Frontoparietal Bone in Extinct Palaeobatrachidae (Anura): Its Variation and Taxonomic Value

ZBYNEK ROCEK,1* RENAUD BOISTEL,2 NICOLAS LENOIR,3 ARNAUD MAZURIER,4 STEPHANIE E. PIERCE,5 JEAN-CLAUDE RAGE,6 SERGEI V. SMIRNOV,7 ACHIM H. SCHWERMANN,8 XAVIER VALENTIN,2 MARTON VENCZEL,9 MICHAEL WUTTKE,10 AND TOMÁS ZIKMUND11

1Department of Palaeobiology, Geological Institute, Academy of Sciences of the Czech Republic, Prague, Czech Republic
2Institut International de Paléoprimatologie et de Paléontologie Humaine, UMR 7262 CNRS, Université de Poitiers, Poitiers, France
3Multiscale Group, Laboratoire Navier, UMR205-CNRS/ENPC/IFSTTAR/Université Paris-Est, Champs-sur-Marne, France
4Institut de Chimie des Milieux et Matériaux de Poitiers, UMR 7285 Université de Poitiers, UFR SFA, Poitiers, France
5Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
6Sorbonne Universités—CR2P—MNHN, CNRS-UPMC-Paris 6, Muséum National d’Histoire Naturelle, Paris, France
7Laboratory of Evolutionary Morphology, a.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia
8Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Bonn, Germany
9Târîi Crişurilor Museum, Oradea, Romania
10Department of Archaeology, General Department of Cultural Heritage Rhineland Palatinate, Section Geological History of the Earth, Mainz, Germany
11X-Ray Micro CT and Nano CT Research Group, CEITEC—Central European Institute of Technology, Brno University of Technology, Brno, Czech Republic

ABSTRACT

Palaeobatrachidae are extinct frogs from Europe closely related to the Gondwanan Pipidae, which includes Xenopus. Their frontoparietal is a distinctive skeletal element which has served as a basis for establishing the genus Albionbatrachus. Because little was known about developmental and individual variation of the frontoparietal, and its usefulness in delimiting genera and species has sometimes been doubted, we investigate its structure in Palaeobatrachus and Albionbatrachus by means of

Grant sponsor: National Geographic Society; Grant number: 8535-08; Grant sponsor: Region Île-de-France; Grant number: 75-77-78-91-93-94-95; Grant sponsor: Région Poitou-Charentes; Grant number: 16-17-79-86; Grant sponsor: European Regional Development Fund; Grant number: FEDER: 34848.

*Correspondence to: Zbyněk Roček, Department of Palaeobiology, Geological Institute, Academy of Sciences of the Czech Republic, Rozvojova 135, CZ-165 00 Prague 6, Czech Republic. Fax: +420 220 922 670. E-mail: rocek@gli.cas.cz

Received 2 February 2015; Revised 29 May 2015; Accepted 2 June 2015.

DOI 10.1002/ar.23203

Published online 1 August 2015 in Wiley Online Library (wileyonlinelibrary.com).
INTRODUCTION

The holotype of Palaeobatrachus diluvianus (Goldfuss, 1831), type species of the genus Palaeobatrachus, believed to be lost by Spinar (1972) but recently rediscovered, is a natural cast of the dorsal side of an almost complete articulated skeleton, recovered from the latest Oligocene (MP 30; Mai, 1995) of Germany (Goldfuss, 1831). As evidenced by ossified carpal elements and moderately convex epiphyses of hindlimb bones, it represents an adult, albeit a not yet fully grown individual. A remarkable feature of its frontoparietal, besides a slight constriction in the middle of its anteroposterior length, is a pair of parasagittal, arch-like, and slightly prominent ridges, which delimit laterally a more or less horizontal and flat frontoparietal table, a feature that is quite unusual in anurans (Fig. 1). Meyer (1860), who studied this fossil nearly 30 years after its discovery, was aware of the significance of this bone for taxonomy of palaeobatrachid frogs, and in order to properly understand its external morphology, he made a simple cast of its dorsal surface from bread (Meyer, 1860, p. 18-2).

