

New lissamphibians and squamates from the Maastrichtian of Hațeg Basin, Romania

ANNELISE FOLIE and VLAD CODREA



Folie, A. and Codrea, V. 2005. New lissamphibians and squamates from the Maastrichtian of Hațeg Basin, Romania. *Acta Palaeontologica Polonica* 50 (1): 57–71.

Numerous remains of amphibians and squamates were discovered in the continental sediments of the Maastrichtian Sânpetru Formation, south of Pui Village (Hațeg Basin, western Romania). The lissamphibians are represented by a salamander-like allocaudatan (*Albanerpeton* sp.) and at least two discoglossid frogs (cf. *Eodiscoglossus* sp. and cf. *Paradiscoglossus* sp.). The numerous lizards are represented by, e.g., the teiid *Bicuspidon hatzeiensis* sp. nov., and for the first time in a Late Cretaceous site, by two species of the paramacellodid *Becklesius* (*Becklesius nopcsai* sp. nov. and *Becklesius* cf. *B. hoffstetteri*). Snakes are also present in this site by an indeterminate madtsoiid, which represents the first occurrence of this family in eastern Europe. The presence of *Albanerpeton* in this site confirms that this genus appeared in Europe by at least the Late Cretaceous instead of Miocene as previously thought. The presence of both *Albanerpeton* and *Bicuspidon* in Hațeg Basin suggests a North American influence on eastern European amphibian and lacertilian faunas by Maastrichtian times.

Key words: Allocaudata, Anura, Lacertilia, Serpentes, palaeobiogeography, Maastrichtian, Romania.

Annelise Folie [annelise.folie@naturalsciences.be], F.R.I.A. grant holder, Department of Palaeontology, Royal Belgian Institute of Natural Sciences, rue Vautier 29, B-1000 Brussels, Belgium (corresponding author);

Vlad Codrea [vcodrea@bioge.ubbcluj.ro], Catedra de Geologie-Paleontologie, Universitatea Babeș-Bolyai, Str. Kogălniceanu 1, 3400 Cluj-Napoca, Romania.

Introduction

The Sânpetru Formation of Hațeg Basin, in western Romania, has yielded some of the richest and most diversified Late Cretaceous continental faunas from Europe. Baron von Nopcsa was the first to describe some of the most significant elements of this fauna, mainly dinosaurs, in a series of papers published from 1897 up to 1929 (see Pereda-Suberbiola 1996, for the detailed list of Nopcsa's papers). Prospecting and excavations resumed in the Hațeg Basin in the late 1970s, mainly by teams from the Faculty of Geology and Geophysics (Bucharest, Romania) and The Deva Museum of Dacian and Roman Civilisation (Deva, Romania). The Pui locality was the first microvertebrate fossil site investigated in the Hațeg Basin. A joint French-Romanian team sieved a small sandy lens (named Pui) and discovered fragmentary remains of fishes, amphibians, turtles, lizards, crocodiles, dinosaurs and multituberculate mammals (Grigorescu et al. 1985). From 1992, small amounts of sediments (25 to 50 kg) were sieved in three new fossiliferous lenses at Pui (named Pui 1, 4, and 5) by the team from the Faculty of Geology and Geophysics of Bucharest (Grigorescu et al. 1999).

From 2000 to 2002, a joint team from the University Babeș-Bolyai (Cluj-Napoca) and the Royal Belgian Institute of Natural Sciences (Brussels) organized three large excavation campaigns in Transylvania (see Codrea et al. 2002; Smith et al. 2002). During the springs of 2000 and 2001, nearly 2500 kg of sediments were sieved from a new large lens at the Pui locality (named Pui Islaz), leading to the dis-

covery of many microvertebrate fossils. The aim of the present paper is to describe and discuss fossils of amphibians, lizards, and snakes discovered at the occasion of these new excavations at Pui.

The new site is situated around 500 m south of Pui village, along the right bank of the Bărbat River, at the level of the last houses (Fig. 1). The GPS co-ordinates of the site are N 45°30'27.6" and E 23°05'41.5". The articles written by Grigorescu et al. (1985 and 1999) do not indicate the exact location of the different sites excavated at Pui. It is therefore difficult to compare our new site with the old ones. Dr. Jimmy Van Itterbeeck and collaborators have recently shown the exact location of the new Pui site (Van Itterbeeck et al. 2004). We refer to this article for more information about the location of this new site. The dominantly red coloured sediments outcrop in the river bed. The site is thus only accessible during the summer months when the water level is relatively low.

The sediments have been attributed to the Sânpetru Formation (Grigorescu and Anastasiu 1990). This formation comprises continental mollassic sedimentary wedges, deposited in the synorogenic Hațeg Basin after the Laramic orogenic pulse. Based on the age of the underlying marine deposits (Grigorescu and Anastasiu 1990) and the palynological content (Antonescu et al. 1983; Grigorescu 1983), the Sânpetru Formation is considered to be late Maastrichtian in age. However, recent palaeomagnetic studies suggest that the entire Sânpetru Formation should be early Maastrichtian in age (Panaiotu and Panaiotu 2002). According to Grigorescu (1983), the sediments were deposited in a northerly

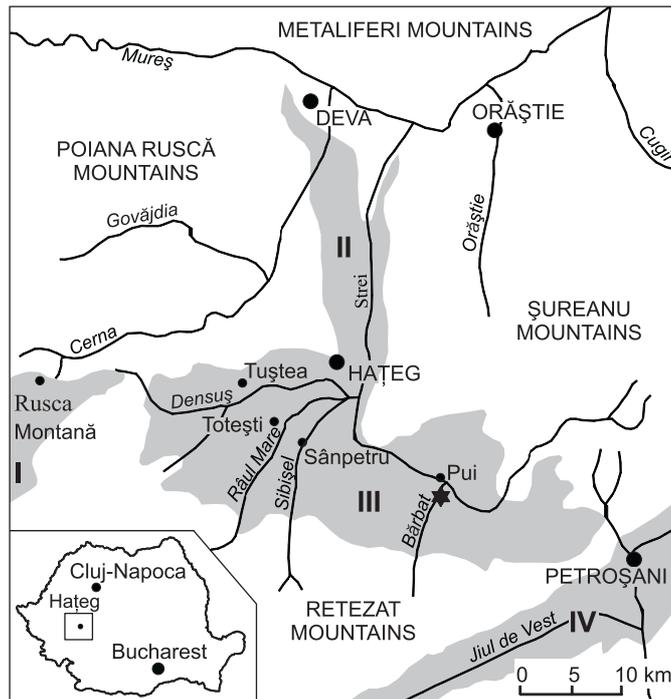


Fig. 1. The outcrop (Pui Islaz, indicated by a star) attributed to the Maastrichtian Sânpetru Formation, is located in the Bârbaț River bed south of the village of Pui. The grey areas indicate the sedimentary basins (I, Rusca Montana Basin; II, Strei Basin; III, Hateg Basin; IV, Petrosani Basin). Modified from Codrea et al. (2002).

flowing braided river system under a warm and humid climate with seasonal fluctuations.

Institutional abbreviations.—PSMUBB, Palaeontology-Stratigraphy Museum, University Babeș-Bolyai, Cluj-Napoca, Romania; RBINS, Royal Belgian Institute of Natural Sciences.

Systematic palaeontology

Class Amphibia Linnaeus, 1758

Subclass Lissamphibia Haeckel, 1866

Order Allocaudata Fox and Naylor, 1982

Family Albanerpetontidae Fox and Naylor, 1982

Genus *Albanerpeton* Estes and Hoffstetter, 1976

Type species: *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, Middle to ?Late Miocene, France (Estes and Hoffstetter 1976; Gardner 1999a); Early/Middle Miocene, Western Styrian Basin, Germany (Wiechmann 2001); and Early Miocene, Randeck Maar, Austria (Sanchez 1998).

Other species: *A. nexuosum* Estes, 1981¹ (Campanian to Maastrichtian, Colorado, Montana, New Mexico, Texas, Utah and Wyoming, USA and Alberta, Canada, Gardner 2000a); *A. arthridion* Fox and Naylor, 1982 (Aptian–Albian, Texas and Oklahoma, USA, Gardner 1999b); *A. galak-*

tion Fox and Naylor, 1982 (Campanian to Maastrichtian, Wyoming, USA and Alberta, Canada, Gardner 2000a); *A. cifellii* Gardner, 1999 (Turonian, Utah, USA, Gardner 1999c); *A. gracile* Gardner, 2000² (Campanian, Texas and Utah, USA and Alberta, Canada, Gardner 2000a); “Paskapoo species” (*sensu* Gardner 2002; Late Paleocene, Alberta, Canada); *Albanerpeton* sp. nov. (Early Pliocene, Hungary, Venczel and Gardner 2003).

Albanerpeton sp.

Fig. 2.

Material.—PSMUBB V 180–V 194 (15 incomplete premaxillae), V 195–V 215 (21 incomplete maxillae), V 216–V 272, V 279–V 302 and V 306 (82 incomplete dentaries), V 273–V 278 and V 303–V 305 (nine indeterminate jaw fragments), V 307–V 316 (10 incomplete frontals), V 317–V 327 (11 incomplete humeri), V 328–V 333 (six incomplete atlantes), V 334–V 339 (six axes) and V340–V352 (13 incomplete post-cervical vertebrae).

Description.—The isolated premaxillae discovered at Pui Islaz are robust. The best-preserved specimen (Fig. 2A) is a 2.2 mm high left part that bears eight loci for teeth. None of the premaxillae is medially fused. A well-developed dorsoventral medial flange forms a “tongue-in-groove” articulation between the paired premaxillae. The entire labial side of the pars dorsalis is slightly ornamented by pustules and anastomosed ridges and is perforated by a few foramina. The dorsal border of the pars dorsalis is straight but the bone is complete and presents a boss (*sensu* Gardner 1999a and 2000a) that covers one-third of the pars dorsalis and is ornamented by polygonal pits enclosed by ridges. It is separated from the rest of the process by a ventral rim. In lingual view, the elliptical suprapalatal pit is set just over the pars palatinum and communicates with the pars dentalis by a short canal. The suprapalatal pit is bordered by two well-developed internal supports. The bases of these supports are located on the pars palatinum and converge dorsally just over the suprapalatal pit. On some specimens, an additional pit is present ventromedially to the suprapalatal pit. This foramen is also linked to the pars dentalis by a short canal.

The best-preserved maxilla (Fig. 2B) is a 3 mm long right specimen whose posterior part is broken off. This maxilla possesses 14 loci for teeth. By comparisons with complete figured material (e.g., Gardner 1999a: pl. 1M), it seems that a complete maxilla of *Albanerpeton* sp. from Pui Islaz was around 4.2 mm long. The lateral process, which articulated with the premaxilla, is short. In lingual view, the pars dentalis is straight. The anterior part of the pars palatinum is wide, but it progressively becomes narrower posteriorly. Labially, the pars facialis thins posteriorly. Its surface is rather smooth, except the presence of a few foramina in the anterior region. The junction between the lateral and nasal processes of the premaxilla forms the inferior and posterolateral margins of the external naris.

¹ Emended from *Albanerpeton nexuosus* Estes, 1981, in order to retain the conformity of the generic and specific genders (ICZN, Article 34.2).

² Emended from *Albanerpeton gracilis* Gardner, 2000, in order to retain the conformity of the generic and specific genders (ICZN, Article 34.2).

