

New frogs from the latest Cretaceous of Hațeg Basin, Romania

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The latest Cretaceous (Maastrichtian) fluvio-lacustrine deposits of Hațeg Basin (Romania) have yielded a number of aquatic and terrestrial microvertebrates, including dissociated skeletal remains of the following anuran taxa: *Hatzegobatrachus grigorescui* gen. et sp. nov., *Paralatonia transylvanica* gen. et sp. nov., and Anura indet. *H. grigorescui* sp. nov. (type species), retaining some leiopelmatid-grade anuran features, is diagnosed as a small-sized primitive frog with still unclear relationships. *P. transylvanica* sp. nov. (type species) is a middle-sized discoglossine frog. Based on the characters of jaw-bones and post-cranial skeletal elements, it appears as intermediate between primitive (*Eodiscoglossus*-like) and more derived (*Latonia*-like) discoglossine discoglossid. In *Hatzegobatrachus* and *Paralatonia* the morphology of the hipbones shows that they differ in saltatorial abilities. Consequently, these forms may have occupied distinct ecological niches, suggesting that the latest Cretaceous microvertebrate assemblages of Hațeg Basin were connected to more complex ecosystems than considered before.

Key words: Cretaceous, Maastrichtian, Amphibia, Anura, Romania.

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Introduction

It is now generally believed that the ancestry of anurans was among late Paleozoic–early Mesozoic temnospondyl amphibians (Roček and Rage 2000a). The rise of anurans was preceded by some proanuran stages, documented in the fossil record by two intermediate forms: *Triadobatrachus* and *Czatkobatrachus*. *T. massinoti* (Piveteau 1936), known from the Early Triassic (Scythian) of Madagascar, shared a number of advanced features with anurans (e.g., presence of a frontoparietal, T-shaped parasphenoid, deeply triradiate pterygoid, toothless dentary) (Roček and Rage 2000b). *Czatkobatrachus polonicus*, described from the early Triassic of Poland (Evans and Borsuk-Białynicka 1998), resembles *Triadobatrachus* in retaining a comparatively long presacral vertebral column and a short tail, but in some characters was more derived (e.g., elongate transverse processes on some presacrals, single atlantal centrum, no atlantal ribs, sacral ribs fused to vertebral centrum).

The earliest recognised anuran is *Prosalirus bitis*, known from the Early Jurassic Kayenta Formation (Pliensbachian) of Arizona (Shubin and Jenkins 1995; Jenkins and Shubin 1998). Further Jurassic anurans (*Enneabatrachus*, *Eodiscoglossus*, *Notobatrachus*, *Rhadinosteus*, and *Vieraella*) are known from Americas and Europe (Sánchez 1998; Roček 2000 and references therein). Recently, the Late Jurassic–Early Cretaceous of Asia produced *Mesophryne beipiaoensis* and *Callobatrachus sanyanensis*, both from the Yixian Formation of western Liaoning Province, China (Wang and Gao 1999; Gao and Wang 2001). The fossil record of Cretaceous anurans (e.g., *Aralobatrachus*, *Baurubatrachus*, *Eodiscoglossus*, *Eopelobates*, *Estesina*, *Gobiatates*, *Gobiatoides*, *Kizyl-*

kuma, *Monsechobatrachus*, *Neusibatrachus*, *Pachybatrachus*, *Palaeobatrachus*, *Paradiscoglossus*, *Procerobatrachus*, *Saltenia*, *Scotiophryne*, *Soevesoederberghia*, *Theatoni*, *Wealdenbatrachus*) is more complete (Roček 2000 and references therein), but in many instances their exact relationships are still unresolved.

The first localities yielding latest Cretaceous vertebrates from the Hațeg Basin, Romania, were described by Baron Franz Nopcsa (see Weishampel and Reif 1984, and references therein), producing a faunal assemblage considered at that time as rather depauperate (Nopcsa 1915). In the late 1970s a team from the Faculty of Geology and Geophysics (Bucharest University) led by Professor Dan Grigorescu made the first re-excavation since Nopcsa's time, and revealed a far more diverse latest Cretaceous vertebrate fauna (Grigorescu et al. 1985). Intensive field campaigns began in 1992, resulting in the discovery of several new fossiliferous sites (e.g., Pui 1, 4, and 5 from the Sânpetru Formation; Tuștea, Vălioara-Fântânele and Vălioara-Budurone from the Densuș-Ciula Formation) yielding abundant microvertebrate remains, including fishes, amphibians and squamates (Grigorescu et al. 1999). Another new fossil locality was discovered quite recently in the central part of the Hațeg Basin at Totești barrage, the microvertebrate assemblage of which included multituberculates, scincomorph squamates, albanerpetontid, and discoglossid lissamphibians (Codrea et al. 2002; Godefroit et al. 2002).

Material.—The frog material used in this study consists of jaw bones and postcranial skeletal elements, housed in the collection of University of Bucharest, Faculty of Geology and Geophysics in Bucharest, Romania. The purpose of the present work is to re-evaluate the taxonomic status of the previously

described specimens (Grigorescu et al. 1999) and to describe the newly discovered remains from the Densuş-Ciula Formation. The specimens are incomplete, but with some important details. They appear to represent two distinct groups: one is a small-sized primitive anuran, resembling by its distinctive ilium gobiatine or bombinatorine frogs, while the other one is a discoglossine frog, as indicated by a combination of features observed on cranial and appendicular bones.

Anatomical conventions.—The common English terms and the standard anatomical orientation system are used in this paper; the classification of frogs follows Sanchíz (1998).

Institutional abbreviations.—FGGUB, University of Bucharest, Faculty of Geology and Geophysics in Bucharest, Romania; HNHM, Hungarian Natural History Museum, Budapest, Hungary; MTC, Țării Crișurilor Museum, Oradea, Romania.

Systematic palaeontology

Class Amphibia Linnaeus, 1758

Superorder Salientia Laurenti, 1768

Order Anura Rafinesque, 1815

Family *incertae sedis*

Genus *Hatzegobatrachus* nov.

Type species: *Hatzegobatrachus grigorescui* sp. nov.

Etymology: *Hatzeg*, Romanian, geographic name of Hațeg Basin, Romania, + *batrachos*, Greek, a frog.

Diagnosis. —As for the type and only known species.

Hatzegobatrachus grigorescui sp. nov.

Etymology: After Prof. Dan Grigorescu, University of Bucharest, whose collecting efforts in the Late Cretaceous of Hațeg Basin, Romania, resulted in discoveries of the microvertebrate localities and frog fossils reported in this paper.

Holotype: FGGUB v. 433, a partial left ilium missing the distal part of iliac shaft and posterior margin of supraacetabular and subacetabular regions (Figs. 1A, 2A).