Since the middle of the 19th century, a comparatively large number of articulated palaeobatrachid skeletons were recovered from various localities in central Europe, ranging from early tadpoles up to large, fully grown adults. Some of them were big and considered separate species (e.g., Palaeobatrachus gigas from the latest Oligocene of Rott in Germany, reaching a length from snout-to-tip of urostyle ~120 mm; Meyer, 1852, 1860). Most of them, however, were medium-sized, so rare large individuals were considered by later authors just extremely old adults (e.g., Spinar, 1972).

In the meantime, various disarticulated bones of palaeobatrachids were recovered, for instance, the ilia, humeri, angulars, and some others from the early Miocene of Mainz-Weisenau (Meyer, 1843). However, isolated bones are sometimes difficult to interpret taxonomically, as they may lack key species-specific features found elsewhere in the skeleton. This holds true for the frontoparietal described as Albionbattrachus wightensis from the late Eocene of England by Meszoely et al. (1984), which was vaguely diagnosed as having “a distinct, hourglass-shaped frontoparietal with a prominently sculptured dorsal surface.” However, “hourglass-shaped,” 18 mm long frontoparietals with signs of sculpture on the frontoparietal table may also be found in large individuals of Palaeobatrachus (Fig. 3—1a). This was the reason why Wuttke et al. (2012) suggested that Albionbattrachus might be congeneric with Palaeobatrachus. Moreover, Hossini and Rage (2000) found that in similar frontoparietals from the early Miocene of France, described as Palaeobatrachus robustus, the elevated frontoparietal table is connected with the compact, basal layer by means of a distinctive intermediate layer. This layer occurs also in medium to large-sized individuals of other Palaeobatrachus species, as can be inferred from the fact that their frontoparietals are often split horizontally, so that the basal layer and dorsal surface layer become associated with the part and counterpart of the specimen, respectively (Wuttke et al., 2012, Fig. 1a). Thus, it may be hypothesised that the elevated frontoparietal table, including parasagittal ridges, is added during the course of development, and that the original frontoparietal of a juvenile is preserved in the adult frontoparietal as its basal layer. This, however, involves partial resorption on the ventral side.

In order to learn how the external morphology of the frontoparietal and of its inner structure vary amongst palaeobatrachid species, we decided (1) to study the internal structure of the frontoparietals in Albionbattrachus and Palaeobatrachus of approximately the same individual size/age, and compare them with each other in order to decide whether differences among them can be assessed at generic or species levels, and (2) to infer developmental variation of external features based on...
comparisons with extant *Xenopus* to decide whether these external features may be used for determination of relative individual age. In addition, we include an examination of an isolated frontoparietal from the early Campanian of France, the earliest doubtless evidence of the Palaeobatrachidae (Buffetaut et al., 1996), which will allow us to assess the evolutionary origins of frontoparietal features in these frogs.

**MATERIALS AND METHODS**

We examined both external morphology and internal structure of the following isolated fossilized frontoparietals (all except for PW 2011/5897-LS were extracted from matrix): an indeterminate palaeobatrachid, MDE-Vil-16, from the late Cretaceous (early Campanian) of Villeveyrac, France (Buffetaut et al., 1996); *Albionbatrachus wightensis*, MCZ 8784, holotype, from the late Eocene of the Isle of Wight, England (Meszoei et al., 1984); *A. oligocenicus*, UBB V 442, holotype, from the early Oligocene of Suceag, Romania (Venczel et al., 2013); *Palaeobatrachus* sp., PW 2011/5897-LS, from the late Oligocene of Enspel, Germany; *P. robustus*, MNHN.F.LAU 7, holotype, from the earliest Miocene of Laugnac, France (Hossini and Rage, 2000); and *Palaeobatrachus* sp., MTC 23195, from the late middle Miocene of Subpiatră, Romania (Venczel, 2007). Because the closest extant relatives of extinct Palaeobatrachidae are members of the family Pipidae, developmental changes were inferred from a series of three developmental stages of recent *Xenopus laevis* (the youngest NMP 6d-24/2014/1, medium-sized DP FNSP 6331, and a 12-year-old female NMP 6d-24/2014/2; see Smirnov, 1994 for further information on this specimen), and from adults of two other species of *Xenopus*, *X. tropicalis* (DP FNSP 6542) and *X. muelleri* (DP FNSP 6541); all were represented by dry skeletons, except for NMP 6d-24/2014/1, which was a complete individual with soft body parts.