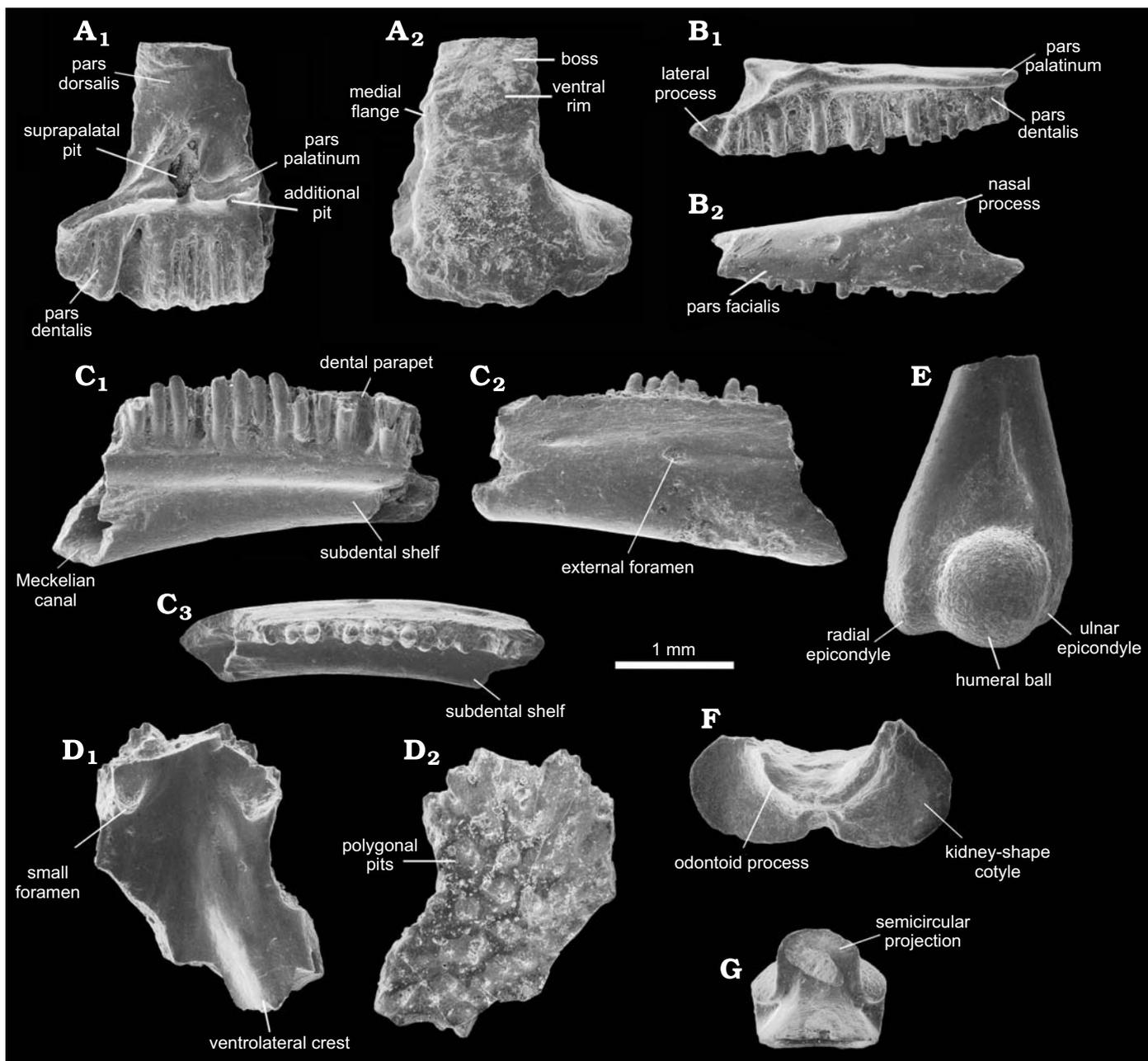


Fig. 2. *Albanerpeton* sp. **A.** PSMUBB V 180, left premaxilla in lingual (A_1) and labial (A_2) views. **B.** PSMUBB V 195, right maxilla in lingual (B_1) and labial (B_2) views. **C.** PSMUBB V 237, left dentary in lingual (C_1), labial (C_2), and occlusal (C_3) views. **D.** PSMUBB V 308, small fragmentary frontal in ventral (D_1) and dorsal (D_2) views. **E.** PSMUBB V 317, distal end of a left humerus in ventral view. **F.** PSMUBB V 328, atlas in anterior view. **G.** PSMUBB V 334, axis in dorsal view. SEM micrographs.

The dentaries (Fig. 2C) are robust and are similar to those described elsewhere for *albanerpetontids* (see, e.g., Gardner 2000b: fig. 3L–P). An association between some of the Pui Islaz fragments indicates that the dentaries probably reached a length of around 6 mm. Anterior prominences correspond to the intermandibular joints between paired dentaries. The labial side of the bone appears rather low anteriorly, but progressively becomes higher rearwards to the level of the Meckelian canal opening. It is perforated by only one row of foramina and some small additional foramina are concentrated in the an-

terior part of the bone. The posterior part of the bone, against which the postdentary bone was attached, is not preserved in the available material from Pui Islaz. The dorsal edge of the dental parapet is straight and rather high. On the ventral side of some specimens, a large ridge marks the insertion area for intermandibular muscles. In lingual view, the Meckelian canal is closed. The dental shelf is low, straight and gutter-shaped. Teeth are pleurodont, non-pedicellate, straight, closely packed and not highly heterodont, with crowns that are labiolingually compressed, faintly tricuspid and chisel-like.

The frontals are usually very fragmentary in the Pui Islaz material. They are rather flat but the area between the ventrolateral crests is dorsally concave. Polygons and ridges ornament their dorsal surface. The best-preserved frontal (Fig. 2D) is 2.5 mm long, but it is incomplete: only the area between the two ventrolateral crests in the anterior part of the frontal, the anterior part of the right ventrolateral crest, a small part of the left ventrolateral crest and two small foramina at the top of the crests are preserved. The ventrolateral crests are triangular in cross-section and appear rather slender but their external parts are missing and they were probably wider. The anterior portion of the frontal is unfortunately always broken off in the Pui Islaz material, so that it is not possible to determine the structure of the anterolateral or internasal processes. Although it is not possible to know the original length of the frontals, the angle between the ventrolateral crests is wide and it is likely that the frontals were characteristically triangular.

Ten distal ends of humeri have been discovered in the investigated lens at Pui Islaz (one of which is illustrated in Fig. 2E). The shaft is straight and the humeral ball is spherical. The ulnar epicondyle is smaller than the radial epicondyle.

The atlas (Fig. 2F) is anteroposteriorly compressed. In anterior view, it bears two wide kidney-shaped cotyles, separated by a gutter-like odontoid process. Only the bases of the neural arches are preserved. The axis (Fig. 2G) is conical in shape and approximately 1 mm long. Dorsally, it bears a semicircular projection that articulated with the atlas (Estes and Hoffstetter 1976).

Some fragments of trunk or caudal vertebrae have also been found in the material from Pui Islaz. These pieces are characteristically hourglass-shaped, amphicoelous (*sensu* Estes and Hoffstetter 1976; Duffaud 2000), and widened in their medial part to form two lateral areas. None of the vertebrae are complete.

Discussion.—Each kind of bones presents the same morphology (e.g., premaxillae are robust and the suprapalatal pits share the same characteristics). The entire albanerpetontid material likely belongs to a single taxon.

The distal ends of humeri found at Pui Islaz are characteristic for the family Albanerpetontidae. In other Amphibia, the shaft is more widened, the distal part is wider, the humeral ball is moved aside and distally flattened, and the ulnar epicondyle is wider than the radial one (Gardner and Averianov 1998; Gardner 1999b).

The vertebrae also display characteristic albanerpetontid morphology: the two first vertebrae (with partially the first trunk vertebra) are specialised to add an atlanto-axial joint that allows movement in a mediolateral plane (McGowan 1998; Gardner 2001). The original diagnosis of *A. inexpectatum* is mainly based on the fusion of the first three vertebrae (Estes and Hoffstetter 1976). However, Gardner (1999a, b) showed that this character is only diagnostic at the familial level and gave a more accurate diagnosis of *A. inexpectatum* based on other features.

McGowan and Evans (1995) showed that the shape of the frontals is diagnostic at the generic level. Although incom-

plete, the specimens discovered at Pui Islaz are likely triangular and are thus characteristic of the genus *Albanerpeton*, whereas *Celtesdens* and *Anoualerpeton* have a more rectangular frontal (Gardner 2000b; Gardner et al. 2003). Venczel and Gardner (2003) recently identified a new *Albanerpeton* species that, e.g., bears a unique ventromedial keel on the frontals. As our specimens do not bear any keel, they cannot belong to this new species.

With the exception of the basalmost species *A. arthridion*, the morphology of the premaxilla allows to group species of *Albanerpeton* into two great clades (Gardner 2002). These clades probably separated during the latest Albian–earliest Cenomanian (Gardner 1999c, d, 2002). In one clade, *A. galaktion*, *A. gracile*, and *A. cifellii* are characterised by gracile-shaped premaxillae with a triangular suprapalatal pit. On the other hand, the premaxillae discovered at Pui Islaz are particularly robust and their suprapalatal pit is elliptical, like in the clade including *A. nexuosum* and *A. inexpectatum* (Gardner 1999a, 2000a).

The size of the suprapalatal pit on the premaxillae from Pui Islaz can be evaluated around 7% of the lingual side of the pars dorsalis. It is closer to the condition observed in *Albanerpeton inexpectatum* (4–7%, Gardner 1999a) and differs from the sizes (9–13%) observed in *A. nexuosum* (Gardner 2000a). Attribution of the Pui Islaz material to the Aptian–Albian species *A. arthridion* can be excluded, because its suprapalatal pit represent only 1% of the lingual side of the pars dorsalis. With the proportion of the suprapalatal pit, the second argument that prevents the attribution of the Pui Islaz material to *A. nexuosum* is the heterodonty of dentary teeth. Those of *A. nexuosum* are distinctly higher and wider in the anterior part of the bone.

The general shape of the albanerpetontid material from the Pui Islaz site is concordant with *A. inexpectatum*. In his revision of *A. inexpectatum*, Gardner identified 5 autapomorphies for this species (Gardner 1999a): pustulate ornamentation on the labial side of the premaxilla; maxilla and dentaries of large individuals weakly ornamented labially; dentary with a low dorsal process that contributes to coronoid process; azygous frontals broad with a equilateral triangle form; and wide ventrolateral crests, deeply concave dorsally in the orbital region. The ornamentation with pustules and ridges is present on the entire labial side of the premaxillae from Pui Islaz even if bones are worn (Fig. 2A₂). Maxillae and dentaries are unornamented but the Pui Islaz specimens are likely not large (Fig. 2B₂, C₂). As mentioned in the description, the posterior part of the bones is not preserved, it is therefore not possible to observe the coronoid process. It is likely that the frontal was triangular and the angle between the ventro-lateral crests is wide so that it is supposed that the shape of the frontal was close to an equilateral triangle (Fig. 2D). The ventrolateral crests are not entirely preserved but they were probably broad. The orbital region of the bone is missing so that it is not possible to observe the deep concavity of the crests.