Holotype locality, horizon, and age: Vălioara-Fântânele microvertebrate locality, about 5 km west of the village Vălioara, Hațeg Basin, Romania; middle member of the Densuş-Ciula Formation (Grigorescu et al. 1999). The sedimentological development indicates the presence of a braided-meandering river system with large and small channels; the microvertebrate bearing sediments are grey-greenish, massive, compact, slightly variegated mudstones of Maastrichtian age (Grigorescu and Csiki 2002).

Referred specimens: FGGUB v. 451, a partial right prearticular (Fig. 4A); FGGUB v. 437, a partial left prearticular (Fig. 4B).

Distribution.—Known only from the holotype locality.

Diagnosis.—A small-sized anuran having an inferred snout-vent length of about 30 mm. Differs from *Ascaphus*, *Leiofelma*, *Mesophryne*, *Notobatrachus*, *Prosalirus*, pelobatoids, and some pipoids (*Rhadinosteus*), in having a well-developed dorsal protuberance of ilium. Differs from discoglossids (including *Alytes*, *Callobatrachus*, *Discoglossus*, *Enneabatrachus*, *Eodiscoglossus*, *Latoglossus*, *Latonina*, *Paradiscoglossus*, and *Wealdenbatrachus*), palaeobatrachids, and most pipids in

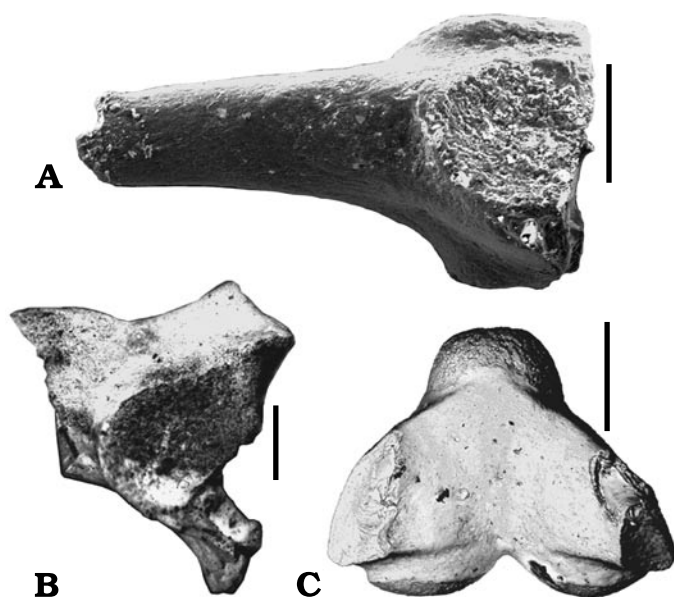


Fig. 1. Frog remains from the Late Cretaceous (Maastrichtian) of Hațeg Basin, Romania. A. *Hatzegobatrachus grigorescui* gen. et sp. nov., holotype left ilium, FGGUB v. 433, left lateral view. B. *Paralatonia transylvanica* gen. et sp. nov., holotype left ilium, FGGUB v. 455, left lateral view. C. Anura indet., fragmentary sacral vertebra, FGGUB v. 438, dorsal view. Scale bars 0.5 mm. A, B, anterior is left; C, anterior is up. All SEM micrographs.

the absence of an individualised dorsal iliac crest. Resembles Bombinatorinae in having a well-developed and undivided dorsal prominence, but differs from them in having its dorso-lateral margin more thickened. Differs from Bombinatorinae and Gobiatinae in the absence of any waisting between the acetabular region and the iliac shaft, resembling in this respect some leiopelmatid-grade anurans (*Notobatrachus*). Differs from rhinophrynids (including *Chelomophrynus*, *Eorhinophrynus*, and *Rhinophrynus*) in having comparatively smaller pre- and supraacetabular regions.

Description.—The holotype specimen preserves the acetabular region and proximal part of the iliac shaft (Figs. 1A, 2A). The supraacetabular and subacetabular regions (somewhat damaged posteriorly) are slightly expanded and are positioned nearly symmetrically in relation to the centrally placed acetabular fossa. In lateral view, the acetabular fossa has the shape of an inverted, rounded, triangle, with a prominent acetabular rim dorsally and anteroventrally. Medially, the posteroventral part of the acetabular region is damaged, but there was a well-developed interiliac tubercle. In posterior view the ilioischadic junction is thickened. The dorsal protuberance is indistinguishable from the dorsal prominence lying entirely above the acetabular fossa. The upper margin of the dorsal prominence is thickened (especially its anterior section) and projects slightly laterally. The preacetabular fossa is rather shallow. Ventrally to the preacetabular fossa there is a low crest for the iliacus internus muscle insertion. The iliac shaft has a rounded cross-section and lacks a dorsal crest; there is no waisting above the acetabular fossa.

Prearticular (Fig. 4).—Specimen FGGUB v. 451 represents a partial right prearticular with the anterior portion of the bone and posteromedial section of spatulate extremity broken off. The bone is slender with its anterior part bent linguallly, while its posterior section is slightly curved labially. The coronoid process is weakly projecting with a smooth convex surface, directed dorsolingually. In its posterior section a rather shallow groove is observed. There is no obvious constriction at the level of coronoid process in the course of Meckel's groove. The spatulate extremity is moderately deep and is delimited laterally by a sharp crest. Above the external mandibular crest, the lateral surface is slightly concave with a small tubercle near the ventrolabial margin. Specimen FGGUB v. 437 (Fig. 4B) belonged to a slightly larger individual. Its anterior and posterior part is lacking, and preserves a convex and somewhat wider coronoid process. However, these morphological differences, compared to FGGUB v. 451, may be interpreted as intraspecific variation.