Internal structure of the frontoparietals was investigated by X-ray high resolution computed tomography (micro-CT). Five specimens (*Albionbatrachus oligocenicus*, *Palaeobatrachus* sp. from Subpiatră, three

---

11In order to support stability of zoological nomenclature, we adhered to Frost (2014), although we acknowledge that alternative concepts exist (e.g., Pyron, 2014).
developmental stages of *Xenopus laevis* were scanned with a GE phoenix v|tome|x L240 equipped with a 240 kV/300 W high-power micro focus X-ray tube (with tungsten reflection target, focal spot size up to 5 μm), in CEI-TEC (Central European Institute of Technology), Brno, Czech Republic; because of their small size, two additional specimens (*Xenopus muelleri* DP FNSP 6541 and *X. tropicalis* DP FNSP 6542) were scanned with a 180 kV/20 W nano focus X-ray tube with a tungsten target transmission, focal spot size up to 0.9 μm, and a flat-panel GE DXR detector array (2,048 × 2,048 pixels of 0.2 mm size). All but one specimen were mounted in glass tubes with the spare space packed out with cotton wool. One sample (*Xenopus laevis* NMP 6d/2014/1) was fixed in agarose gel to avoid soft tissue vibrations. The tomographic measurements were performed at the temperature of 21°C. Raw micro-CT data were reconstructed using three-dimensional (3D) computed tomography software datoslx 2.0. Images of the 3D volume rendering were made with VGStudio Max 2.2, using the volume

Fig. 2. Frontoparietals of *Albionbatrachus*. 1: *Albionbatrachus wightensis*, holotype (MCZ 8784) from the late Eocene of the Isle of Wight, England, in dorsal (1a) and ventral (1b) views; longitudinal section of the same specimen in the midline (1c), and transverse sections in the narrowest part of the bone marked as “section A” (1d), and in the widest part of the parietal portion of the bone marked as “section B” (1e). Note that the anterior part of the bone is broken away. 2: *Albionbatrachus oligocenicus*, holotype (UBB V 442) from the early Oligocene of Suceag, Romania, in dorsal (2a) and ventral (2b) aspects. Sections on the right side are at the same levels as in *A. wightensis*. Anterior is to the left in 1c and 2c. White arrows mark the position of the foramen for pineal complex; the black arrows mark the ventral orifice of the canal for pineal complex. Broken lines mark the position of the sections illustrated in 1c–e and 2c–e.
rendering algorithm with two light sources and shadows on.

 Albionbatrachus wightensis was scanned using a SkyScan 1173 in the Museum of Comparative Zoology, Harvard University. The scanner combines a sealed vacuum polychromatic X-ray source with a tungsten filament and a beryllium target, an X-ray spot of 5 μm and an 8 watt source (130 kV/300 μA). The detector has a distortion-free flat-panel sensor with a resolution of 2,240 × 2,240 pixels. The specimen was mounted by carefully sandwiching it in a small cavity between layers of styrofoam, with the styrofoam then parafilm-wrapped onto a brass mounting disc. The raw X-ray projections were reconstructed using NRecon version 1.6.6.0 and the 3D volume rendering was made with Mimics Materialise software version 17.0.

 Palaeobatrachus sp. from Enspel was scanned with GE phoenix v|tome|x L240 in the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn. The internal structure of the frontoparietal could not be scanned in higher resolution because the specimen was too large due to being scattered in surrounding matrix.

 Palaeobatrachus robustus was scanned with RX solutions UltraTom in the Laboratoire Navier, École des Ponts, Paris Institute of Technology (ParisTech), using a Hamamatsu micro spot 240 kV 220 W source, and a Varian-Paxscan 2520DX CsI detector. The frontoparietal of the oldest known Palaeobatrachidae from Villeveyrac was scanned in the Centre of Microtomography of the University of Poitiers, with RX solutions EasyTom XL Duo, using a Hamamatsu micro spot 150 kV 75 W source and a Varian-Paxscan 2520DX CsI detector. In both these samples, 3D volume rendering was performed using Avizo v.8.1 (Visualization Sciences Group, Inc.).