Albanerpetontid material was previously known from several localities in Europe: middle–late Campanian of La Neuve, France; late Campanian of Laño, Spain; ?early Maas-

trichtian of Cruzy, France; late Maastrichtian of Cassagnau, France and late Maastrichtian of various localities in the Hațeg Basin (Duffaud 2000). Duffaud (2000) attributed all these specimens to a single species. Because of the presence of a boss on the dorsal part of the premaxilla and of the ornamentation of the bone that is stronger in the upper part than in the lower part, he identified this taxa as being close to *A. nexuosum*. The new albanerpetontid material found at Pui Islaz differs from the material described by Duffaud (2000) by the pars dentalis that is more laterally projected (Fig. 2A and Duffaud 2000: fig. 1). However, both the material from Pui Islaz and material described by Duffaud seems to belong to the same taxa. The presence of the boss on the dorsal border of the premaxilla prevents the attribution of this taxa to *A. inexpectatum* but the characters observed on the Pui Islaz material indicate that the Late Cretaceous albanerpetontid species was nevertheless closer to this species than to *A. nexuosum* as concluded by Duffaud (2000).

It is clear that the material discovered at Pui Islaz is not sufficient to assign it to *A. inexpectatum*. Nevertheless, the Pui Islaz material seems to be closer to this species than to all the other species of the genus *Albanerpeton*. The characters that are non-concordant with *A. inexpectatum* or that are unknown on the Pui Islaz material, are not sufficient to erect a new species. Moreover, this taxon was previously described from Miocene sediments, while the site of Pui Islaz is Maastrichtian in age. If the taxonomic assignment is confirmed, the temporal range of *A. inexpectatum* would extend over more than 40 millions years. Such exceptional longevity is suspected in another albanerpetontid species, *Celtesdens megacephalus*, which is known from the Late Jurassic to the Albian of Western Europe (Gardner 2002; McGowan 2002).

Order Anura Rafinesque, 1815

Family Discoglossidae Günther, 1859

Cf. *Eodiscoglossus* sp.

Fig. 3A.

Material.—PSMUBB V 356 (one incomplete left ilium).

Description.—Only a single posterior part of an ilium recovered at Pui Islaz can be attributed to this taxon (Fig. 3A). It is 2 mm long, 1.5 mm high and displays a small anterior part of the acetabulum, the base of the pars ascendens, a small but well-marked supraacetabular fossa and a shallow tubercle instead of a tuber superius. The angle between the tubercle and the pars ascendens is open, the junction between the acetabular region and the shaft is not sharply waisted, the pars descendens is lost and the pars ascendens is postero-dorsally oriented.

Discussion.—A postero-dorsally elongated pars ascendens on the ilium is characteristic for the family Discoglossidae (Rage and Hossini 2000). Moreover, an iliac crest is only present in the members of the *Discoglossus* group (*sensu* Rage and Hossini 2000) that includes the genera *Discoglossus*, *Latonia*, *Eodiscoglossus*, *Paralatonia*, and probably also *Paradiscoglossus* (Duffaud and Rage 1999).

This ilium recovered from Pui Islaz differs from *Latonia* in that the ilium of the latter is about 10 times larger and has a tuber superius that is mediolaterally thicker with the angle between the tuber superius and the pars ascendens that is slightly more open (Rage and Hossini 2000). Moreover, *Latonia* possesses an additional fossula tuberis superioris developed behind the acetabulum, the base of the pars ascendens is narrower and the junction between the acetabulum and the shaft is waisted (Roček 1994). The juvenile form of *Latonia* and the adult of *Discoglossus* are very similar although the latter is smaller. They share a thick tuber superius, the presence of an additional fossula tuberis superioris, a narrow base of the pars ascendens and a waisted junction between the shaft and the acetabulum (Roček 1994; Duffaud and Rage 1999; Rage and Hossini 2000). Grigorescu et al. (1999) referred fragmentary ilia from the Sânpetru Formation to the genus *Eodiscoglossus*. Recently, Venczel and Csiki (2003) revised these fragments and attributed them to the new genus *Paralatonia*. Some characters are concordant with the ilia from Pui Islaz as the size and the great angle between the tuber superius and the pars ascendens. But some characters are different: the supraacetabular fossa is wider and deeper, the tuber superius is more crest-like and continuous with the iliac shaft, and the acetabular rim is not as prominent and does not project beyond the ventral margin of the bone. The presence of an iliac tubercle instead of a tuber superius prevent the attribution of this ilium to the genus *Paradiscoglossus*.

The iliac crest of PSMUBB V 356 is not well visible. Therefore, it cannot be proved that this ilium really belongs to a discoglossid frog. However, this specimen closely resembles the ilium of *Eodiscoglossus* Villalta, 1957 by the presence of a dorsal tubercle instead of a crest (Evans et al. 1990). Two species are currently referred to this genus: *E. santonjae* Vergaud-Grazzini and Wenz, 1975 (type species) and *E. oxoniensis* Evans et al., 1990. *Eodiscoglossus santonjae* (Estes and Sanchiz 1982a) differs from PSMUBB V 356 by a more waisted junction between the acetabular region and the shaft (instead of less marked on the fragments from Pui Islaz), and by a lateral ridge between the iliac crest and the pars cylindroformis giving a triangular section to the bone (instead of a groove giving a drop-shaped bone section). *Eodiscoglossus oxoniensis* seems to be more similar to the fragments from Pui Islaz because the junction between the shaft and the acetabular area is not waisted, and the iliac crest and the pars cylindiformis are separated by a groove (Evans et al. 1990). However, differences can be observed: in *E. oxoniensis*, dorsal and ventral pits separate the tubercle from the remainder of the bone and the supraacetabular fossa is longer and deeper (Evans et al. 1990). Duffaud and Rage (1999) described very similar discoglossid ilia from the Late Cretaceous of Laño (Spain). According to these authors, those specimens cannot be referred to *Eodiscoglossus* because the pars ascendens is less developed and the supraacetabular fossa of the ilium is shallower. In the specimen from Pui Islaz, the pars ascendens is not very well preserved

and it is therefore impossible to assess whether it was rather strong or frail. It is also difficult to compare the depth of the supraacetabular fossa.

This ilium fragment found at Pui Islaz is very similar to *Eodiscoglossus oxoniensis* but the differences described above prevent the attribution of the fossil to this species.

Cf. *Paradiscoglossus* sp.

Fig. 3B, C.

Material.—PSMUBB V 357 (one incomplete right ilium) and V 358–V 360 (three incomplete left ilia).

Description.—These four posterior parts of ilia collected at Pui Islaz are between 2 and 3.5 mm long and 1 to 3 mm high. Two of these fragments (V 357 and V 360) are approximately twice as large as the two other fragments (V 358 and V 359) but they share several characters in common. In lateral view, the iliac shaft is not strongly curved. The junction between the acetabular region and the shaft is not sharply waisted. The pars descendens is lost. The pars ascendens is postero-dorsally oriented. The angle between the tuber superius and the pars ascendens is open. The pars ascendens is lost except on PSMUBB V 357 (Fig. 3B) where a small but wide part is present. The supraacetabular fossa seems to be wide and deep. The acetabulum is incomplete as it displays only a well-marked anterior edge. The tuber superius is elongate, mesiodistally compressed and does not pass the well-developed iliac crest (Fig. 3C). This crest is separated from the pars cylindriformis by a groove.

Discussion.—As mentioned for cf. *Eodiscoglossus* sp., the presence of a postero-dorsally elongated pars ascendens on the ilium is characteristic of the Discoglossidae and the iliac crest is a characteristic of the members of the *Discoglossus* group (Rage and Hossini 2000). For the reasons mentioned for the previous taxa, these ilia cannot be attributed to *Latonina*, *Discoglossus*, or *Paralatonina* and the presence of a crest-like tuber superius instead of a tubercle prevent the attribution of these specimens to *Eodiscoglossus*. However, they share several characters in common with *Paradiscoglossus americanus* Estes and Sanchiz, 1982: they are similarly curved, they have well-developed dorsal crest continuous with the elongate and compressed dorsal tuber superius, which is not clearly separated from the crest (Estes and Sanchiz 1982b), an open angle between the tuber superius and the pars ascendens, and a wide supraacetabular fossa and pars ascendens. However, the posterior part of the bones is lost on the larger fragments and the tuber superius seems to be more compressed than in *P. americanus* on the smaller one, thus precluding confident referral of the specimens from Pui Islaz to *P. americanus*.

Discoglossidae indet.

Fig. 3D, E.

Material.—PSMUBB V 353, V 354 (two incomplete urostyles), V 355 (one sacral vertebra).

Description.—Two proximal portions of urostyles were discovered in the excavated lens. Only the two oval anterior cotyles for articulation with the sacral vertebra and the anterior part of the neural canal are preserved in the first specimen. The second, better-preserved specimen (Fig. 3D) is 4 mm long, 2 mm high, and 2 mm wide (at the level of the cotyles). The two anterior cotyles, two broken transverse processes and a small part of the dorsal crest are preserved on this specimen. The transverse processes are triangular in cross-section and inclined posterolaterally. Behind them, two spinal foramina are posteriorly open. The dorsal crest is not complete along the fragment. Ventrally, the bone is smooth.

The sacral vertebra founded at Pui Islaz is 1.5 mm long, 2 mm wide and bears an anterior and two posterior condyles (Fig. 3E). The neural arch is lost. Ventrally, the posterior condyles are separated by a shallow sagittal canal.

Discussion.—A single pair of transverse processes and a poorly developed neural crest on the urostyle, and a posteriorly bicondylar sacral vertebra indicate that the specimens are referable to the family Discoglossidae. However, these elements are not specific to the generic or specific level. Moreover, the presence of two taxa referred to this family at Pui Islaz prevent the attribution of these elements to cf. *Eodiscoglossus* sp. or cf. *Paradiscoglossus* sp.

Class Diapsida Osborn, 1903

Order Squamata Oppel, 1811

Suborder Lacertilia Owen, 1842

Infraorder Scincomorpha Camp, 1923

Family Paramacellodidae Estes, 1983

Genus *Becklesius* Estes, 1983

Type species: *Becklesius hoffstetteri* Seiffert, 1973 (late Kimmeridgian, Guimarota lignite mine, Leiria, Portugal; Portlandian of Purbeck, England; middle Cretaceous of Morocco). (= *Macellodus brodei* Hoffstetter, 1967; non *Macellodus brodei* Owen, 1854; *Becklesisaurus hoffstetteri* Seiffert, 1973).

Other species: *Becklesius cataphractus* Richter, 1994 and *Becklesius* sp. Richter, 1994 (upper Barremian, Uña, Spain).

Becklesius nopcsai sp. nov.

Fig. 3G.

Holotype: PSMUBB V 361, fragment of dentary with four complete teeth and two empty loci.

Type locality: Pui Islaz, Hațeg Basin, Transylvania, Romania, Europe.

Type horizon: Sânpetru Formation, Maastrichtian, Late Cretaceous.

Derivation of the name: After Baron Francis von Nopcsa, pioneer in palaeontological researches in Hațeg Basin.

Diagnosis.—*Becklesius nopcsai* differs from both *Becklesius hoffstetteri* and *Becklesius cataphractus* by having the apex of the labial cusp that is less developed in height, giving a square shape to the crown (whereas the crowns of *B. hoffstetteri* and *B. cataphractus* are more triangular); and by a wide lingual cusp reaching nearly 75% of the width of the labial cusp (whereas about 40% in both *B. hoffstetteri* and *B. cataphractus*).