Remarks.—The ilium of *Hatzegobatrachus* shows a number of primitive features (little expansion of preacetabular and supraacetabular processes, lack of dorsal crest, dorsal prominence of low height, no waisting between the acetabular region and iliac shaft) in combination with few derived ones (dorsal protuberance projects laterally, well developed interiliac tubercle). The combination of the above features is often present in the extinct Gobiatinae (Roček and Nessov 1993; Roček 2000), and in living Bombinatorinae. The posterior margin of the supraacetabular region in the holotype is somewhat damaged, but the outline of the dorsal margin is suggestive of a relatively small supraacetabular expansion, resembling *Barbourula*, *Bombina*, and Gobiatinae. The preacetabular process is lacking in *Barbourula* (Clarke 1987; Evans and Manabe 1998) but is present at least in some members of *Bombina* (Fig. 2B₂). Contrary to *Hatzegobatrachus*, in bombinatorine and gobiatine a little waisting is present between the acetabular region and the iliac shaft (Fig. 2B₂, Roček 2000: fig. 16), while the dorsal tuberosity (also projecting laterally) is weakly developed. However, in gobiatine frogs the latter structure displays a wide range of intra- or interspecific variation (see Roček and Nessov 1993: text-fig. 25A–E, pl. 9: 5, pl. 10: 4). The interiliac tubercle of the ilium is relatively small in *Bombina* (Fig. 2B₁), versus more strongly developed in *Barbourula* (Clarke 1987: figs. 6, 7) and *Gobiatas* (Roček 2000: fig. 16). Other distinctive features of *Hatzegobatrachus* include the laterally oriented acetabular fossa (oriented slightly dorsolaterally in discoglossids) and the dorsally prominent acetabular rim (undeveloped in discoglossids). The undivided and laterally projecting dorsal prominence may be reminiscent of some leiopelmatid-grade anurans (e.g., *Notobatrachus*) (Báez and Basso 1996). Another anuran with the ilium somewhat resembling *Hatzegobatrachus* is *Scotiophryne pustulosa*. But it lacks a dorsal protuberance of the ilium. A morphological resemblance between *Scotiophryne* and *Zaphrissa* was pointed out by Estes (1969), the latter taxon actually being a synonym of *Pelobates* (Böhme et al. 1982; Sanchíz 1998). Within extinct pipids, the ilium of some members (e.g., *Shelania laurenti*, *Xenopus romeri*) lacks a dorsal

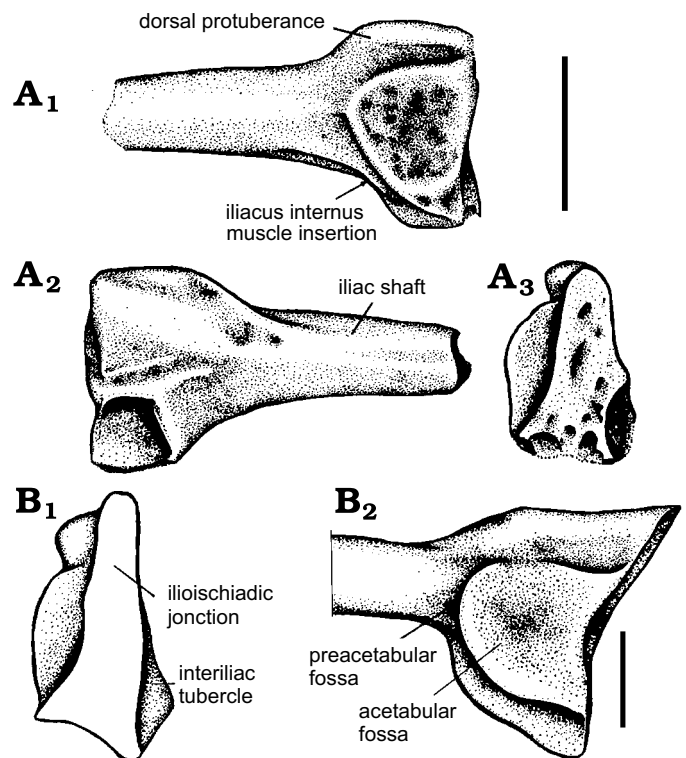


Fig. 2. Ilium of *Hatzegobatrachus grigorescui* gen. et sp. nov. (A), and recent *Bombina bombina* (B). A. Holotype left ilium, FGGUB v. 433 in lateral (A₁), medial (A₂), and posterior (A₃) views. B. Left ilium in recent *B. bombina* in posterior (B₁) and lateral (B₂) views. Scale bars 1 mm.

crest, but the morphology of the acetabular region and the size and orientation of the dorsal protuberance is different (Báez and Pugener 1998; Sanchíz 1998).

The prearticular assigned to *Hatzegobatrachus* has a small, elongated and dorsally convex coronoid process. In *Eodiscoglossus*, *Barbourula*, and to a lesser degree *Alytes* and *Bombina* (Fig. 4C), the dorsomedial surface of the coronoid process is smooth and convex, but much wider than in *Hatzegobatrachus*. In prearticular, assigned with some doubts to *Gobiatoides* (Roček and Nessov 1993: text-fig. 24A; pl. 14:10, and text-fig. 24B; pl. 14: 9), the morphology of the coronoid process approaches the condition seen in FGGUB v. 437 (Fig. 4B). The spatulate extremity in *Hatzegobatrachus* is not widened posteriorly with sharp lateral margins. In *Bombina* the lateral crest delimiting the pars spatulata is similarly sharp with its lateral surface concave and somewhat crinkly; it bears a tubercle near the posterolateral margin. In *Hatzegobatrachus* a tubercle is present on the ventrolateral surface, but in a more anterior position.

In order to ascertain the closer relationships of *Hatzegobatrachus*, further skeletal material is needed from the type locality.

Family Discoglossidae Günther, 1859 Subfamily Discoglossinae Günther, 1859

In recent classifications of frogs the discoglossids are placed either in a single family (Duellman and Trueb 1986; Clarke 1988;