 See Table 1 for further information.

 To compare the scanned frontoparialets, we used the midline section and two transverse sections: section A is the narrowest diameter of the interorbital portion, and section B is the widest diameter of the parietal portion (see Fig. 2—1a, b, and elsewhere). Descriptive terminology of a generalized palaeobatrachid frontoparietal is shown in Fig. 1.

**RESULTS**

**The Frontoparietal Bone in Palaeobatrachidae**

 Micro-CT reveals that in most fossilized frontoparialets, the bone tissue is organized into a superficial, dorsal layer (either smooth or ornamented on its outer surface), and an inner, basal part, consisting of compact bone with superimposed layers of deposition, separated by a middle layer of cancellous bone. This middle layer is characterized by vascular cavities of various sizes which may be arranged in a single layer and, due to extensive process of erosion, may fuse together (Castanet et al., 2003). The cavities are surrounded by more or less distinct layers of bone matrix, and are connected with the dorsal surface of the bone by thin canals. These canals are inclined anteriorly in the anterior portion of the bone, and slightly posteriorly in the posterior portion of the bone. The canals pass through the dorsal layer of compact bone. Below we provide information on external features of the bone that might be used for taxonomic

**TABLE 1. Technical data of micro-CT scans**

<table>
<thead>
<tr>
<th>Sample System</th>
<th>Sample</th>
<th>System</th>
<th>Isotropic voxel size (μm)</th>
<th>Acceleration voltage (kVp)</th>
<th>X-ray tube current (μA)</th>
<th>Filter</th>
<th>Integration time (ms)</th>
<th>No. projections per 360°</th>
<th>Projection diameter (μm)</th>
<th>Material (mm)</th>
<th>Integration time (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albionbatrachus wightensis MCZ 8784</td>
<td>SkyScan 1173</td>
<td>9.59573</td>
<td>127</td>
<td>70</td>
<td>61</td>
<td>1 mm Al</td>
<td>500</td>
<td>1,200</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albionbatrachus oligocenicus UBB V 442</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>15</td>
<td>70</td>
<td>80</td>
<td>1 mm Cu</td>
<td>333</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeobatrachus robustus MNHN.F.LAU 7</td>
<td>RX solutions UltraTom</td>
<td>7.95</td>
<td>100</td>
<td>80</td>
<td>1 mm Cu</td>
<td>333</td>
<td>1,800</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeobatrachus sp. Subpiatr/C21 MTC 23195</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>10</td>
<td>70</td>
<td>80</td>
<td>1 mm Al</td>
<td>500</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeobatrachus sp. Enspel PW 2011/5897-LS</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>10</td>
<td>70</td>
<td>80</td>
<td>1 mm Al</td>
<td>500</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeobatrachidae indet. Villeveyrac MDE-Vil-16</td>
<td>RX solutions EasyTom XL Duo</td>
<td>12.79</td>
<td>60</td>
<td>60</td>
<td>1 mm Al</td>
<td>333</td>
<td>1,800</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeropus laevis NMP 6d-24/2014/1</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>8</td>
<td>60</td>
<td>150</td>
<td>0.5 mm Al</td>
<td>400</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeropus laevis $DPI$ FNSP 6331</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>8</td>
<td>60</td>
<td>150</td>
<td>0.5 mm Al</td>
<td>400</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeropus laevis $DPI$ FNSP 6d-24/2014/2</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>12</td>
<td>50</td>
<td>200</td>
<td>0.1 mm Al</td>
<td>700</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeropus muelleri # DPI FNSP 6541</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>5.5</td>
<td>50</td>
<td>200</td>
<td>0.1 mm Al</td>
<td>700</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xeropus tropicalis DP FNSP 6542</td>
<td>GE phoenix v</td>
<td>tome</td>
<td>x L240</td>
<td>5</td>
<td>50</td>
<td>200</td>
<td>0.1 mm Al</td>
<td>700</td>
<td>1,800</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1852 ROČEK ET AL.
diagnoses, as well as microanatomical details in which the specimens differ from this general pattern.