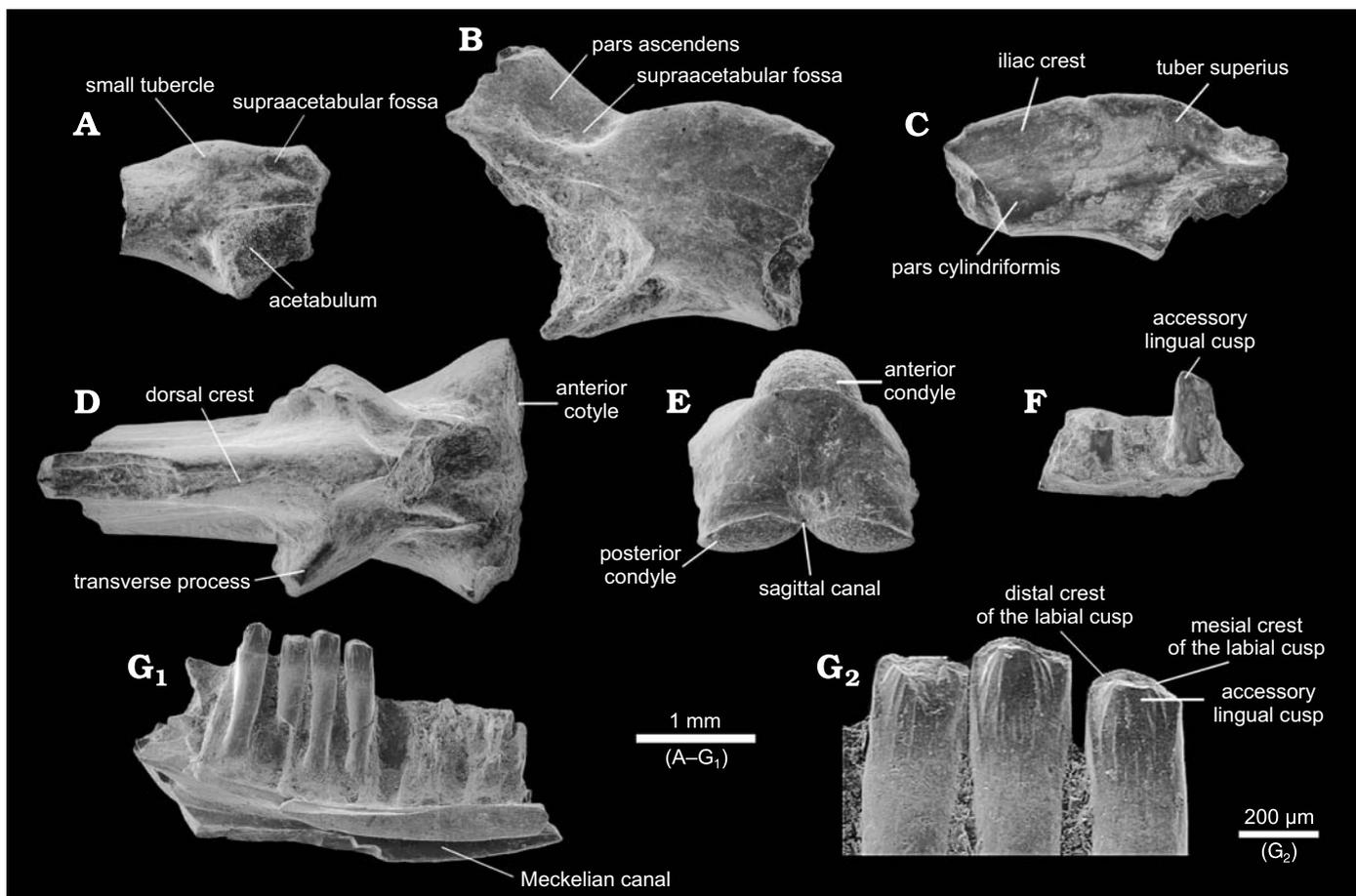


Fig. 3. A–E. Discoglossidae. A. PSMUBB V 356, cf. *Eodiscoglossus* sp., left ilium in lateral view. B, C. cf. *Paradiscoglossus* sp. B. PSMUBB V 357, great form, right ilium in lateral view. C. PSMUBB V 358, small form, left ilium in lateral view. D, E. Discoglossidae indet. D. PSMUBB V 353, urostyle in dorsal view. E. PSMUBB V 355 sacral vertebra in ventral view. F, G. *Becklesius*. F. PSMUBB V 365, *B.* cf. *hoffstetteri*, left dentary in lingual view. G. PSMUBB V 361, holotype of *B. nopcsai* sp. nov., fragment of left dentary (G₁) and tooth crown (G₂) in lingual view. SEM micrographs.

Material.—PSMUBB V 361, V 362 (two incomplete dentaries), V 363, V 364 (two incomplete maxillae).

Description.—The holotype PSMUBB V 361 is 3.7 mm long, with four complete teeth and two empty loci (Fig. 3G₁). The Meckelian canal is open. The labial side of the dentary is smooth and bears a series of aligned foramina. Teeth are pleurodont, high, straight, slender, enlarged lingually in the middle of their height and they extend beyond the dental parapet for more than third of their height. The crowns are curved lingually and ornamented by vertical ridges. The teeth bear a wide and flattened lingual cusp (*cuspis lingualis sensu* Richter 1994) that extends nearly over 75% of the width of the labial cusp. The lateral borders of the crown are straight-sided and parallel (Fig. 3G₂). The *anguli mesialis* and *distalis sensu* Richter 1994 are pointed and reach nearly 90 degrees, and the labial cusp is nearly the same height as the *anguli*. The crown is therefore square-shaped. The mesial crest is slightly longer than the distal crest resulting in posterior displacement of the apex of the tooth crown that is displaced posteriorly (Fig. 3G₂).

Discussion.—Richter (1994) showed that the family Paramacellodidae is, e.g., characterised by strongly built teeth

with crowns bearing a mesial crest longer than the distal one. In this family, only the genus *Becklesius* possesses robust, chisel-shaped teeth with the mesial crest always longer than the distal crest, pronounced angles between the lateral sides of the crown and the labial crests, and an additional lingual cusp (Kosma 2003). In the type species, *Becklesius hoffstetteri* (see Seiffert 1973: fig. 18), this lingual cusp is about 40% of the width of the labial cusp. It is therefore distinctly narrower than on the specimens from Pui Islaz where the lingual cusp reach 75% of the width of the labial cusp. The lateral sides of the crowns are slightly curved to the apex, and the angles are more obtuse and not pointed, such that the crown appears triangular in lingual view (Hoffstetter 1967). In *B. cataphractus* (see Richter 1994: fig. 9), the crests and the lateral sides of the crown are clearly separated by pointed angles like on the specimen from Pui Islaz. However, *B. cataphractus* possesses a narrow lingual cusp that represents about 40% of the width of the labial cusp. Moreover, this latter cusp is well-developed in height giving a triangular aspect to the crown whereas the crown of *B. nopcsai* is more square-shaped. We believe that these differences justify the

erection of the new species *Becklesius nopcsai* for this *Becklesius* material recovered from Pui Islaz.

Becklesius cf. *B. hoffstetteri*

Fig. 3F.

Material.—PSMUBB V 365 (one incomplete left dentary).

Description.—The fragment found at Pui Islaz is 1.5 mm long and bears 3 loci (Fig. 3F). The only completely preserved tooth is lingually enlarged and passes the dental parapet on about the half of its height. The implantation is pleurodont. The tip of the crown is slightly curved lingually, chisel-like or truncated, and bears a narrow and slightly striated lingual cusp that is far from the middle of the crown. The lingual cusp extends on about 40% of the width of the labial cusp. The mesial crest is longer than the distal one and the angles between the lateral sides of the crown and the labial crests are not very acute (around 125 degrees for the mesial angle and 140 degrees for the distal one). The labial side of the bone is smooth and does not bear any foramen.

Discussion.—This specimen is identified as a dentary because a labiolingual concave facet (interpreted as the dorsal part of the Meckelian canal) is developed on its ventral side. It bears a chisel-shaped tooth with the mesial crest that is longer than the distal crest, the angles are pronounced and an additional lingual cusp is present. This dentary can therefore be attributed to the genus *Becklesius* (*sensu* Kosma 2003). However, it significantly differs from other fossils from Pui Islaz referred to *B. nopcsai* sp. nov., because the tooth is proportionally shorter, the lingual cusp bears only a few striations and represents only about 40% of the width of the labial cusp, and the crown is more lingually curved and not square in outline. This specimen more closely resembles *B. hoffstetteri* (Hoffstetter 1967: fig. 7C, C', C''; Seiffert 1973: figs. 16, 18); however, in *B. hoffstetteri*, the teeth are larger and the lingual cusp is more striated preventing the strict attribution of the described fragment from Pui Islaz to *B. hoffstetteri*. According to Seiffert (1973), posterior dentary teeth of *B. hoffstetteri* bear a cusp located in the middle of the tooth whereas this cusp is more displaced posteriorly on more anterior teeth. This observation indicates that PSMUBB V 365 seems to be the anterior part of a left dentary.

Superfamily Lacertoidea Fitzinger, 1826

Family Teiidae Gray, 1827

Subfamily Polyglyphanodontinae Estes, 1983

Genus *Bicuspidon* Nydam and Cifelli, 2002

Type species: *Bicuspidon numerosus* Nydam and Cifelli, 2002 (Mussentuchit Member of Cedar Mountain Formation, Albian–Cenomanian boundary, Emery County, Utah).

Remarks.—Nydam and Cifelli (2002) recognized that *Bicuspidon* can be a Polyglyphanodontinae and indicates arguments to consider this relationship. However, the lack of cranial material, the presence of active polyphyodonty in *Bicuspidon* and the frail phylogenetic results prevent for the moment, the confident assignment to this subfamily. Neverthe-

less, *Bicuspidon* and *Polyglyphanodon sternbergi* may be closely related together and the dental morphology in *Bicuspidon* might be the morphological and temporal antecedent of *Polyglyphanodon sternbergi*. We refer to the article of Nydam and Cifelli (2002) for more explanations about the relationships of the genus *Bicuspidon*. We consider the genus *Bicuspidon* as a member of Polyglyphanodontinae in the present paper.

Bicuspidon hatzeiensis sp. nov.

Fig. 4A–D.

Holotype: PSMUBB V 368, posterior part of a left dentary with two complete teeth (Fig. 4C).

Type locality: Pui Islaz, Hațeg Basin, Transylvania, Romania, Europe.

Type horizon: Sânpetru Formation, Maastrichtian, Late Cretaceous.

Derivation of the name: After “Hațeg”, the name of the synorogenic basin in Romania where this new species was found.

Diagnosis.—Differs from *B. numerosus* in teeth bearing well-developed labial and lingual striae; and by having the posteriormost tooth only slightly smaller than the other ones, bearing a conical crown devoid of sharp and V-shaped transverse ridge.

Material.—PSMUBB V 366–V 374 (nine incomplete dentaries), V 375, V 376 (two incomplete maxillae), V 377–V 379 (three indeterminate jaw fragments), V 380 (one isolated tooth), V 381–V 384 (four ?cervical vertebrae centra), V 385, V 386 (two ?caudal vertebrae centra).