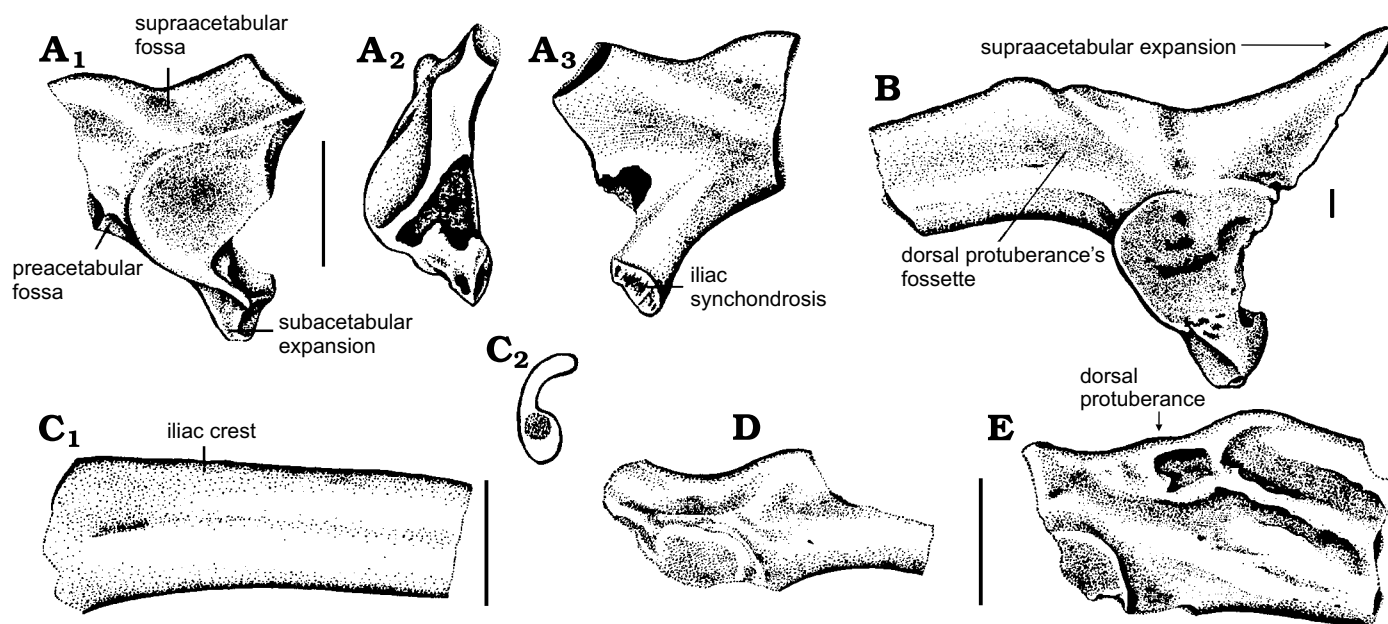


Fig. 3. Fragmentary ilia of *Paralatonia transylvanica* gen. et sp. nov. (A, C, D, E), and *Latonia gigantea* (B). A. Left ilium, holotype, FGGUB v. 455 in left lateral (A₁), posterior (A₂), and medial (A₃) views. B. Left ilium, HNHM. No. V.99.2, in left lateral view. C. FGGUB v. 410 in right lateral (C₁) and anterior (C₂) views. D. FGGUB v. 439 in right lateral view. E. FGGUB v. 452 in right lateral view. Scale bar 1 mm.

Roček 1994), or as distinct subfamilies (Gobiatinae, Alytinae, Bombinatorinae, and Discoglossinae) within Discoglossidae (Sánchez 1998). According to Gao and Wang (2001), the monophyly of Discoglossidae is supported by four synapomorphies: postchoanal process of vomer forms an acute angle with the anterior portion of the bone, clavicle overlapping scapula anteriorly, coracoid elongate with little expansion of its medial end, trigeminal and facial foramina separated by prefacial commissure. However, the latter authors excluded a number of fossil discoglossid taxa (*Gobiates*, *Wealdenbatrachus*, and *Latonia*) from their phylogenetic analysis, on the basis of their “doubtful taxonomic status or morphological ambiguity”. Part of the material from Hațeg Basin, closely resembling discoglossine frogs (see below), was assigned to this subfamily. Unfortunately, up to now, no skeletal material bearing any synapomorphy of the group, *sensu* Gao and Wang (2001), has been recovered from the studied localities.

Genus *Paralatonia* nov.

Type species: *Paralatonia transylvanica* sp. nov.

Etymology: “Para”, Greek, similar, but not identical, + *Latonia*, an extinct discoglossid genus.

Diagnosis.—As for the type (and only included) species.

Paralatonia transylvanica sp. nov.

Eodiscoglossus sp.; Grigorescu et al. 1999: 305–308, fig. 3: 3–11.

Etymology: After “Transsylvania”, Latin, geographic name of Transylvania, Romania.

Holotype: FGGUB v. 455, partial left ilium missing most of iliac shaft and supraacetabular expansion (Figs. 1B, 3A).

Holotype locality, horizon, and age: Vălioara-Budurone microvertebrate locality, about 4 km west of the village Vălioara, Hațeg Basin, Romania; middle member of the Densuș-Ciula Formation (Grigorescu et

al. 1999). The sedimentological development indicates the presence of a braided-meandering river system and channels; the microvertebrate bearing sediments are grey-bluish to blackish mudstones of Maastrichtian age (Grigorescu and Csiki 2002).

Referred specimens: FGGUB v. 446 (Fig. 5D), v. 447 (Fig. 5B), v. 448 (Fig. 5C), v. 402, v. 461, v. 462, partial maxillae; FGGUB v. 449 (Fig. 4E), v. 450 (Fig. 4D), v. 403, v. 404, v. 405, partial prearticulars; FGGUB v. 442 (Fig. 6E), v. 443 (Fig. 6F), partial scapulae; FGGUB v. 410 (Fig. 3), v. 439 (Fig. 3D), v. 452 (Fig. 3E), v. 409, v. 411, partial ilia.

Distribution.—Latest Cretaceous (Maastrichtian), Romania.

Diagnosis.—A small discoglossid frog having an inferred snout-vent length of about 40–50 mm. The ilium of *Paralatonia* differs from *Hatzegobatrachus*, as well as from Alytinae, Bombinatorinae, and Gobiatinae discoglossids in having prominent iliac crest. Differs from *Callobatrachus* and *Enneabatrachus* in having a higher iliac crest. Differs from *Discoglossus* in having a smaller preacetabular process. Differs from *Eodiscoglossus* in having a more expanded acetabular rim and by presence of an iliac synchondrosis. Differs from *Latoglossus* and *Latonia* in having a comparatively smaller inferred body size and by lack of waisting between the acetabular region and iliac shaft. Differs from *Paradiscoglossus* in having shallower supraacetabular fossa and a more expanded acetabular rim. Differs from *Wealdenbatrachus* in the lack of waisting between the acetabular region and the iliac shaft, and in having smaller iliac synchondrosis.

Description.—The holotype specimen preserves the acetabular region and the base of iliac shaft (Figs. 1B, 3A). The supraacetabular region is relatively wide, with the supraacetabular expansion oriented posterodorsally. The latter structure is broken off, but was strongly developed extending to the dorsal limit of the ischium. The subacetabular region is relatively small,

