paroticus is prominent above the dorsal margin of the lamella. The ramus paroticus is not extensive medially, which suggests that the lamella was closely adjacent to the crista parotica of the otic capsule.

The praearticulare bears a typical, lingually prominent tubercle (often called the processus coronoideus) with a wrinkled surface for insertion of the m. adductor mandibulae (sometimes even with a small foramen or foramina on its surface). The tubercle can be compressed dorso-ventrally in young individuals (25/16, 28/12, 41/20, 44/1), whereas it is rounded in cross-section in older ones. In some specimens (e.g., 40/4, 40/5) the outer surface of the tubercle is irregularly concave. The sulcus pro cartilago Meckeli is, at the level of the tubercle, deep and V or U-shaped in cross-section. The tubercle may be well delimited so that it is distinctly separated from the lateral edge of the groove. In some specimens (e.g., 35/25) the dorsomedial surface of the tubercle is flat, and the tubercle is connected with the medial margin of the sulcus for Meckel's cartilage by a ridge which is elevated in a point when it joins the medial margin of the groove. A similar point is developed on the opposite margin of the groove (Text-fig. 8E). More anteriorly the groove turns onto the labial surface of the bone where its formerly lateral edge becomes a narrow and sometimes even rounded horizontal ledge delimiting the sulcus ventrally, and its medial edge (crista paracoronoidea) becomes a sharp dorsal edge of the bone. However, in some specimens (e.g., 47/3), the groove is delimited ventrally by a sharp crista on the lateral surface of the bone. In large individuals, a low but distinct ridge splits away from the crista paracoronoidea and runs posteromedially towards the processus coronoideus (Text-fig. 8D). The outer surface of the bone beneath the lateral margin of the groove is distinctly concave (see also Vergnaud Grazzini & Młynarski, 1969: pl. I, fig. 16). This lateral depression is delimited ventrally by a rounded irregularly lobate ridge which no doubt served as an insertion area for jaw muscles, and at the basis of which are two comparatively large foramina (seen in ventro-lateral aspect).

The atlas has no median crista on its ventral surface, and both articular fossae for the occipital condyles are fused, with their lateral parts reaching nearly the level of the roof of the neural canal. The



Text-fig. 14 - Anura indet. A - right praearticular, 54/4. B - Left praearticular, 23/6. C - Right maxilla in outer (a) and inner (b) view, 5/30. D - Left squamosum in outer (a) and inner (b) view, 44/11 (possibly *Palaeobatrachus* sp.). E - Right frontoparietal in dorsal (a) and ventral (b) view, 40/25. F - Left frontoparietal in dorsal (a) and ventral (b) view, 6/31. All in the same scale.



Text-fig. 15 - Percentage representation of the identified taxa in the sample of the amphibian fauna from Rudabanya.

posterior condyle is large, dorso-ventrally compressed, and slightly concave on its dorsal side. Morphology of praesacral vertebrae is essentially the same as described by Vergnaud Grazzini & Młynarski (1969). The centrum is compressed ventrally, so the cotyle is typically semilunar in shape. The roof of the neural canal is reaching up to the level of the cotyle. The spinal process is long and nearly horizontal. The synsacrum is a typical feature of the Palaeobatrachidae (Vergnaud-Grazzini & Młynarski, 1969: pl. I, figs 1, 2; Vergnaud-Grazzini & Hoffstetter 1972: 165-166, pl. 1, figs 1a,b, 4a,b; Špinar, 1972: 65-67, text-figs 18, 19, 20). It consists of one or more praesacral vertebrae fused with the sacral. Specimen 52/1 consists of two praesacrals and sacral; the latter displays a large area for articulation with the urostyle, only moderately compressed and thus subdivided in the midline.