Description.—The jaw fragments are between 1.5 and 3.5 mm long with a mean of 2 mm and bear from 1 to 5 teeth. Bones and teeth are thick and robust. In labial view, the fragments bear a few aligned foramina and are smooth or ornamented by some longitudinal ridges, giving them some wooden aspect. In lingual view, subcircular replacement pits at the base of the teeth are present on some fragments (Fig. 4A). The dentition is heterodont. Teeth are subpleurodont, closely packed and extend beyond the dental parapet for more than half of their height. At approximately three-quarters of their height, a constriction marks the separation between the root and the crown of the teeth. The crowns are circular to slightly elliptic in cross-section and ornamented by external vertical ridges (Fig. 4B₁). In occlusal view, teeth are approximately 250 μm wide except for the fragment PSMUBB V 367 that is approximately 500 μm wide. Two morphotypes of crowns can be observed in the sample from Pui Islaz. The first is molariform, formed by two distinct cusps separated by a labiolingual V-shaped, transverse ridge (Fig. 4B₂). From the wider labial cusps, one anterior and one posterior ridges extend lingually around the crowns, but do not reach the smaller lingual cusp. The second morphotype is conical and monocuspid. Both morphotypes are associated on the holotype (PSMUBB V 368): the anterior tooth has molariform crown, whereas the posterior one, which corresponds to the last dentary tooth position, is conical and monocuspid (Fig. 4C). The molariform crown is slightly wider labiolingually and more compressed antero-posteriorly than the conical crown.

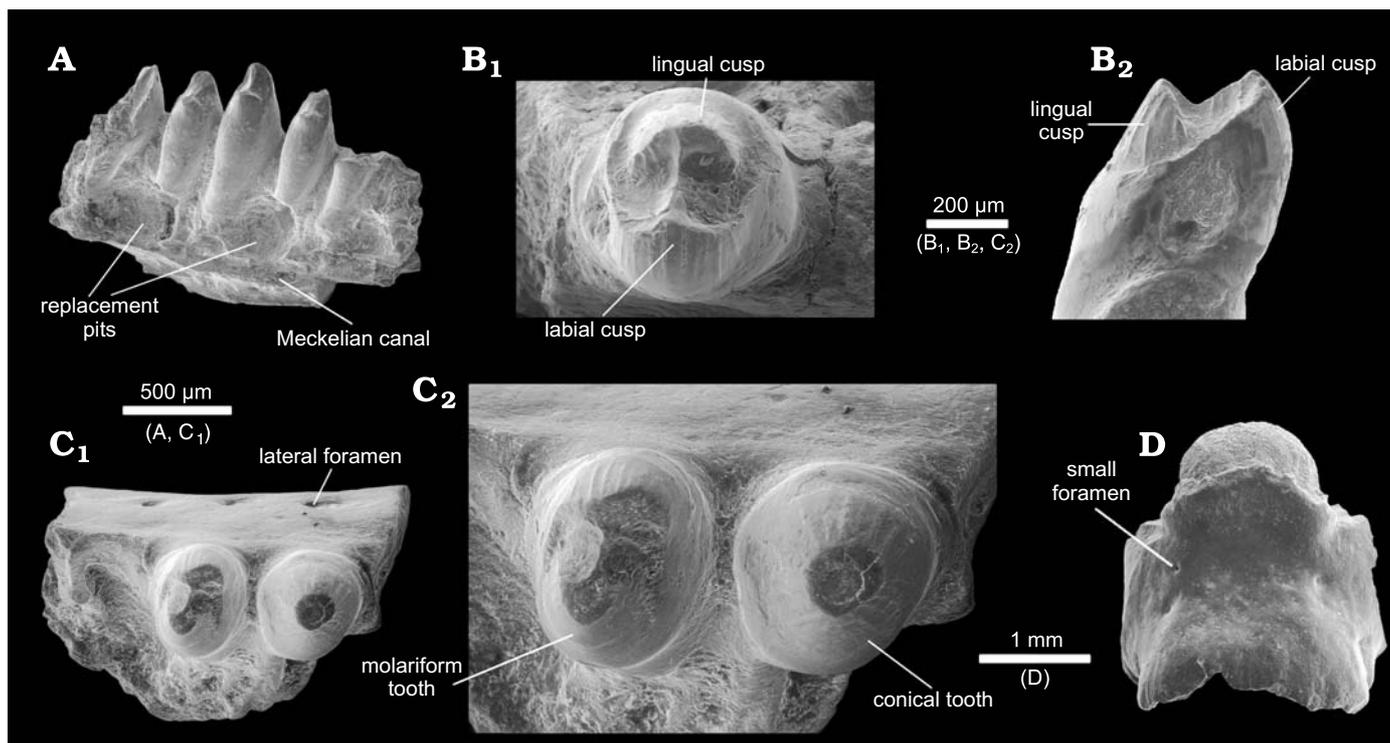


Fig. 4. *Bicuspidon hatzeziensis* sp. nov. **A.** PSMUBB V 366, dentary in lingual view. **B.** PSMUBB V 367, molariform tooth in occlusal (B_1) and lateral (B_2) views. **C.** PSMUBB V 368, holotype in general (C_1) and detailed (C_2) occlusal views. **D.** PSMUBB V 381, cervical vertebra in ventral view. SEM micrographs.

Several incomplete vertebrae have been found on the site of Pui Islaz and are tentatively assigned to *Bicuspidon hatzeziensis*. All are procoelous. The cervical vertebrae (Fig. 4D) are short and their dorsal side is perforated by two small foramina near the middle of their length. The neural arch is lost. The dorsal vertebrae are similar, but are more elongated and narrower than the cervical ones.

Discussion.—A heterodont dentition with transversely expanded teeth is similar to that occurring in the Polyglyphanodontinae (Estes 1983). Among this clade *Polyglyphanodon*, *Paraglyphanodon*, *Dicothodon*, *Peneteius*, and *Bicuspidon* are five North American genera bearing transversely bicuspid and molariform teeth (Nydam 1999; Nydam et al. 2000; Nydam and Cifelli 2002) whereas the Mongolian representatives of this family and the North American genus *Haptosphenus* Estes, 1964 (sometimes considered as a member of the Teiinae; Gao and Fox 1996) have mono-, tri- or polycuspid teeth (Gilmore 1943; Estes 1964; Sulimski 1975).

Polyglyphanodon and *Paraglyphanodon* (maybe a juvenile form of *Polyglyphanodon*; Gilmore 1943; Nydam 1999) have medial and lateral cusps connected by a horizontal or U-shaped transverse ridge (instead of V-shaped in *Bicuspidon*) and mediolaterally expanded teeth (instead of not expanded). Moreover, *Polyglyphanodon* appears to have suppressed tooth replacement, so that replacement pits cannot be observed (Gilmore 1942; Nydam and Cifelli 2002). Similar to *Bicuspidon numerosus*, replacement pits are clearly visible on *B. hatzeziensis* sp. nov.

Peneteius Estes, 1969 bears maxillary teeth with a V-shaped transverse ridge, but these teeth also possess a more complex morphology with multicuspids crowns (Nydam et al. 2000) whereas the tooth crowns in *Bicuspidon* are strictly bicuspid.

Dicothodon Nydam, 1999 is a Polyglyphanodontinae-like genus known in North America that bears V-shaped crowns. It differs from *Bicuspidon* by the presence of anterior and posterior ridges connecting the two cusps together and limiting two associated basins (Nydam 1999).

The attribution of the fragments of Pui Islaz to the American genus *Bicuspidon* Nydam and Cifelli, 2002 is based on the presence of the following characters: teeth crowns not transversally expanded, formed by a labiolingual, V-shaped, transverse ridge and with anterior and posterior ridges lingually going around the tooth without contact with the smaller lingual cusp. However, the fragments show some differences with *Bicuspidon numerosus*. The posteriormost tooth crown is perfectly conical, without a transverse ridge or any additional cusps (instead of last tooth bicuspid with a small medial cusp near the lateral cusp), and bear some vertical external ridges (instead of internal crenulations). Moreover, except for the fragment PSMUBB V 367, the teeth are around half the size of those of *Bicuspidon numerosus*. These differences support the erection of the new species *Bicuspidon hatzeziensis*, to represent these specimens recovered from Pui Islaz.

To date, vertebrae have not been described for *Bicuspidon*. However, the vertebrae described herein are only

tentatively referred to *B. hatzeziensis* because they closely resemble those of *Polyglyphanodon* (Gilmore 1942).

Lacertilia indet.

Genus and species indet. A

Fig. 5A.

Material.—PSMUBB V 389–V 391 (three nearly complete frontals).

Description.—The best-preserved frontal that can be referred to this taxon (PSMUBB V 390) is 2.7 mm long (Fig. 5A). Its posterior part splits into two symmetrical branches, whose ends are broken off. The interorbital region is particularly narrow. The frontal widens out anteriorly into an oval and slightly dorsally concave plate. An open canal joins the anterior and posterior parts of the specimen. The frontal is not ornamented dorsally. The two other frontals are very similar, but lack the right branch of the posterior part and a great portion of the anterior part.

Discussion.—The proportions and the general shape of the first form closely resemble those of the gekkonid *Rodanogekko* Hoffstetter, 1946, from the Late Eocene of France (compare with Estes 1983: fig. 14D). In other Gekkonidae, the interorbital region is distinctly wider. However, the dorsal surface of the frontal is ornamented by anastomosing ridges in *Rodanogekko*, although PSMUBB V 390 is completely smooth. Moreover, the processus descendens of the frontal meet medially its counterpart in Gekkonidae (Estes 1983), whereas they approach, but do not meet on PSMUBB V 390. These specimens cannot be attributed to any of the taxa identified at Pui Islaz, because most Scincomorpha are characterised by two wide coossified frontals that are rectangular in shape whereas PSMUBB V 390 is azygous and narrow (e.g., Estes 1983: fig. 15).

Genus and species indet. B

Fig. 5B.

Material.—PSMUBB V 392–V 404 (13 incomplete frontals).

Description.—The best-preserved fragment (PSMUBB V 398) is 3.5 mm long and 2 mm wide (at the widest part of the bone). The ventral side bears a ventrolateral crest on one edge and what seems to be a suture on the other edge (Fig. 5B₁). One of the ends is wider than the other and corresponds to a widest part of the ventrolateral crest. This end is apparently digitated. The other end seems to be broken off; it is narrow and it bears a more laterally compressed ventrolateral crest with a small foramen on its external side. No area for attachment with other bones is present. The ventrolateral crests were apparently not fused ventrally when the frontals were in contact. The dorsal surface is ornamented with strong anastomosing ridges on the wider end and smaller ridges on the narrower end (Fig. 5B₂). A small foramen is situated nearby the middle of the bone, at the limit between the two ornamentations.

Discussion.—The best-preserved fragment of this form bears a ventrolateral crest and the suture-like structure indi-

cating that it was probably the left part of paired frontals. A strong dorsal ornamentation may correspond to the posterior part of a scincomorph frontal. The shallower ornamentation on the anterior part of the bone indicates the interorbital region (Estes 1983). For the moment, it is not possible to group these fragments with one of the described taxa because of lack of information about the frontals in many scincomorph taxa (Estes 1983).