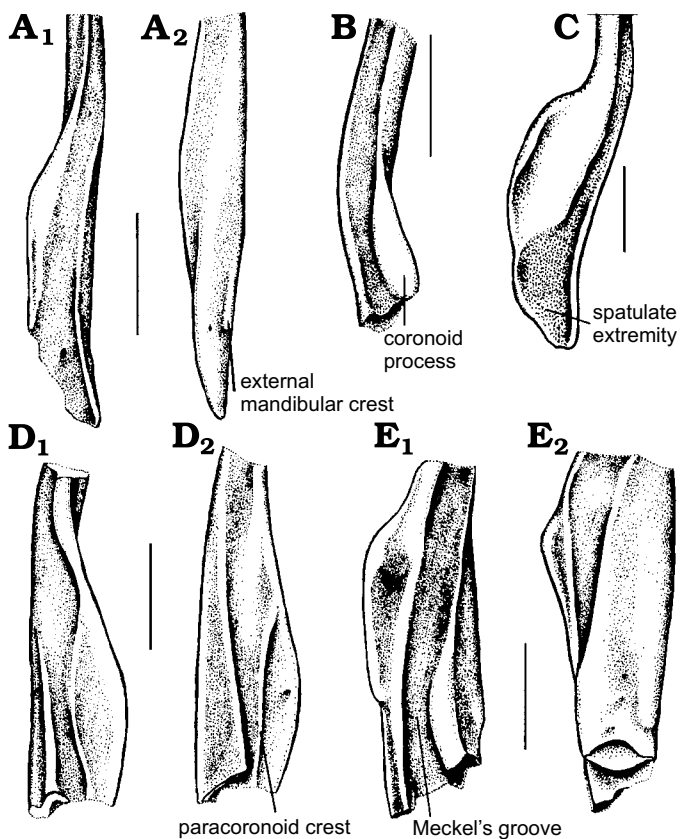


Fig. 4. Prearticulars of *Hatzegobatrachus grigorescui* gen. et sp. nov. (A, B), recent *Bombina bombina* (C), and *Paralatonia transylvanica* gen. et sp. nov. (D, E). A. Right prearticular, FGGUB v. 451 in dorsolabial (A₁) and labial (A₂) views. B. Left prearticular, FGGUB v. 437 in dorsolabial view. C. Right prearticular, MTC uncatologued in dorsolabial view. D. Left prearticular, FGGUB v. 450 in dorsolabial (D₁) and labial (D₂) views. E. Right prearticular, FGGUB v. 449 in dorsolabial (E₁) and labial (E₂) views. Scale bars 1 mm. Anterior is up.

with a short subacetabular expansion. On the medial side of the latter there is an area not covered by periosteum. The acetabular fossa is nearly circular with a posteriorly widened acetabular rim. The latter is prominent anteroventrally and projects beyond the ventral margin of the bone. Dorsally the acetabular rim is nearly imperceptible, but near the posterodorsal margin of the acetabular region it is raised again delimiting a rather shallow supraacetabular fossa. In the vicinity of the anteroventral margin a small preacetabular fossa is observed. The posterior border of the acetabular fossa is broken off. In posterior view the ilioischadic junction displays the typical discoglossid pattern, being distinctly widened ventrally. In lateral view there is a relatively high dorsal crest. The dorsal protuberance, formed by the thickened posterodorsal margin of the dorsal crest, is elongated and moderately prominent. Ventrally to the latter there is a shallow fossette (= dorsal protuberance's fossette).

Maxilla (Fig. 5B–D).—All the available specimens are fragmentary, preserving various parts of the maxilla. The labial surface is smooth without secondary bony ornament; there are few small nutritive foramina. The facial part of maxilla was proba-

bly of moderate height (Fig. 5C), with a distinct palatine process (Fig. 5D), and a somewhat raised zygomaticomaxillaris process (Fig. 5B, C). The horizontal lamina is rather wide and with a convex lingual surface. The tooth row extends posteriorly to the base of the pterygoid process. The tip of the latter structure is not preserved. There is a deep posterior depression (Fig. 5B, C).

Prearticular (Fig. 4D₁, D₂, E₁, E₂).—The specimens belonged to various sized individuals. In all the specimens the dorsal surface of the coronoid process is concave and projects lingually, with the lingual margin slightly bent dorsally. The paracoronoid crest is better developed posteriorly. Meckel's groove is well marked and is slightly constricted at the level of the coronoid process. In specimen FGGUB V. 403 (see Grigorescu et al. 1999: fig. 3: 4), a moderately wide, deep spatulate extremity is preserved. The labial surface above the external mandibular crest is concave, the latter structure ending posteriorly in a small tubercle.

Scapula (Fig. 6E, F).—The bone is relatively short and cleft, with a deeply concave posterior margin. The acromial part of scapula projects well beyond the glenoid margin.

Ilium (Fig. 3C–E).—Part of the material was already described under the generic name *Eodiscoglossus* (Grigorescu et al. 1999: fig. 3: 7–11). The FGGUB v. 439 (Fig. 3D), representing a partial right ilium, preserves a relatively large supraacetabular expansion, projecting posterodorsally. The supraacetabular

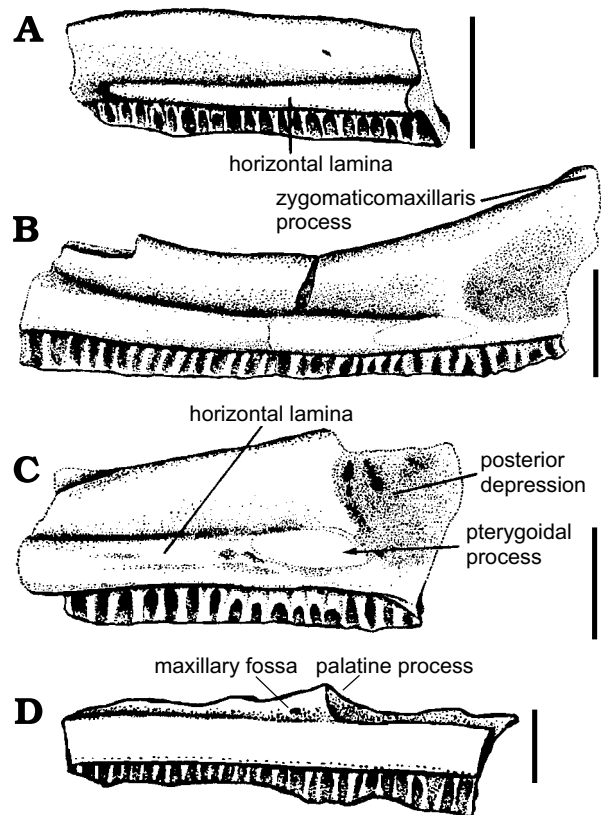


Fig. 5. Fragmentary anuran maxillae in lingual view. A. Partial left maxilla of *Anura* indet., FGGUB v. 435. B–D. Partial right maxillae of *Paralatonia transylvanica*, FGGUB v. 447 (B), FGGUB v. 448 (C), and FGGUB v. 446 (D). Scale bars 1 mm. A, anterior is right; B, C, D, anterior is left.