The urostyle has two condylar fossae anteriorly. In younger individuals there is usually a flat, horizontal outgrowth, termed the processus intercondylicus by Špinar (1972: 68, text-fig. 21B), that protrudes from the ventral part of the bone between the two condylar fossae, reinforcing the original articulation between the urostyle and sacral vertebra (in 27/16). The neural canal is comparatively narrow and low. There is a rounded median dorsal ridge (sometimes subdivided into two parts) from which an oblique surface slants ventro-laterally on each side, extending in a horizontal lamina of various anterior-posterior extent (see also Hodrová, 1982: pl. I, fig. 4). Between the anterior margin of this horizontal lamina and the lateral margin of the condylar fossa is an oblique groove directed postero-ventrally, well illustrated by Fejérváry (1917: pl. II, fig. 2).

The coracoid (Text-fig. 9I; see also Špinar, 1972: pl. 15) has its proximal part divided into two parts, the intumescentia glenoidalis for articulation with the scapula, and the processus rostriformis (sensu Špinar, 1972: 79, text-fig. 31) for articulation with the clavicle (see Špinar, 1972: text-fig. 33, pl. 14/2). The articulation surface can be seen in internal, but not in the external view. The processus rostriformis coracoidei is a typical feature of the palaeobatrachids.

The scapula (for illustration see also Hodrová, 1982: pl. II, figs 4-6) has its pars suprascapularis short so the lateral basis of the pars glenoidalis, seen in dorsal aspect, is approximately in the middle of the medio-lateral diameter of the bone. The pars glenoidalis is separated from the pars acromialis by a deep incisure which, itself, shallows ventrally; hence, the ventral margin of the bone between the two parts is continuous and convex. Anteriorly, there is a thin osseous lamina (tenuitas cranialis) stretched between the pars suprascapularis and pars acromialis. On the ventral, slightly concave surface of the pars suprascapularis there is a shallow crista running parallel to the margin of the tenuitas.

The medial epicondyle of the humerus is larger than the lateral one, and its lower margin is separated from the caput humeri by a distinct incisure, whereas the margin of the lateral epicondyle continues smoothly towards the lower surface of the caput (see also Vergnaud-Grazzini & Hoffstetter, 1972: pl. 1, fig. 2, Vergnaud Grazzini & Młynarski, 1969: pl. I, fig. 21). There are, however, large humeri (e.g., 36/1) which bear the epicondyles of approximately same size. The medial epicondyle of these large specimens reaches beyond the caput, the lateral one is somewhat less extensive, though it is also well defined and separated from the caput. The main character pointing to the

Palaeobatrachidae is absence of the fossa cubitalis ventralis (Vergnaud Grazzini & Hoffstetter, 1972: 164). Although 49/2 is larger than 49/1, both are uniform also in that the crista medialis is pierced by two distinct foramina: one (smaller) approximately at mid-heigth of the caput humeri, the second (larger) is located higher. Both medial and lateral cristae are widely rounded. The proximal section of the bone (42/27) is compressed laterally, extending in a prominent ventral crista which, however, soon joins the medial margin of the bone. The middle and most prominent part of the crista is bent laterally toward a short parallel lateral crista, so as to make a partial roof over a broad groove between the two structures. When viewed in ventral aspect, the humerus is slender, except for its distal part. It should be noted that the palaeobatrachid humerus 50/2 (the fossa cubitalis ventralis is absent) differs from other humeri in that the lateral crista is subdivided in rounded lobes. Besides, the lateral epicondyle is well developed, closely adjoining the ventro-lateral part of the caput humeri. It is difficult to decide whether this morphology is taxonomically significant or represents only a malformation.