*Albionbatrachus wightensis* Meszoely, Spinar et Ford, 1984. The frontoparietal is incomplete anteriorly; its longest anteroposterior length is 18.8 mm and it can be estimated that it was smaller than the frontoparietal of *A. oligocenicus* (Fig. 2—1). It seems to be as broad anteriorly as posteriorly, and slightly constricted in the interorbital part. The original width of its anterior portion could have exceeded the width of the parietal portion, as is the case with *A. oligocenicus*. The frontoparietal table is flat, markedly prominent from the dorsal surface of the bone (Fig. 2—1d and e), and ornamented by a pit-and-ridge sculpture, which is less pronounced anteriorly. It seems that the table was slightly depressed anterior to the pineal foramen (Fig. 2—1c). The lateral surfaces of the bone are smooth. Posterolaterally, the table extends onto prominent, slender paroccipital processes, which extend beyond the level of the posterior margin of the bone in the midline. The frontoparietal incrassation (smooth part of the ventral surface, which might indicate that the latter individual is older. The middle, cancellous portion of the bone consists of large cavities arranged in a single layer, interconnected anteroposteriorly (Fig. 2—2c–e), reaching the posterior periphery of the bone. In contrast, the layer of cancellous bone does not reach the anterior, flat part of the bone; here, the layer is substituted by a system of anteroposteriorly oriented thin canals in the compact bone which open on the ventral surface, between the frontoparietal and sphenethmoid.

*Palaeobatrachus* sp., *Enspel*. The length of the frontoparietal is 25.3 mm (Fig. 3—1), which is similar to that of *Albionbatrachus oligocenicus*. Judging by the length of the frontoparietals in some individuals from the late Oligocene of Bechlejovice (e.g., 17.5 mm in NMP Pv 10025, which corresponds to SVL of 63.5 mm), this was a large individual. But a still larger individual was recovered from Enspel (PW 1999/5007-LS) in which the frontoparietal probably attained ~30 mm; however, the bone was not preserved. The taxonomic status of *Palaeobatrachus* from Enspel is not yet clarified, but a remarkable feature of its frontoparietal is that it is unusually thin and flat. It is complete, thus it may be used as a tool for inferring information on fragmentary specimens. Its most distinctive feature is that the most prominent structures on its dorsal surface are the parasagittal ridges, whereas the area between them (the frontoparietal table) is seemingly depressed; but, in fact, it sits at a level equivalent to other parts of the dorsal surface of the bone. Posteriorly, the parasagittal ridges reach the paroccipital processes, which are only slightly prominent on the posterolateral margins of the bone. Thus, they do not extend beyond the level of the posterior median process. Both parasagittal ridges are interconnected posteriorly by a similar, but less pronounced, transverse ridge, from which another ridge runs down posteroventrally towards the posterior median process. Another peculiar feature of this frontoparietal is that there is another pair of ridges parallel to the orbital margins (termed parorbital ridges in Fig. 1); they, however, reach neither the anterior nor posterior parts of the bone. On the ventral surface, the frontoparietal incrassation is well delimited posteriorly, but covered by irregular grooves. These may be artifacts, as can be inferred from the fact that they extend onto the posterior, striated contact area with the otic capsules. The internal structure of the bone can only be inferred from blurry transmission images. Although there are small and large cavities or canals in the bone, they seem to be arranged in a single layer only in the anterior and posterior parts of the bone (Fig. 3—1c), and much of the bone seems to be compact. A single foramen for the pineal complex and the canal (including its ventral opening) are present.