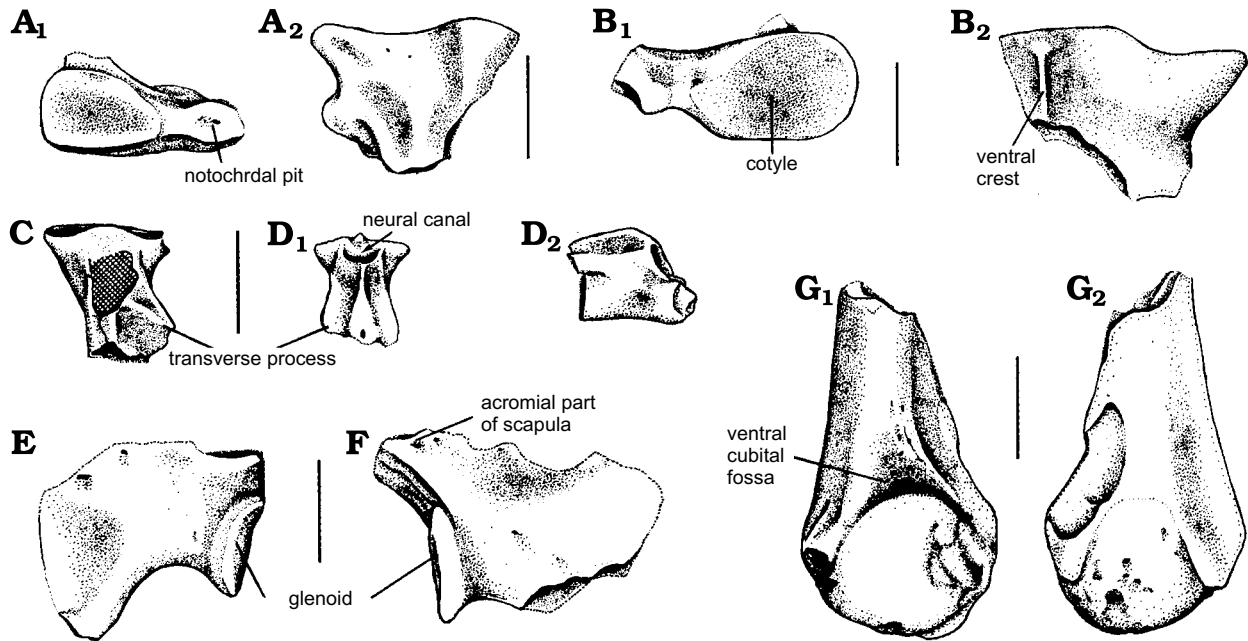


Fig. 6. *Paralatonia transylvanica* gen. et sp. nov. (E, F), and Anura indet. (A, B, C, D, G). A, B. Fragmentary atlases, FGGUB v. 453 (A) and FGGUB v. 454 (B) in anterior (A₁, B₁) and ventral (A₂, B₂) views. C, D. Fragmentary urostyles, FGGUB v. 441 (C), and FGGUB v. 440 (D) in dorsal (C, D₁), and lateral (D₂) views. E, F. Fragmentary scapulae, FGGUB v. 442 (E) and FGGUB v. 443 (F) in lateral views. G. Fragmentary left humerus, FGGUB v. 445 in ventral (G₁) and dorsal (G₂) views. A₁, B₁, dorsal is up; A₂, B₂, C, D₁, anterior is up; D₂, anterior is right; G, proximal is up. Scale bars 1 mm.

tabular fossa is rather shallow and extends parallel to the dorsal acetabular rim. The dorsal protuberance is elongated and barely swollen along the posterodorsal margin of the iliac shaft. In FGGUB v. 452 (Fig. 3E), the acetabular rim is prominent anteriorly and there is a small preacetabular fossa. The dorsolateral surface of the iliac shaft shows clear signs of anomaly. Laterally there are several grooves and pits, while part of the muscular insertion surface on the dorsal protuberance is shifted medially. FGGUB V.410 (Fig. 3C), figured in Grigorescu et al. 1999 (fig. 3: 9–11), preserves a right iliac shaft provided with a moderately high and strongly medially inclined dorsal crest.

Remarks.—The ilium in *Paralatonia* shows a combination of derived features (well-developed and strongly medially bent dorsal crest, crest-like dorsal protuberance, anteroventrally expanded acetabular rim, and small interiliac synchondrosis), that morphologically approaches the condition seen in *Latonia* (Fig. 3B). In posterior view, the shape of ilioischadic junction of *Paralatonia* closely resembles that of *Discoglossus* and *Latonia* (Hodrova 1987: text-fig. 1: 6; Bailon 1999: pl. 19A).

The coronoid process of prearticular in *Paralatonia* is more derived than that of *Eodiscoglossus*, approaching the condition seen in *Discoglossus*, in which the coronoid process is elongated and has a concave surface (see Bailon 1999: pl. 9A). In *Latoglossus* the coronoid process has a nearly flat dorsal surface and forms a rather thick sub-rectangular lamina (Hossini 2000: fig. 1A, B). To the contrary, the prearticular in *Latonia* is provided with two coronoid processes (Hodrova 1987; Roček 1994).

The maxilla lacks a labial sculpture, condition similar to other discoglossids, except some members of *Latonia* (e.g., *Latonia gigantea*) and *Gobiates* (Špinar and Tatarinov 1986).

The well-developed pterygoidal process of maxilla, as well as the presence of a posterior depression and a relatively high zygomaticomaxillaris process is reminiscent of *Discoglossus*, *Latoglossus* and *Latonia* (see Bailon 1999: pl. 2G–I; Hossini 2000: fig. 1C, D; Roček 1994: fig. 9). In the maxilla of *Eodiscoglossus* there is no prominent pterygoidal process, and the posterior depression is lacking (Evans et al. 1990; Sanchíz 1998: fig. 39D).

The scapula assigned to *Paralatonia* is short and cleft, similarly to most members of Discoglossidae. According to Borsuk-Białynicka and Evans (2002), the cleft scapula of many primitive anurans (including *Prosalirus*, *Notobatrachus*, some *Leiopelma*, and *Eodiscoglossus oxoniensis*) represents the basal anuran condition. In *Wealdenbatrachus*, contrary to other discoglossine frogs, there is a long *Leiopelma*-like scapula (Sanchíz 1998).

Considering all the above features, *Paralatonia* appears as a transitional form between primitive (*Eodiscoglossus*-like) and more derived discoglossids (e.g., *Latonia*).

Anura indet.

Material.—FGGUB v.435 (Fig. 5A), v. 436, v.437, v. 460, partial maxillae; FGGUB v. 453 (Fig. 6A), v. 454 (Fig. 6B) partial atlases; FGGUB v. 438 (Fig. 1C), v. 456–459, partial sacral vertebrae; FGGUB v. 440 (Fig. 6D), v. 441 (Fig. 6C), partial urostyles; FGGUB v. 445 (Fig. 6G), v. 406–408, partial humeri.

Description.—A partial left maxilla, FGGUB v. 435 (Fig. 5A), preserves a low postorbital facial part, its orbital margin being nearly parallel with the horizontal lamina. The latter has

a convex lingual margin, ended posteriorly in a small pterygoid process. The tooth row extends posterior to the pterygoid process. The labial surface is smooth.

Atlas (Fig. 6A, B).—Only fragmentary centra were recovered. The centrum is dorsoventrally flattened. The anterior cotyles are ovaloid in shape, and are separated medially by an intercotylar region with a small notochordal pit. There is no medial notch in ventral or dorsal outline. In ventral view, FGGUB v. 454 has a distinct ventral crest (Fig. 6B₂), while FGGUB v. 453 (Fig. 6A₂) has a low and wide ridge only. The posterior margin is damaged in all available specimens.