The ilium is essentially the same as that illustrated in Vergnaud Grazzini & Młynarski (1969: pl. I, fig. 17) in that it has a large acetabulum (typical feature of the Palaeobatrachidae), and its anteroventral margin protrudes beyond the outline of the bone. The tuber superius is only moderately prominent dorsally (but well defined in lateral aspect), separated from the pars ascendens ilii by an oblique groove which, however, does not continue anteromedially onto the medial surface of the bone (see also Młynarski et al., 1984: fig. 2/1). A similar groove separates the tuber and anterodorsal and dorsal sections of the acetabular margin (well developed in 43/5). In some specimens (47/10) the latter groove is involved in the acetabulum, which is probably a malformation. The tuber superius of large individuals (43/9) can be rimmed by an elevated ridge, apparent in lateral aspect. The pars ascendens extends postero-dorsally (41/12). Specimen 46/1 (Text-fig. 9H) obviously represents a young individual of Palaeobatrachus because, besides its small size, it has a large acetabulum extending beyond the anteroventral margin of the bone. The dorsal margin is straight (only the pars ascendens is slightly elevated), and the tuber superius is moderately prominent laterally (hence, it is separated by a distinct groove from the acetabulum, but it does not extend beyond the dorsal outline of the ilial shaft).

Remarks

The posterior part of the frontoparietal is essentially different from that described from the Upper Pliocene (Csarnótan) of Ivanovce locality, Slovakia (Hodrová, 1982) in that the posterior part of the flat ventral surface is bifurcated. This might be one of characters separating genera Palaeobatrachus and Pliobatrachus. Besides, there is also some variation in morphology of frontoparietals (as well as of the ilia and humeri) from Rudabánya, which is ascribed here to ontogenetic (or individual) variation, but which also might reflect taxonomic differences (especially that in the frontoparietal).

cf. *Palaeobatrachus* sp.

Material

Left squamosum (41/44, 44/12), left praearticulare (49/5).

Description

The lamella alaris squamosi is only tentatively associated with Palaeobatrachus on the basis of its size and proportions similar to that in articulated individuals (Špinar, 1972: text-figs 11, 12). It is smooth on its outer surface, extended anteriorly but narrow posteriorly. The dorsal margin separating the outer surface of the lamella from the dorsal surface of the ramus paroticus is only an indistinct rounded ridge. The lower part of the lamella breaks towards its ventral margin in a sharp horizontal ridge (similar to those on the dorsal surface of the frontoparietal) curved ventrally in its posterior section. The outer surface of the lamella is continuous with the proximal part of the processus posterolateralis.

The praearticulare bears the lingual tubercle which is typical for palaeobatrachids, however, it differs from other praearticulars assigned here to Palaeobatrachus sp. in that the sulcus pro cartilago Meckeli is much shallower. In its anterior section, the sulcus is represented only by a flat labial surface between the bone‘s dorsal edge and indistinct rounded horizontal ridge ventrally.

Pelobatidae indet.

Material

Left praearticulare (23/6, Text-fig. 10B; 38/4, Text-fig. 10A), right praearticulare (4/4; 27/15), right coracoid (5/16-17, Text-figs 10C, D), left humerus (27/4), right humerus (8/2; 36/6, 46/11, Text-fig. 10E), left ilum (15/4, Text-fig. 10H), right ilium (10/21, Text-fig. 10F).

Description

The praearticular is characteristic by its groove for Meckel's cartilage turned in its anterior section entirely onto the outer surface of the bone, so that it is not visible in dorsal aspect, and in that the coronoid process is compressed dorso-ventrally and its anterior part is located at the level of the medial ridge delimiting the groove. The groove itself is comparatively shallow at the level of the coronoid process.

The medial epicondyle of the humerus is large, with a broad vertical ridge projecting onto its surface and extending superiorly on the lower side. Because of this, it is separated from the caput humeri by a deep and broad incisure. There is a deep fossa cubitalis ventralis proximal to the caput, with its slanting proximal side pierced by a foramen. The bottom of the fossa cubitalis ventralis is pierced by a foramen which is a characteristic feature of most pelobatid humeri. However, the foramen may be absent in some specimens.

The ilium has its shaft rounded in cross-section, and its pars ascendens is prominent. The tuber superius is absent; instead, there is an oblique shallow groove running antero-medially over the dorsal margin of the bone onto its medial surface where it is delimited by a low, distinct crista projecting from the pars ascendens. In all these characteristics, the ilium is identical with that of contemporary *Pelobates*.