*Palaeobatrachus* sp., *Subpiatrà*. As the anterior part of the bone is broken off, its length cannot be reconstructed (Fig. 3—2). The distance between the most anterior tip of the fragment and the tip of the posterior median process is 17.8 mm. The most remarkable
Fig. 3. Frontoparietals of *Palaeobatrachus*. 1: *Palaeobatrachus* sp. (PW 2011/S897-LS) from the late Oligocene of Enspel, Germany. The internal structure of the transverse sections could not be scanned in higher resolution because the specimen was too large due to being embedded in surrounding rock matrix. 2: *Palaeobatrachus* sp. (MTC 23195) from the middle Miocene of Subpiatra, Romania. 3: *Palaeobatrachus robustus*, holotype (MNHN.F.LAU 7) from the early Miocene (Aquitanian) of Laugnac, France. Longitudinal sections (1c, 2c, 3c) are oriented with their anterior ends to the left. White arrow marks the position of the pineal complex foramen, black arrow marks the ventral orifice of the canal for pineal complex (note that the canal does not run strictly in a vertical, anteroposteriorly oriented plane, so it cannot be observed completely in one section). Cross-sections are at the same levels as in Fig. 2. The frontoparietal in 3a, b is reversed horizontally if compared with the original publication by Hossini and Rage (2000, Fig. 1; 1).
feature is that both parasagittal ridges take their origin on the anterior flat part of the bone, not on its orbital margin. Both ridges are prominent as in *Palaeobatrachus* from Ens pel, thus in the interorbital part, they delimit a longitudinal depression. Anteriorly, there is another V-shaped depression containing the foramen for the pineal complex (seen in longitudinal section; Fig. 3—2c). Posteriorly, the divergent parasagittal ridges are declined laterally and produce an obtuse process on either side. This posterior part of the frontoparietal table is horizontal, smooth and flat, and its posterior, transverse ridge is straight. As in *Palaeobatrachus* from Ens pel, there is a median ridge running down onto the posterior median process, but it is steeper. Both paroccipital processes do not extend beyond the level of this median process. The frontoparietal incrcassation is similar to that in *Albionbtrachus oligocenicus*, except for the fact that its middle and posterior surface is robustly sculptured. The contact surfaces for the sphenethmoid and otic capsules are also similar, but the striation is less pronounced. The lanceolate area extending onto the ventral surface of the posterior median process is similar to that in *Albionbtrachus*. The inner structure of the bone is characterized by compact bone along the dorsal and ventral margins that is dominated by numerous growth lines; the middle layer of cancellous bone is represented only by small cavities aggregated horizontally along a dark, less dense dividing layer, which anteriorly forms a clear horizontal split in the bone (Fig. 3—2d). There are no canals which would connect the middle, cancellous portion of the bone with its dorsal surface. The canal for the pineal complex opens in the posterior part of the V-shaped depression on the anterior part of the dorsal surface of the bone; then it runs posterolaterally and appears on the ventral surface of the frontoparietal incassation (Fig. 3—2b). It displays no sign of obliteration.

*Palaeobatrachus robustus* Hossini et Rage, 2000. Judging from the available fragment (about 14 mm anteroposteriorly) (Fig. 3—3), the total length of the bone could have been about 25 mm. The frontoparietal table is flat, sharply limited and unsculptured, with only a few pores on its surface. It does not extend posterolaterally onto the paroccipital processes, and the paroccipital processes do not extend beyond the level of the posterior median process, similar to other *Palaeoba-

**Palaeobatrachidae indet., Villeveyrac.** The length of the fragment moderately exceeds 11 mm (Fig. 4). Taking into account that a substantial portion of the anterior margin, and also part of posterior margin, are broken away, the total length of this frontoparietal may be estimated to 20–25 mm, which corresponds to large representatives of this family. This is rather surprising, because Mesozoic anurans are on average smaller than Cenozoic anurans. The dorsal surface of the frontoparietal table is horizontal and flat, well delimited laterally and covered with irregular pitted sculpture. The inner structure of the bone is difficult to compare with the other specimens because of the lower resolution of the scan, but there are thin dark, perhaps less dense layers running parallel to the ventral surface of the bone (Fig. 4—1c, d, e); the superficial layer of the frontoparietal table is dark and clearly distinguishable from the lighter and deeper portion of compact bone (Fig. 4—1c, e), and cavities occur mainly in the deep marginal parts of the frontoparietal table (Fig. 4—1e). Therefore, it appears that the middle, cancellous layer is restricted to the lateral parts of the bone.