Sacral vertebra (Fig. 1C).—Only the centrum is preserved. There is a single anterior condyle and two posterior ones. Thus, the sacrococcygeal articulation is bicondylar.

Urostyle (Fig. 6C, D).—The two condyloid fossae are well separated from each other. FGGUB v. 440 (Fig. 6D) has a small median tubercle. The neural canal is relatively large, while the neural crest is low. The transverse process is directed posterolaterally in FGGUB v. 441 (Fig. 6C), but hooked posteriorly in that of FGGUB v. 440 (Fig. 6D₁).

Humerus (Fig. 6G).—In FGGUB v. 445 (Fig. 6G₁), the humeral ball is shifted slightly laterally and the medial crest is more or less similarly developed by comparison with the lateral crest. In consequence the olecranon scar has a medial position. In contrary, in FGGUB V.406 (Grigorescu et al. 1999; Fig. 3: 5, 6) the medial crest is better developed than the lateral one, and the olecranon scar is displaced laterally. However, the latter condition may be related to sexual dimorphism. There is a well-developed ventral cubital fossa.

Remarks.—The morphology of the maxilla somewhat resembles that of *Kizylkuma*, known from the Upper Cretaceous of Uzbekistan (Roček and Nessov 1993), provided with a low postorbital section. However, specimen LU-N 6/271 (see Roček and Nessov 1993: text-fig. 9J, K), *versus* FGGUB v. 435, has a lingually prominent posterior section of horizontal lamina. The notochordal pit, seen in the atlas of specimens FGGUB v. 453 and v. 454 is also present in *Eodiscoglossus* (Evans et al. 1990; Estes and Sanchíz 1982), and *Leiopelma* (Worthy 1987). A ventral crest in atlas is also present in *Discoglossus* and *Latonia*, but it is unknown in *Paradiscoglossus* and *Wealdenbatrachus*. It is noticeable that a similar atlas with the interglenoidal tubercle broken, described from the Belgian Paleocene as belonging to a salamander by Groesens-Van Dyke (1981), bears a conspicuous ventral ridge, too (Estes and Sanchíz 1982). The size, morphology and the orientation of transverse process in the available urostyles suggest that these may have belonged to two different forms. The morphology of the humerus suggests that the available specimens may represent indeterminate discoglossid frogs.

Paleoecology

Based on paleomagnetic studies, the paleolatitude $21^{\circ} \pm 9^{\circ} \text{N}$ for the Sânpetru Formation shows, that during Maastrichtian times

the Hațeg Basin was situated at tropical latitude, and in a southern position with respect to Europe (Panaiotu and Panaiotu 2002). The sedimentological development of the Sânpetru Formation and that of the middle member of the Densuș-Ciula Formation (from which the overwhelming part of the microvertebrate remains have come) indicates the presence of a braided-meandering river system with large and small channels, and floodplains in which well-drained and poorly-drained conditions alternated periodically (Grigorescu and Csiki 2002). One may assume that *Hatzegobatrachus* and *Paralatonia* could have been closely associated with aquatic habitats, too. At the same time they would have been involved in different ecological niches in these ecosystems. The morphology of the available ilia suggests that the jumping and/or swimming ability of *Hatzegobatrachus* and *Paralatonia* was quite different. It is known that the latter character in frogs depends among others by the configuration of the caudopelvic complex (Jenkins and Shubin 1998). The ilium, provided with high dorsal crest, enlarges considerably the surface of attachment for muscles involved in jumping and/or swimming (e.g., coccygeo-iliac muscle). Consequently, *Paralatonia*, with a better ability of saltatorial movement, could have been associated with a broader spectrum of environments than *Hatzegobatrachus*, as suggested analogously by the fossil record of *Latonia* from the Tertiary of Western Europe (Böhme 2002). The larger bodied *Paralatonia*, more frequent in the fossil material from Hațeg Basin, probably inhabited rivers, channels or marshlands, and may have fed on small fishes, worms, molluscs, and arthropods. The smaller *Hatzegobatrachus*, based on the conformation of its ilium, could have been a hopper, rather than a jumper, and may have inhabited channels, marshlands, or even temporary ponds, feeding mainly on arthropods.

Conclusions

- The latest Cretaceous (Maastrichtian) microvertebrate deposits of Hațeg Basin, Romania have yielded a number of skeletal elements belonging at least to two new genera and species of anurans. Based on the morphology of ilium (and perhaps prearticular), *Hatzegobatrachus grigorescui* gen. et sp. nov. resembles gobiatine and bombinatorine frogs. However, it retains some leiopelmatid-grade anuran features. *Paralatonia transylvanica* gen. et sp. nov., based on cranial- and postcranial characters, appears as a transitional form between primitive (*Eodiscoglossus*-like) and more derived discoglossine frogs (e.g., *Discoglossus*, *Latoglossus*, and *Latonia*).
- The morphological differences seen in the ilia of *Hatzegobatrachus* and *Paralatonia* indicate that the jumping and/or swimming ability of these forms was quite different, and consequently they could have occupied different ecological niches in the ecosystems.
- The fluvio-lacustrine deposits of the studied localities suggest that the Late Maastrichtian vertebrate assemblages of Hațeg Basin area were part of more complex ecosystems than considered previously.