Remarks

The foramen piercing the fossa cubitalis is in the deepest part of the fossa in contemporary *Pelobates*, whereas it is shifted more proximally in the fossil specimens. Nevertheless, its referral to the Pelobatidae is beyond doubt. In contrast, it is not possible to distinguish whether the fossil humerus belongs to Pelobates or Eopelobates, for the postcranial skeleton is similar in the both genera.

Pelodytidae Bonaparte, 1850

Pelodytes sp.

Material

Left ilium (2/2, Text-fig. 11A; 3/15; 42/33, Text-fig. 11B).

Description

The ilium is characteristized by its shaft lacking dorsal crista, by an oblique groove projecting postero-laterally from the medial surface of the bone onto its lateral side (towards the dorsal side of the acetabulum), and by the anterior margin of the acetabulum being markedly lifted laterally. In all these characters the bone is similar to that in Pelobatidae, however, it differs by a rounded ridge arising on the lateral surface of the shaft and becoming in its antero-dorsal course a well developed lateral crista running parallel and exceeding in depth the dorsal margin of the shaft. Farther anteriorly, both delimit a longitudinal groove on the dorsal surface of the shaft, similar to contemporary *Pelodytes punctatus*. Although the anterior part of the shaft is broken off, it appears that the lateral crista does not exceed the medial one to such an extent as it is the case in *P. punctatus*.

Hylidae Gray 1825 (1815)

Hyla sp.

Material

Right praearticulare (35/29, Text-fig. 12A), right humerus (36/22, Text-fig. 12C), left ilium (8/10, Text-fig. 12F; 37/23; 40/20, Text-fig. 12B), left scapula (14/17, Text-fig. 12E). Middle section of the left maxilla 4/19 (Text-fig. 12D) can be associated with *Hyla*, on the basis of its small size and outer surface smooth.

Description

The praearticulare bears a large, medially directed and dorso-ventrally compressed tubercle, widely separated from Meckel's groove. The groove is shallow and turns onto the lateral side of the bone, at the level of the posterior margin of the medial tubercle. Although the bone is more stout, in both features the praearticular is in agreement with contemporary *Hyla*.

The scapula is comparatively long, with its middle part (collum scapulae) being slender. In ventral view, there is a deep cleft (sinus interglenoidalis) between the pars glenoidalis and pars acromialis; the cleft is situated in the long axis of the bone.

Although the medial epicondyle of the humerus is broken off it is obvious that it extended considerably medially. The lateral epicondyle is shifted proximally, as a swollen margin of the lateral crista. The fossa cubitalis ventralis is well developed. In all these characters the humerus agrees with contemporary *Hyla*.

The tuber superius ilii is prominent above the dorsal margin of the bone, located at the level of the anterior part of the acetabulum. At the same time, it is also prominent laterally. Seen in lateral aspect, it is well delimited ventrally having a knob-like aspect. A broad lamina is stretched between the ventral margin of the ilial shaft and the anterior margin of the pars descendens. Both of these characters are typical for contemporary *Hyla*. The dorsal margin of the ilial shaft is rounded, bearing no crista.

Ranidae Gray, 1825

Rana sp.

Material

Right frontoparietale (36/12; Text-fig. 13A), 8th praesacral vertebra (14/10; 43/11), sacral vertebra (14/9-10; 5/20; 31/8; 46/8), urostyle (? 31/5), sternum (42/45), left humerus (15/21; 25/25, Text-fig. 13C; 37/59; 42/31, Text-fig. 13B), right humerus (13/2; 19/18; 37/56, Text-fig. 13D), left ilium (1/9; 2/6; 14/13; 15/6; 19/34; 25/19, 35/6; 42/34; 44/8; 46/2, Text-fig. 13E; 54/9), right ilium (6/15; 10/22; ? 15/3; 15/8; 19/32-33; 25/17-18; 31/6; 37/21; 37/22; 37/26; 42/37; 43/4; 45/4, Text-fig. 13F).