Genus and species indet. C

Fig. 5C, D.

Material.—PSMUBB V 387 and V 388 (two isolated teeth).

Description.—These two teeth are short, tricuspid, slightly flared and curved lingually, and devoid of longitudinal striations. PSMUBB V 387 is 2 mm high, 1.5 mm long and 1 mm wide (Fig. 5C). The central cusp has a blunt tip, is labiolingually compressed and slightly posteriorly hooked, bears lateral crests and is twice higher and 3–4 times wider than the well-marked lateral cusps. The latter have a circular section in occlusal view. The tip of the anterior cusp is lost, whereas the posterior one is acute. The base of this tooth is enlarged. The root of the tooth has been replaced by a concave, circular to slightly labiolingually compressed resorption cavity on which a small foramen opens. The second tooth (PSMUBB V 388) is smaller (a little more than 1 mm high and a little less than 1 mm long and wide), but quite similar to the first tooth except that the lateral cusps are less markedly developed (Fig. 5D).

Discussion.—We tentatively assume that the two specimens from Pui Islaz belong to the same taxon. In this case, the small specimen would be an anterior tooth, while the wider would have occupied a more posterior position.

As noted by Gao and Fox (1996), tricuspid teeth are commonly seen in the Xantusiidae, Iguanidae, and Teiidae. Teeth of the Xantusiidae are more tubercular and cusps are only weakly tricuspid (Estes 1983) whereas PSMUBB V 387 is clearly tricuspid with well-developed anterior and posterior smaller cusps. It is likely that PSMUBB V 387 and V 388 do not belong to the Xantusiidae. The specimens from Pui Islaz possess flared tricuspid teeth with a wide apical cusp and smaller anterior and posterior cusps like the Iguanidae (Gao and Fox 1996). The teeth of the Iguanidae are often high-crowned and they are commonly less than 1 mm wide (see Estes 1983: fig. 6A) whereas PSMUBB V 387 and V 388 likely belong to a low-crowned taxon with teeth wider than 1 mm. However, taxa with wide and low-crowned teeth also exist within this family (see Estes 1983: fig. 8D). The two isolated teeth discovered at Pui Islaz could therefore belong to the Iguanidae. “Enlarged molariform or multicusped teeth” is a diagnostic derived character state for the Teiidae (Estes 1983) that is present on PSMUBB V 387 and V 388. Within this family, several taxa possess a heterodont dentition with low-crowned, medially concave teeth bearing triconodont crowns (Estes 1983). Neither of the descriptions of these taxa allowed a confident assignment of PSMUBB V 387 and V 388 to the Teiidae. Isolated teeth without a bone fragment

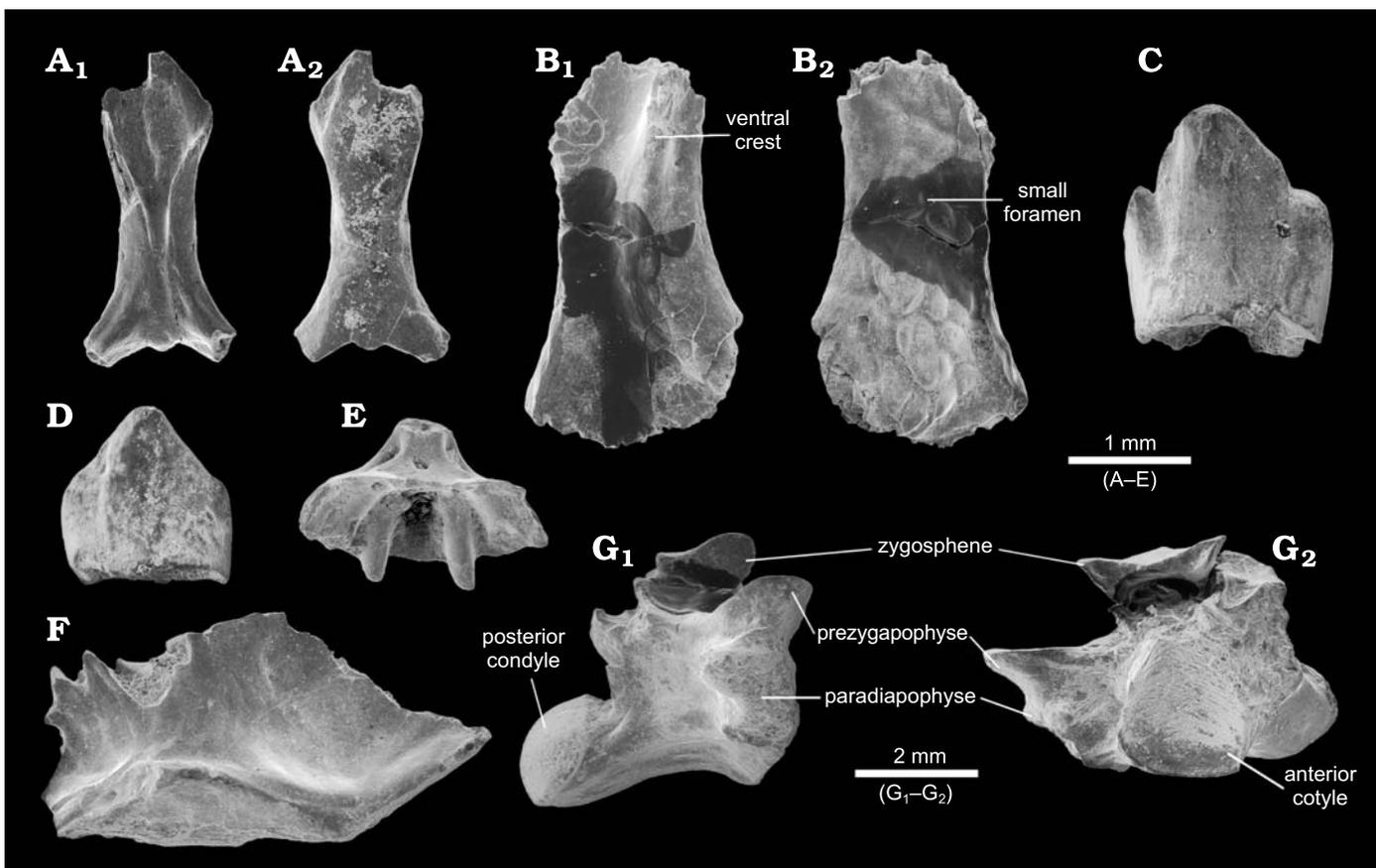


Fig. 5. A–F. Lacertilia indet. A. PSMUBB V 390, genus and species indet. A, azygous frontal in ventral (A₁) and dorsal (A₂) views. B. PSMUBB V 398, genus and species B, frontal in ventral (B₁) and dorsal (B₂) views. C, D. Genus and species C. C. PSMUBB V 387, greater (posterior?) tooth. D. PSMUBB V 388, smaller (anterior?) tooth. E. PSMUBB V 406, genus and species E, premaxilla in lingual view. F. PSMUBB V 405, genus and species D, postdentary bone in lingual view. G. Madtsoiidae indet., PSMUBB V 407, vertebra in right lateral (G₁) and anterior (G₂) views. SEM micrographs.

prevent the formal attribution of PSMUBB V 387 and V388 to the Iguanidae or the Teiidae.

Genus and species indet. D

Fig. 5F.

Material.—PSMUBB V 405 (one ?post-dentary bone).

Description.—This thin fragment is 3.5 mm long and 1.5 mm high. In lingual view, a sinuous crest covers its ventral part (Fig. 5F). The anterior part bears the beginning of what seems to be a fossa. The middle part of the bone is in relief. The posterior part presents a structure with a wide base, which supports two crests. In occlusal view, those crests are as wide as the bone, parallel and obliquely to perpendicularly arranged from the axis of the bone. In labial view, the surface presents an ornamentation with small polygons in the upper part and wider ones in the lower part.

Discussion.—This incomplete bone seems to be a post-dentary bone at the junction between the surangular, the pre-articular and the articular (Romer 1956). The anterior fossa would represent the posterior part of the adductor fossa of the surangular and the posterior structure is probably the anterior part of the articular. A separation between the different parts

can be made as follow: the articular is represented by the posterior part of the bone (with the structure) up to the fossa, the surangular is the anterior part with the fossa, and the pre-articular is the ventral part of the bone delimited dorsally by the sinuous crest (Romer 1956: fig. 105). For the moment, the informations about this specimen are not sufficient to place this bone in a more precise taxonomic context.

Genus and species indet. E

Fig. 5E.

Material.—PSMUBB V 406 (one premaxilla).

Description.—This small premaxilla is 2 mm wide and 1.5 mm high (Fig. 5E). It bears 5 loci. The external loci display only tooth bases, the second and the fourth teeth are more complete and the middle tooth is lost leaving a wide cavity. In the middle of the pars palatinum, a small foramen is open and probably communicated ventrally with the pars dentalis. The pars dorsalis presents two narrow vertical crests stuck on the pars palatinum. Two foramina are open beside the crests. The labial side is smooth and bears no foramina. This premaxilla is convex labially. Teeth are pleurodont, conical, sharp, and do not bear any ornamentation.

Discussion.—This azygous premaxilla with a convex labial side and two high posterior processes is undoubtedly lacertilian (Estes 1983). There is currently no information about the premaxilla of *Bicuspidon* or *Becklesius*. This element might therefore belong to any of the small lacertilians discovered at Pui Islaz.

Suborder Serpentes Linnaeus, 1758
Family Madtsoiidae Hoffstetter, 1961
Madtsoiidae indet.

Fig. 5G.

Material.—PSMUBB V 407 (one incomplete vertebra).

Description.—This vertebra is 5.5 mm long, 5 mm wide, 4 mm high (Fig. 5G). It is deformed, as the cotyle is not aligned with the rest of the vertebra. Anteriorly, a wide and slender zygosphene is present and there is no prezygapophysial process. Posteriorly, the postzygapophysis and the zygantum are lost. The condyle is dorso-ventrally compressed. Laterally, only the right part of the bone is preserved. The paradiapophysis is very expanded and rather low on the bone. The diapophysis is wider than the parapophysis. There is no parapophysial process. Dorsally, the neural spine is lost. The prezygapophysial articular facets are wide, nearly horizontal, not tilted upward with an antero-lateral great axis. Ventrally, there is no hypapophysis but a wide and poorly defined haemal keel. The paracotylar, subcentral and lateral foramina are present but not well visible.

Discussion.—The absence of prezygapophysial process is a primitive character present in rare Ophidia such as the Madtsoiidae (Sigé et al. 1997). But it is not always easy to see whether this element is present or not (Rage 1973). This family is mainly defined as follows: presence of parazygantral and paracotylar foramina and absence of prezygapophysial process (e.g., Rage 1996). The two latter characters can be observed in the Pui Islaz sample.

Sigé et al. (1997) attributed two fragmentary vertebrae from the Campanian of Champ-Garimond (France) to the Madtsoiidae because of the presence of a parazygantral foramen and the absence of prezygapophysial process. Only the latter character is shared with the specimen from Pui Islaz. A more detailed comparison is therefore impossible.