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References

- Báez, A.M. and Basso, N.G. 1996. The earliest known frogs of the Jurassic of South America: review and cladistic analysis. *Münchener Geowissenschaftliche Abhandlungen A* 30: 131–158.
- Báez, A.M., Basso, N.G., and Pugener, L.A. 1998. A new paleogene pipid frog from northwestern Patagonia. *Journal of Vertebrate Paleontology* 18 (3): 511–524.
- Bailon, S. 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France. In: J. Dresse and N. Dresse-Berset (eds.), *Fiches d'ostéologie animale pour l'archéologie, série C: varia*, 1–42. Centre de Recherches Archéologiques du CNRS, APDCA, Antibes.
- Borsuk-Białynicka, M. and Evans, S.E. 2002. The scapulocoracoid of an Early Triassic stem-frog from Poland. *Acta Palaeontologica Polonica* 47 (1): 79–96.
- Böhme, M. 2002. Lower vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin—palaeoecological, environmental and palaeoclimatical implications. *Beiträge zur Paläontologie* 27: 339–353.
- Böhme, W., Roček, Z., and Špinar, Z.V. 1982. On *Pelobates decheni* Troschel, 1861, and *Zaphrissa eurytelis* Cope, 1866 (Amphibia: Salientia: Pelobatidae) from the early Miocene of Rott near Bonn, West Germany. *Journal of Vertebrate Paleontology* 2 (1): 1–7.
- Clarke, B.T. 1987. A description of skeletal morphology of *Barbourula* (Anura: Discoglossidae), with comments on its relationships. *Journal of Natural History* 21: 879–891.
- Clarke, B.T. 1988. *Evolutionary Relationships of the Discoglossid Frogs. Osteological Evidence*. 431 pp. Ph.D. thesis. City of London Polytechnic, London.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P., and Van Itterbeek J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *Comptes Rendus Palevol* 1 (3): 173–180.
- Duellman, W.E. and Trueb, L. 1986. *Biology of Amphibians*. 670 pp. McGraw Hill, New York.
- Estes, R. 1969. A new discoglossid frog from Montana and Wyoming. *Breviora* 328: 1–7.
- Estes, R. and Sanchíz, B. 1982. Early Cretaceous lower vertebrates from Galve (Teruel), Spain. *Journal of Vertebrate Paleontology* 2: 21–39.
- Evans, S.E. and Borsuk-Białynicka, M. 1998. A stem-group frog from the Early Triassic of Poland. *Acta Palaeontologica Polonica* 43 (4): 573–580.
- Evans, S.E., Borsuk-Białynicka, M., and Manabe, M. 1998. Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleontological Research* 2 (4): 275–278.
- Evans, S.E., Borsuk-Białynicka, M., Milner, A.R., and Mussett, F. 1990. A discoglossid frog from the Middle Jurassic of England. *Palaeontology* 33: 299–311.
- Gao, K. and Wang, Y. 2001. Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaebatrachian anuran clades. *Journal of Vertebrate Paleontology* 21 (3): 460–476.
- Godefroit, P., Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., and Van Itterbeek, J. 2002. Dinosaur egg nests, mammals and other vertebrates from the new Maastrichtian site of the Hațeg Basin (Romania). *Seventh European Workshop on Vertebrate Palaeontology, Sibiu (Romania)*, 21. Ars Docendi, Bucharest.
- Grigorescu, D. and Csiki, Z. 2002. Geological introduction to the uppermost Cretaceous formations with dinosaurs and other vertebrates of the Hațeg Basin. *Seventh European Workshop on Vertebrate Palaeontology, Sibiu (Romania)*, 51–58. Ars Docendi, Bucharest.
- Grigorescu, D., Csiki, Z., Hartenberger, J.-L., Rădulescu, C., Samson, P., and Sudre, J. 1985. Découverte de mammifères et dinosaures dans le Crétacé supérieur de Pui (Roumanie). *Comptes Rendus de l'Académie des Sciences, Paris, série 2* 301: 1365–1368.
- Grigorescu, D., Csiki, Z., Venczel, M., Csiki, Z., and Limborea, R. 1999. New latest Cretaceous microvertebrate fossil assemblages from the Hațeg Basin (Romania). *Geologie en Mijnbouw* 78: 301–314.
- Groessens-Van Dyke, M. 1981. Étude des amphibiens du Montien continental de Hainin. *Société Belge de Géologie, Bulletin* 90: 87–101.
- Günther, A. 1859. On sexual differences found in bones of some recent and fossil species of frogs and fishes. *Annals and Magazine of Natural History* 3 (7): 377–387.
- Henrici, A.C. 1998. A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology* 18 (2): 321–332.
- Hodrova, M. 1987. Lower Miocene frogs from the Dolnice locality in the Cheb Basin (Czechoslovakia). *Acta Universitatis Carolinae Geologica* 2: 97–115.
- Hossini, S. 1993. A new species of *Latonia* (Anura, Discoglossidae) from the lower Miocene of France. *Amphibia-Reptilia* 14: 237–245.
- Hossini, S. 2000. Un nouveau discoglossidé (Amphibia, Anura) dans le Miocène supérieur du gisement marocain "Oued Zra". *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes* 331: 621–626.
- Jenkins, F.A. and Shubin, N.H. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology* 18 (3): 495–510.
- Laurenti, J.N. 1768. *Specimen medicum, exhibens synopsis Reptilium emendatum cum experimentis circa venena et antidota Reptilium Austriacorum*. 214 pp. J.T. de Trattum, Wien.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Laurentius Salvius, Stockholm.
- Nopcsa, F. 1915. Erdélyi dinoszauruszai. *A Magyar királyi Földtani Intézet Évkönyve* 23: 3–24.
- Panaiotu, C. and Panaiotu, C. 2002. Paleomagnetic studies. *Seventh European Workshop on Vertebrate Palaeontology, Sibiu (Romania)*, 59. Ars Docendi, Bucharest.
- Piveteau, J. 1936. Une forme ancestrale des amphibiens anoures dans le Trias inférieur de Madagascar. *Comptes Rendus de l'Académie des Sciences, Paris* 102: 1607–1608.
- Rafinesque, S.C. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. 224 pp. Privately printed, Palerme.
- Roček, Z. 1994. Taxonomy and distribution of Tertiary discoglossid (Anura) of the genus *Latonia* v. Meyer, 1843. *Geobios* 27 (6): 717–751.
- Roček, Z. 2000. Mesozoic anurans. In: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology, vol. 4, Palaeontology: The Evolutionary History of Amphibians*, 1295–1331. Surrey Beatty and Sons, Sydney.
- Roček, Z. and Nessov, L.A. 1993. Cretaceous anurans from Central Asia. *Palaeontographica A* 226: 1–54.
- Roček, Z. and Rage, J.-C. 2000a. Anatomical transformations in the transition from temnospondyl to proanuran stages. In: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology, vol. 4, Palaeontology: The Evolutionary History of Amphibians*, 1274–1282. Surrey Beatty and Sons, Sydney.
- Roček, Z. and Rage, J.-C. 2000b. Proanuran stages. In: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology, vol. 4, Palaeontology: The Evolutionary History of Amphibians*, 1283–1294. Surrey Beatty and Sons, Sydney.
- Sanchíz, B. 1998. Salientia. In: P. Wellnhofer (ed.), *Encyclopedia of Paleoherpétology* 4: 1–276. Dr. Friedrich Pfeil Verlag, München.
- Shubin, N.H. and Jenkins, F.A. 1995. An Early Jurassic jumping frog. *Nature* 377: 49–52.
- Špinar, Z.V. and Tatarinov, L.P. 1986. A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi Desert. *Journal of Vertebrate Paleontology* 6 (2): 113–122.
- Wang, Y. and Gao, K. 1999. Earliest Asian discoglossid frog fossil from western Liaoning. *Chinese Science Bulletin* 44: 636–641.
- Weishampel, D.B. and Reif, W.-E. 1984. The work of Franz Baron Nopcsa (1877–1933): dinosaurs, evolution and theoretical tectonics. *Jahrbuch der Geologischen Bundesanstalt Wien* 127: 187–203.
- Worthy, T.H. 1987. Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil *Leiopelma* species. *Journal of the Royal Society of New Zealand* 17: 201–251.