Description

The frontoparietal is smooth and nearly flat on its dorsal surface, with only indistinct impressions of blood vessels. The lateral (i.e., orbital) margin is abbreviated in a vertical wall by a sharp crista, which is a typical feature distinguishing this frontoparietal from those of contemporary ranids. The medial margin (taking part in the median suture) is nearly straight. The posterior part of the frontoparietal incrassation (*sensu* Jarošová & Roček, 1982) is widely separated from the medial margin, which is the most important evidence for distinguishing this fragmentary frontoparietal from that of *Bufo*.

The centrum of the 8th vertebra is bi-concave and pierced by a comparatively broad canal. The neural arches are short antero-posteriorly, with their anterior margins directed postero-medially (consequently, a comparatively long section of the neural canal is uncovered dorsally). The carina neuralis is a short but prominent median crest extending onto the posterior surface of the neural arches, separating depressions on either side of the bone. The bases of the transverse processes are perpendicular to the long axis of the vertebra. The articular surfaces of zygapophyses are extremely declined. In general, the morphology of this vertebra does not differ from that of contemporary generic representatives. The sacral vertebra's centrum bears a large condyle anteriorly, and two condyles for sacro-urostylar articulation, posteriorly. The latter are separated from one another by a comparatively wide cleft.

The sternum does not differ from that in modern species of *Rana*.

The distal end of the humerus is markedly asymmetrical, bearing a large medial epicondyle which extends distally beyond the level of the caput; both are separated from one another by a deep and broad incisure. The lateral epicondyle is absent, and only a short lateral crista joins the surface of the caput. The fossa cubitalis ventralis is well developed and delimited medially by a rounded ridge extending up to the medial epicondyle. The crista medialis is poorly developed.

The ilium is characteristic by a depressed triangular area between the lower, thickened part of the ilial shaft, and the obliquely located tuber superius, which is more or less prominent laterally, and either confluent with the anterodorsal margin of the acetabulum, or well separated from it by a groove (45/4). Posterior to the tuber, the dorsal margin of the bone is bent ventrally towards the acetabulum. Anteriorly, the dorsal part of the ilial shaft is represented by only a thin vertical lamina. The anterior margin of the acetabulum is prominent laterally. There are several foramina entering the lateral surface of the bone along the anterior acetabular margin and within the area of the ventral part of the tuber superius.

Remarks

Although the sacral vertebral centra in discoglossids (*Latonia*, *Discoglossus*) and *Rana* are essentially the same, the posterior condyles in ranids are separated by comparatively broad cleft whereas in discoglossids they are close to one another.

Anura indet.

Material

Left frontoparietal (6/31, Text-fig. 14F), right frontoparietal (40/25, Text-fig. 14E), right maxilla (5/30), right praearticulare (54/4, Text-fig. 14A), left praearticular (23/6, Text-fig. 14B). Except for the praearticulars, these elements apparently do not belong to the same taxon.

Description

The dorsal surface of the frontoparietal is flat, pierced laterally by tiny foramina with their orifices directed anteriorly. A characteristic feature is a wide rounded process extending laterally into the posterior part of the orbit. The posterior lateral process, which originally was adjoining the dorsal surface of the otic capsule, is smooth, with only a groove running postero-anteriorly along the elevated dorsal surface of the bone, toward the orbit. There is a well delimited frontoparietal incrassation on the ventral surface of the bone. In the praearticulare, the lingual process for attachment of the m. adductor mandibulae ("processus coronoideus") is dorsoventrally compressed. The groove for Meckel's cartilage is very shallow at the level of the anterior part half of the process; consequently, the dorsal surface of the process passes into the groove by an indistinct ridge. The groove becomes deeper both anteriorly (where it turns onto the labial side of the bone) and posteriorly. In its posterior part, the medial ridge delimiting the groove is more acute than the lateral which is rounded. The lateral surface of the bone is flat or even moderately concave.