**Development of the Frontoparietal in Postmetamorphic Xenopus laevis**

The frontoparietal of the youngest studied individual (SVL 41.5 mm) is 9.4 mm long (Fig. 5—3a). The bone, similar to other dermal bones of the skull, is
Fig. 5. Developmental changes in the external morphology and inner structure of the frontoparietal bone in Xenopus laevis (Pipidae). 1a: Hyperossified, extremely old (min. 12 years) adult (NMP 6d-24/2014/2, $\triangleright$), in dorsal view. Note complete fusion with the otic capsules. Parapi-neal and pineal foramina marked by arrows. Section A is at the level of the posterior pineal foramen, section B at the level of ventral orifice of the posterior pineal canal. Section C in the widest area of the parietal portion of the bone, inferred from transverse serial sections (cf. 1e). 1b: Longitudinal section of the same specimen along the midline. Black arrow marks the ventral orifice of the posterior pineal canal. 1c–e: Transverse sections A–C, as indicated in 1a. Note the laminar structure of the bone. 2a: Adult individual (DP FNSP 6331) in dorsal view. Parapineal and pineal foramina are marked by arrows. Section A is at the level of the anterior parapineal foramen, section B at the level of the ventral orifice of the posterior pineal canal, section C in the middle of the parietal portion. 2b: Longitudinal section of the same specimen along the midline. White arrows point to the parapineal and pineal foramen; black arrows point to the ventral orifice of parapineal and pineal canals. 2c–e: Transverse sections A–C, as indicated in 2a. 3a: Juvenile, 1–2 years old individual (NMP 6d-24/2014/1; SVL 41.5 mm) in dorsal view. Sections at the same levels as in 1a and 2a. 3b: Longitudinal section of the same specimen along the midline. White arrows mark the parapineal and pineal foramina; black arrows mark the ventral orifices of the parapineal and pineal canals. 3c–e: Transverse sections A–C, as indicated in Fig. 3a. Longitudinal sections (1b, 2b, 3b) are oriented with their anterior ends to the left.
The median keel is well developed, especially in its posterior stage. The frontoparietal is 13.5 mm long, but its proportions of the bone are similar to those in medium-sized individuals, and the same holds for the posterior part of the bone. Anteriorly, however, the bone becomes wider than posteriorly, and the keel becomes wider, which is reminiscent of the frontoparietal table (this process already started in previous stages; see Fig. 5—2a), with the dorsal surface slightly convex and smooth. The lateral walls of the keel are shallower towards the anterior and disappear well before reaching the anterior margin of the bone. Both the anterior parapineal foramen and posterior pineal foramen are completely obliterated, as are the associated canals, and can be recognized only as shallow depressions (marked by arrows in Fig. 5—1a); ventral opening of the vestigial parapineal canal may be recognized on longitudinal and transverse sections (Fig. 5—1b, d). The most remarkable features of the inner structure of the bone are, besides absence of a layer of cancellous bone, growth lines that anteriorly and posteriorly continue onto the ventral portion of the bone. Judging by layers that terminate on the suture between the frontoparietal and nasal, it joins the orbital margin. It cannot be ascertained whether the canal opens on the ventral surface of the bone, because the frontoparietal is coalesced to the sphenethmoid. The posterior pineal foramen is obliterated and obscured by sculpture, but its original position may be inferred by a slight swelling of the keel. The frontoparietal is fused with the braincase and also the sutures with both otic capsules are almost completely obliterated.