Rage (1996) described two madtsoiid snakes from the late Campanian of Laño (Spain). In the first, *Madtsoia*, the haemal keel is less marked off from the centrum, like in the specimen from Pui Islaz, but the zygosphene is thicker and the centrum is shorter. The second form, *Herensugea*, shares the following characters with the vertebra from Pui Islaz: a wide and thin zygosphene; nearly horizontal, oval and anterolaterally oriented prezygapophysial facets, and a wide and not markedly salient haemal keel. But the paradiapophyses of *Herensugea* are not as large as in PSMUBB V 407 and the prezygapophysial facets are wider and shorter. According to the same author, the small size of PSMUBB V 407

and the wide and thin zygosphene are characteristic for small Madtsoiidae.

Palaeobiogeography

The geographical contacts and faunal exchanges between Asia, North America, and Europe during Cretaceous times are still discussed (Rage 1981; Le Loeuff 1991; Russell 1993; Gardner and Averianov 1998; Nydam 2002).

The oldest reported member of the genus *Albanerpeton* is *A. arthridion* Fox and Naylor, 1982, from the uppermost Aptian–middle Albian of the Antlers Formation of Oklahoma and Texas (USA), indicating that this genus probably originated in North America (Gardner 1999b) and persisted in the New World until the Paleocene (Gardner 2002). In Europe, this genus is represented in the Neogene deposits by *A. inexpectatum* (Miocene of France, Germany and Austria) and by a new species in the Pliocene of Hungary (Venczel and Gardner 2003). For the moment, *Albanerpeton* is rare in the Late Cretaceous of Europe, being only represented in France (Duffaud 2000) and in Romania (Grigorescu et al. 1999, this paper). The story of the albanerpetontid family seems to be complex and the present paper can only indicate that the genus *Albanerpeton* came into Europe during the Late Cretaceous rather than during the Tertiary as previously thought. The question of how these genera came to Europe remains unresolved. Albanerpetontid fragments were also discovered in the Cenomanian and Coniacian deposits of Uzbekistan but they were too fragmentary to be identified at the family level (Gardner and Averianov 1998).

Up to now, *Becklesius* was only known from the Late Jurassic of England and Portugal and from the Early Cretaceous of Spain and Morocco (Richter 1994). The finding of *Becklesius* in the Late Cretaceous extends the stratigraphical range of this genus over 60 Ma but involves a major gap of occurrence between the Barremian (Early Cretaceous) and the Maastrichtian (Late Cretaceous). This occurrence of *Becklesius* might be relictual or represent a reintroduction from an other region. No similar fossils are known for the moment from other Late Cretaceous sites of Europe, e.g., Laño (Spain, Astibia et al. 1999) or Champ-Garimont (France, Sigé et al. 1997).

To explain the presence of a polyglyphanodontine taxon in Europe, the route via Asia is dismissed and a direct contact between North America and Europe is envisaged as suggested by Rage (1981) and Russell (1993). The European and American taxa are rather similar, whereas European and Mongolian taxa are very different from each other. However, Gardner and Averianov (1998) and Le Loeuff (1991) suggested that the Proto-Atlantic Ocean was uncrossable. A way via Asia would involve an influence of the North American Polyglyphanodontinae on the Mongolian fauna, but this is not the case (Sulimski 1975; Nydam 1999). Nevertheless, the absence of *Bicuspidon* or other

taxa with transversally expanded teeth in Mongolia may be also the result of a collecting bias.

Paradiscoglossus (if its presence is confirmed at Pui Islaz) was previously known only from the Maastrichtian of North America (Estes and Sanchiz 1982b). *Bicuspidon* is known from the Albian–Cenomanian boundary of North America (Nydham and Cifelli 2002). The presence of at least these two taxa in Europe suggests a North American influence on the East European amphibian and lacertilian faunas. Up to now, no specimens belonging to *Paradiscoglossus* has been discovered in Asia. A direct contact between North America and Europe could therefore also be supported for these taxa.

At the end of the Cretaceous, the Gondwanan family Madtsoiidae, crossed the Tethys Ocean and arrived in Europe (Rage 1996; Le Loeuff 1991). Previously, madtsoiids were known only from the Campanian–Maastrichtian of Laño (Spain, Astibia et al. 1999) and the Campanian of Champ-Garimont (France, Sigé et al. 1997). If the vertebra found in the Maastrichtian layers of Pui Islaz belongs to Madtsoiidae, it would represent the third occurrence of this family in Europe and the first occurrence in Eastern Europe.

Nopcsa (1914) noted that the Late Cretaceous representatives of local faunas from the Hațeg Basin included animals smaller in size than their the North American and East African relatives and suggested that this area was an island. It spread on 7500 km² and was 200 to 300 km apart from the rest of Europe (Benton 1996). Later, de Lapparent (1947) proposed the presence of a set of islands between the Hațeg Basin and the rest of Europe permitting limited faunal interchanges between these two regions (Grigorescu et al. 1985). Jianu and Boekschoten (1999), who studied the tectonics and sedimentology of this region, suggested that the Hațeg Basin was not an island but an outpost formed by a long but narrow mountain range, projecting from the south-east of Europe into the Late Cretaceous epicontinental seas. The results presented herein seem to confirm the contact between the Hațeg Basin and the rest of Europe, implying that the endemism of Hațeg Basin proposed by Nopcsa (1914) is not supported for all the amphibians and lacertilians. The studies of the other faunas (e.g., mammals and dinosaurs) discovered in the Hațeg Basin likely confirm that the Romanian faunas were in contact with the rest of Europe (Csiki and Grigorescu 2000; Pelaez-Campomanes et al. 2000; Weishampel et al. 2003). The presence of the genus *Bicuspidon* indicates that European faunas could be influenced by North American faunas.

Acknowledgements

The present paper is a part of the Ph. D. thesis of Annelise Folie, supervised by Professor Alain Herbosch (Department of Earth and Environmental Sciences, Université Libre de Bruxelles), to whom she expresses here sincere thanks. The authors are grateful to all the participants in the fieldwork of the 2000 and 2001 excavations campaign in Hațeg Basin, including Virgil Benedek, Paul Dica, Cristina Fărcaș,

Géraldine Garcia, Pascal Godefroit, Stijn Goolaerts, Paul Grovu, Emanoil Săsăran, Thierry Smith, Jimmy Van Itterbeeck, and Suzanne Watrin. At the RBINS Julien Cillis made the SEM photographs and Suzanne Watrin provided technical assistance. Jimmy Van Itterbeeck furnished the sedimentological description and the first figure of this paper. Thanks are due to Pascal Godefroit and Thierry Smith for numerous discussions and useful comments. The authors are also very grateful to Jean-Claude Rage, Randall L. Nydam, James D. Gardner, Annette Broschinski, Ralf Kosma, Thomas Martin, Marc Filip Wiechmann, Paul Sartenaer and his wife for their useful help to this article. Randall L. Nydam and James D. Gardner reviewed the manuscript and made helpful comments. This paper is a contribution to Research Project MO/36/004 financially supported by the Belgian Federal Science Policy Office.

References

- Antonescu, E., Lupu, D., and Lupu, M. 1983. Corrélation palynologique du Crétacé terminal du sud-est des monts Metaliferi et des dépressions de Hațeg et de Rusca Montana. *Annales de l'Institut de Géologie et de Géophysique* 59: 71–77.
- Astibia, H., Corral, J.C., Murelaga, X., Orue-Etxebarria, X., and Pereda-Suberbiola, X. 1999. Introduction to Laño discovery: Palaeontological and geocultural setting. *Estudios del Museo de Ciencias Naturales de Alava* 14 (1): 7–12.
- Benton, M.J. 1996. *The Penguin Historical Atlas of Dinosaurs*. 144 pp. Penguin Group, London.
- Camp, C. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History* 48: 289–481.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P., and Van Itterbeeck, J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *Comptes Rendus Palevol* 1: 173–180.
- Csiki, Z. and Grigorescu, D. 2000. Teeth of multituberculate mammals from the Late Cretaceous of Romania. *Acta Palaeontologica Polonica* 45 (1): 85–90.
- Duffaud, S. 2000. *Les faunes d'amphibiens du Crétacé à l'Oligocène inférieur en Europe: paléobiodiversité, évolution, mise en place*. Unpublished Ph.D. thesis. 221 pp. Muséum National d'Histoire Naturelle Laboratoire de Paléontologie, Paris.
- Duffaud, S. and Rage, J.C. 1999. Amphibians from the Upper Cretaceous of Laño (Basque Country, Spain). *Estudios del Museo de Ciencias Naturales de Alava* 14 (1): 111–120.
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation Eastern Wyoming. *University of California Publications in Geological Sciences* 49: 1–180.
- Estes, R. 1969. Relationships of two Cretaceous lizards (Sauria, Teiidae). *Breviora* 317: 1–8.
- Estes, R. 1981. *Encyclopedia of Paleoherpétology*. Part 2A, *Gymnophiona, Caudata*. 115 pp. Gustav Fischer Verlag, Stuttgart, New York.
- Estes, R. 1983. *Encyclopedia of Paleoherpétology*. Part 10A, *Sauria terrestria, Amphisbaenia*. 249 pp. Gustav Fischer Verlag, Stuttgart, New York.
- Estes, R. and Hoffetter, R. 1976. Les Urodèles du Miocène de la Grive-Saint-Alban (Isère, France). *Bulletin du Muséum National d'Histoire Naturelle* 3^{ième} série 398 (57): 297–343.
- Estes, R. and Sanchiz, B. 1982a. Early Cretaceous lower vertebrates from Galve (Teruel), Spain. *Journal of Vertebrate Paleontology* 2 (1): 21–39.
- Estes, R. and Sanchiz, B. 1982b. New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *Journal of Vertebrate Paleontology* 2 (1): 9–20.
- Evans, S.E., Milner, A.R., and Mussett, F. 1990. A discoglossid frog from the Middle Jurassic of England. *Palaeontology* 33 (2): 299–311.