CONCLUSIONS

As in other Neogene localities in Europe, *Chelotriton*, *Latonia* and *Palaeobatrachus* were common also in Rudabánya. However, precise taxonomic assignment of *Chelotriton* cannot be given unless an articulated skeleton is analyzed and a thorough revision of the material from other parts of Europe is made. Until now, some isolated dermal bones of Chelotriton remain indeterminate. As regards *Latonia*, specimen 5/1 (Text-fig. 5E) suggests that the material from Rudabánya has certain affinities to *Latonia seyfriedi* from Öhningen. Since in other characters it is similar to *L. gigantea*, it may help to clarify taxonomic relations of *L. seyfriedi* and *L. gigantea*.

The majority of disarticulated anuran elements belong to *Palaeobatrachus*. Although the amount of material is comparatively large (Text-fig. 15), it does not permit a decision whether its morphological variation reflects taxonomic diversity (occurrence of more than one species) or if it is a result of individual or developmental variation. It is even difficult to decide whether part of the material does not belong to *Pliobatrachus* and on the basis of which diagnostic characters both genera can be distinguished. In contrast to the three mentioned genera, rather surprising is the abundance of *Mioproteus* (Text-fig. 15). It is comparatively rare in other localities, though its vertebral morphology is characteristic. Since the morphological variation of the vertebrae from Rudabánya includes typical features of both *M. caucasicus* and *M. wezei*, it seems highly probable that both taxa are conspecific and the latter form is a junior synonym. This was the reason why the material described in the present paper (which includes also some specimens with completely preserved transverse processes) was assigned to *M. caucasicus*.

There is a problem of discoglossids other than *Latonia*. Some postcranial elements are similar to those of contemporary *Discoglossus* though, as was mentioned elsewhere, it is difficult to distinguish the postcranial skeleton of juvenile *Latonia* from that of adult Discoglossus and this is even more difficult in case of disarticulated elements. Nevertheless, presence of *Discoglossus* is not excluded because of occurrence (though extremely rare) of this genus in other European localities (e.g., *Discoglossus troscheli* from the late Oligocene MP 30 of Rott, Germany). Rare occurrence of

Bombina seems to be justified by fragmentary praearticulars. *Bombina* was also reported from MN 7-8 of Opole, Poland (Młynarski *et al.*, 1982) and from MN 9 of Suchomasty, Czech Republic (Hodrová, 1987). Hence, *Bombina* from Rudabánya may be considered to be one of the earliest records of the genus.

Of similar importance is *Hyla*, which is evidenced by typical ilia and humeri. It represents one of the earliest *Hyla* in Europe (after that from MN6 of Devinska Nová Ves, Slovakia; Hodrová, 1988; Mátraszölös 2, Hungary, Gál *et al.*, 2000; MN7-8 of Felsötárnány, Hungary, Hír et al., 2001).

Ranids also occurred in Rudabánya, but were less numerous than palaeobatrachids and *Latonia*. Size differences of ranid ilia may suggest that there were at least two forms at Rudabánya.

Rather surprising is a weak occurrence of the pelobatids; only several ilia but none of the cranial elements document the presence of these frogs at Rudabánya. As in the case of some other taxa, it is difficult to decide on the basis of postcranial elements only whether they belong to *Eopelobates* or to *Pelobates*. This is especially important because the latest *Eopelobates* recorded on the basis of cranial elements was reported from MN9 of Suchomasty, Czech Republic (Hodrová, 1987). Moreover, it may be taken for granted that *Eopelobates* and *Pelobates* coexisted at the same localities (e.g., in Rott, Germany and Sansan, France).

Absence of bufonids may be explained by ecological conditions in the locality. Bufonidae are, similar to pelobatids, more associated with terrestrial environment, whereas abundant palaeobatrachids are indicative of aquatic environments. Together with the tailed amphibians, palaeobatrachids suggest their sampling from the Pannonian lake.

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