- Fitzinger, L.I. 1826. *Neue Classification der Reptilien Nach Ihren Naturalischen Verwandtschaften*. 66 pp. J.G. Hübner Verlag, Vienna.
- Fox, R.C. and Naylor, B.G. 1982. A reconsideration of the relationships of the fossil amphibian *Albanerpeton*. *Canadian Journal of Earth Sciences* 19: 118–128.
- Gao, K. and Fox, R. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 33: 1–107.
- Gardner, J.D. 1999a. Redescription of the geologically youngest albanerpetontid (?Lissamphibia): *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, from the Miocène of France. *Annales de Paléontologie* 85(1): 57–84.
- Gardner, J.D. 1999b. The amphibian *Albanerpeton arthridion* and the Aptian–Albian biogeography of albanerpetontids. *Palaeontology* 42 (3): 529–544.
- Gardner, J.D. 1999c. New albanerpetontid amphibians from the Albian to Coniacian of Utah, USA—bridging the gap. *Journal of Vertebrate Paleontology* 19 (4): 632–638.
- Gardner, J.D. 1999d. Current research on albanerpetontid amphibians—a North American perspective. *Canadian Association of Herpetologists Bulletin* 13 (1): 12–14.
- Gardner, J.D. 2000a. Albanerpetontid amphibians from the Upper Cretaceous (Campanian and Maastrichtian) from North America. *Geodiversitas* 22 (3): 349–388.
- Gardner, J.D. 2000b. Revised taxonomy of albanerpetontid amphibians. *Acta Paleontologica Polonica* 45 (1): 55–70.
- Gardner, J.D. 2000c. Comments on the anterior region of the skull in the Albanerpetontidae (Themnospondyli; Lissamphibia). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2000: 1–14.
- Gardner, J.D. 2001. Monophyly and affinities of albanerpetontid amphibians (Themnospondyli; Lissamphibia). *Zoological Journal of the Linnean Society* 131 (3): 309–352.
- Gardner, J.D. 2002. Monophyly and intra-generic relationships of *Albanerpeton* (Lissamphibia; Albanerpetontidae). *Journal of Vertebrate Paleontology* 22 (1): 12–22.
- Gardner, J.D. and Averianov, A.O. 1998. Albanerpetontid amphibians from the Upper Cretaceous of Middle Asia. *Acta Palaeontologica Polonica* 43 (3): 453–467.
- Gardner, J.D., Evans, S.E., and Sigogneau-Russell, D. 2003. New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. *Acta Palaeontologica Polonica* 48 (2): 301–319.
- Gilmore, C.W. 1942. Osteology of *Polyglyphanodon*, an Upper Cretaceous lizards from Utah. *Proceedings of the United States National Museum* 92 (3148): 229–265.
- Gilmore, C.W. 1943. Osteology of Upper Cretaceous lizards from Utah, with a description of a new species. *Proceedings of the United States National Museum* 93(3163): 209–214.
- Gray, J. 1827. Synopsis of the genera of saurian reptiles, in which some new genera are indicated and the others reviewed by actual examination. *Philadelphia Magazine* 2: 54–58.
- Grigorescu, D. 1983. A stratigraphic taphonomic and paleoecologic approach to a “forgotten land”: the dinosaur-bearing deposits from the Hațeg Basin (Transylvania-Romania). *Acta Palaeontologica Polonica* 28 (1–2): 103–121.
- Grigorescu, D. and Anastasiu, N. 1990. Densus-Ciula and Sinpetru formations (Late Maastrichtian–?Early Paleocene). In: D. Grigorescu, E. Avram, G. Pop, M. Lupu, N. Anastasiu, and S. Radan (eds.), *International Geological Correlation Program (Project 245: Nonmarine Cretaceous Correlation; Project 262: Thetyan Cretaceous Correlation): Guide to Excursion*, 42–45. Institute of Geology and Geophysics, Bucharest.
- Grigorescu, D., Hartenberger, J.-L., Radulescu, C., Samson, P., and Sudre, J. 1985. Découverte de mammifères et de dinosaures dans le Crétacé supérieur de Pui (Roumanie). *Comptes Rendus de l'Académie des Sciences de Paris* 301 (19): 1365–1368.
- Grigorescu, D., Venczel, M., Csiki, Z., and Limerea, R. 1999. New latest Cretaceous microvertebrate fossil assemblage from the Hațeg Basin (Romania). *Geologie en Mijnbouw* 78: 301–314.
- 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.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. vol. 1, 574 pp. and vol. 2, 462 pp. Georg Reimer, Berlin.
- Hoffstetter, R. 1946. Sur les Gekkonidae fossiles. *Bulletin du Museum National d'Histoire Naturelle* 18: 195–203.
- Hoffstetter, R. 1961. Nouveaux restes d'un serpent boidé (*Madtsoia mada-gascariensis* nov. sp.) dans le Crétacé supérieur de Madagascar. *Bulletin du Muséum national d'Histoire naturelle* 33 (2): 152–160.
- Hoffstetter, R. 1967. Coup d'œil sur les sauriens (= Lacertilien) des couches de Purbeck (Jurassique Supérieur d'Angleterre). *Colloques internationaux du CNRS* 163: 349–371.
- ICZN 1999. *International Code of Zoological Nomenclature*, 4th Edition. 306 pp. International Trust for Zoological Nomenclature, c/o The Natural History Museum, London.
- Jianu, C.-M. and Boekschoten, G.J. 1999. The Hațeg—Island or outpost? In: J.W.F. Reumer and J. de Vos (eds.), *Elephants have a snorkel! Papers in honour of Paul Y. Sondaar*. *Deinsea* 7: 195–198.
- Kosma, R. 2003. *The Dentition of Recent and Fossil Scincomorph Lizards (Lacertilia, Squamata)—Systematics, Functional Morphology, Paleology*. 188 pp. Unpublished Ph. D. dissertation, Dem Fachbereich Geowissenschaften der Universität Hannover, Hannover.
- Lapparent, A.F., de 1947. Les Dinosaures du Crétacé supérieur du Midi de la France. *Mémoires de la Société Géologique de France* 56: 1–54.
- Le Loeuff, J. 1991. The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research* 1991 (12): 93–114.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.
- McGowan, G.J. 1998. The development and function of the atlanto-axial joint in albanerpetontid amphibians. *Journal of Herpetology* 32 (1): 116–122.
- McGowan, G.J. 2002. Albanerpetontid amphibians from the Early Cretaceous of Spain and Italy: a description and reconsideration of their systematics. *Zoological Journal of the Linnean Society* 135: 1–32.
- McGowan, G.J. and Evans, S.E. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. *Nature* 373: 143–145.
- Nopcsa, F. 1914. Über das Vorkommen der Dinosaurier in Siebenbürgen. *Verhandlungsband Zoologischen Botanischen Gesellschaft* 54: 12–14.
- Nydam, R.L. 1999. Polyglyphanodontinae (Squamata, Teiidae) from the medial and Late Cretaceous: new records from Utah, USA and Baja California del Norte, Mexico. In: D.D. Gillette (ed.), *Vertebrate Paleontology in Utah*, 303–317. Utah Geological Survey, Salt Lake City.
- Nydam, R.L., Gauthier, J.A., and Chiment, J.J. 2000. The mammal-like teeth of the Late Cretaceous lizard *Peneteius aquilonius* Estes 1969 (Squamata, Teiidae). *Journal of Vertebrate Paleontology* 20 (3): 628–631.
- Nydam, R.L. and Cifelli, R.L. 2002. A new teiid lizard from the Cedar Mountain Formation (Albian–Cenomanian boundary) of Utah. *Journal of Vertebrate Paleontology* 22 (2): 276–285.
- Oppel, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien als Prodom einer Naturgeschichte derselben*. 86 pp. Joseph Lindauer Verlag, München.
- Osborn, H.F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memories of the American Museum of Natural History* 1 (8): 449–508.
- Owen, R. 1842. Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science* (1841): 60–204.
- Owen, R. 1854. On some fossil reptilian and mammalian remains from the

- Purbeck. *Quaternary Journal of the Geological Society of London* 10: 420–33.
- Panaiotu, C. and Panaiotu, C. 2002. Paleomagnetic studies. In: *7th European Workshop on Vertebrate Palaeontology—Sibiu (Romania)—July 2–7, 2002*, 59. Ars Docenti, Bucharest.
- Peláez-Campomanes, López-Martínez, N., Álvarez-Sierra, A., and Daams, R. 2000. The earliest mammal of the European Paleocene: the multi-tuberculate *Hainina*. *Journal of Paleontology* 74 (4): 701–711.
- Pereda-Suberbiola, X. 1996. La contribución del Barón Nopcsa al estudio de las faunas de vertebrados continentales del cretácico final de Europa. *Gaia* 13: 43–66.
- Rafinesque, S.C. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. 224 pp. Privately printed, Palerme.
- Rage, J.-C. 1973. Présence de *Dunnophis* dans l'Eocène et l'Oligocène européens. *Compte rendu sommaire des séances de la Société Géologique de France* 3: 76–78.
- Rage, J.-C. 1981. Les continents péri-atlantiques au Crétacé supérieur: migration des faunes continentales et problèmes paléogéographiques. *Cretaceous Research* 2 (1): 65–84.
- Rage, J.-C. 1996. Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une dispersion transthéthysienne. *Comptes rendus de l'Académie des Sciences de Paris* 322 (2): 603–608.
- Rage, J.-C. and Hossini, S. 2000. Les Amphibiens du Miocène moyen de Sansas. *Mémoires du Muséum National d'Histoire Naturelle* 183: 177–217.
- Richter, A. 1994. Lacertilia aus der Unteren Kreide von Una und Galve (Spanien) und Anoual (Marokko). *Berliner geowissenschaftliche Abhandlungen E* 14: 1–147.
- Roček, Z. 1994. Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. *Geobios* 27 (6): 717–751.
- Romer, A.S. 1956. *Osteology of the Reptiles*. 772 pp. The University of Chicago Press, Chicago.
- Russell, D.A. 1993. The role of central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences* 30 (10–11): 2002–2012.
- Sanchiz, B. 1998. Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria): 2. Amphibia. *Annalen des Naturhistorischen Museums Wien* 99A: 13–29.
- Seiffert, J. 1973. Upper Jurassic lizards from central Portugal. *Serviços geológicos de Portugal* 22: 1–85.
- Sigé, B., Buscalioni, A.D., Duffaud, S., Gayet, M., Orth, B., Rage, J.-C., and Sanz, J.L. 1997. Etat des données sur le gisement Crétacé supérieur continental de Champ-Garimond (Gard, Sud de la France). *Münchner geowissenschaftliche Abhandlungen A* 34: 111–130.
- Smith, T., Codrea, V., Sasaran, E., Van Itterbeeck, J., Bultynck, P., Csiki, Z., Dica, P., Farcas, C., Folie, A., Garcia, G., and Godefroit, P. 2002. A new exceptional vertebrate site from the Late Cretaceous of the Hațeg Basin (Romania). *Studia Universitatis Babeș-Bolyai, Geologia. Special issue* 1: 321–330.
- Sulimski, A. 1975. Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. *Palaeontologia Polonica* 33: 25–102.
- Van Itterbeeck, J., Săsăran, E., Codrea, V., Săsăran, L., and Bultynck, P. 2004. Sedimentology of the upper Cretaceous mammal and dinosaur bearing sites along the Râul Mare and Barbat rivers, Hațeg Basin, Romania. *Cretaceous Research* 25 (4): 517–530.
- Venczel, M. and Gardner, J.D. 2003. The geologically youngest albanerpetontid amphibian. *Journal of Vertebrate Paleontology* 23 (Supplement to No. 3): 106A.
- Venczel, M. and Csiki, Z. 2003. New frog from the Latest Cretaceous of Hațeg Basin, Romania. *Acta Palaeontologica Polonica* 48 (4): 609–616.
- Vergaud-Grazzini, C. and Wenz, S. 1975. Les discoglossidés du Jurassique supérieur du Montsech (Province de Lerida, Espagne). *Annales de Paléontologie (Vertébrés)* 61: 19–36.
- Villalta, J.F. 1957. *Eodiscoglossus santonjae* Vill., la Rana mas antigua conocida, que ha sido encontrada en el Jurásico superior de Santa Maria de Meya (Lérida). In: B. Meléndez (ed.), *La evolución biológica*, 146. Ediciones Fax, Madrid. [Adaptation of Leonardi, P. 1950. *L'evoluzione dei viventi*. 360 pp. Morcelliana, Brescia]
- Weishampel, D.B., Jianu, C.-M., Csiki, Z., and Norman, D.B. 2003. Osteology and phylogeny of *Zalmoxes* (n.g.), an unusual Euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology* 1 (2): 65–123.
- Wiechmann, M.F. 2001. Albanerpetontids from the Randeck Maar (Lower/Middle Miocene, southern Germany). *Journal of Vertebrate Paleontology* 21 (Supplement to No. 3): 114A.