In the adult, 12-year-old female (NMP 6d-24/2014/2, Fig. 5—1), the frontoparietal is about 14.5 mm long. It is well delimited anteriorly, but completely fused with the otic capsules posteriorly; its posterior outlines may be inferred only from external morphology of the occipital region of the skull (Fig. 5—1a). The shape and general proportions of the bone are similar to those in medium-sized individuals, and the same holds for the posterior part of the bone. Anteriorly, however, the bone becomes wider than posteriorly, and the keel becomes wider, which is reminiscent of the frontoparietal table (this process already started in previous stages; see Fig. 5—2a), with the dorsal surface slightly convex and smooth. The lateral walls of the keel are shallower towards the anterior and disappear well before reaching the anterior margin of the bone. Both the anterior parapineal foramen and posterior pineal foramen are completely obliterated, as are the associated canals, and can be recognized only as shallow depressions (marked by arrows in Fig. 5—1a); ventral opening of the vestigial parapineal canal may be recognized on longitudinal and transverse sections (Fig. 5—1b, d). The most remarkable features of the inner structure of the bone are, besides absence of a layer of cancellous bone, growth lines that anteriorly and posteriorly continue onto the ventral portion of the bone. Judging by layers that terminate on the suture between the frontoparietal and nasal, it joins the orbital margin. It cannot be ascertained whether the canal opens on the ventral surface of the bone, because the frontoparietal is coalesced to the sphenethmoid. The posterior pineal foramen is obliterated and obscured by sculpture, but its original position may be inferred by a slight swelling of the keel. The frontoparietal is fused with the braincase and also the sutures with both otic capsules are almost completely obliterated.

Variation of the Frontoparietal Within the Genus Xenopus

Besides the developmental stages of the frontoparietal in Xenopus laevis described above, interspecific variation was also studied on two additional individuals from two Xenopus species: X. muelleri and X. tropicalis.
**Xenopus muelleri** (Peters, 1844). Our individual (Fig. 6—1) is a juvenile, medium-sized male, as can be judged by the only partly calcified epiphyses of the long bones and the cartilaginous tectum synoticum. Fully grown males can reach a SVL of 50 mm (Harper et al., 2010). The frontoparietal is completely separated from all surrounding bones; its length is 8.8 mm. In dorsal aspect (Fig. 6—1a), the bone is of about the same width anteriorly (at the level where the frontoparietal-nasal suture joins the orbital margin) as posteriorly (at the level where the frontoparietal-prootic suture joins the orbital margin). The anterior margin of the bone projects in a broad, widely rounded median process, which inserts between the posteromedia! margins of the coalesced nasals. The parietal portion of the bone is rounded, without paroccipital processes. The anterior portion of the dorsal surface of the bone is almost smooth and moderately convex transversely, but a low, poorly developed table may be recognized on the posterior two thirds of the bone; the posterior margin of the table is widely rounded and parallel with the margin of the bone. In the posterior half of the interorbital portion of the bone, the lateral surface of the bone is deep and almost vertical. There is only one (anterior parapineal)
foramen piercing the dorsal surface of the bone, and the canal is only moderately inclined posteriorly. A short, vestigial posterior (pineal) canal that joins the anterior parapineal canal close to its ventral opening can be traced on transverse sections (Fig. 6—1c, d). A thin, not too dense layer of small cavities can be recognized in the anterior third of the bone, extending up to its most lateral margin (Fig. 6—1c, d).

**Xenopus tropicalis** (Gray, 1864). Although this individual (female) is of similar size as our representative of *X. muelleri* (length of the frontoparietal is 7.9 mm; Fig. 6—2a), it seems that it is a fully grown adult. This can be inferred from the ossified epiphyses of the long bones and fusion of some cranial bones with one another (e.g., frontoparietal with sphenethmoid, Figs. 6—2b, d; frontoparietal with prootics and opisthotics, Fig. 6—2e); in contrast, some other bones, such as the nasals, remain separated (they are fused together in other species of *Xenopus*; e.g., *X. laevis*). The frontoparietal is short and broad (as in *X. muelleri*, its anterior part is of the same width as the posterior part), constricted in the middle of the orbital margin. Its anterior margin projects in a pointed median process and inserts between both nasals, whereas each nasal inserts posteriorly in a distinct concavity on the lateral part of its anterior margin. The posterior part of the frontoparietal tapers towards its most posterior end in the midline, which is rounded. On the posteralateral margins of the bone, close to its posterior end, there are signs of short and pointed paroccipital processes. The bone is firmly coalesced to the tectum synoticum (Fig. 6—2b). The frontoparietal table is narrow, delimited laterally by comparatively sharp but low parasagittal ridges. The table is the narrowest in the parietal portion of the bone, and reaches almost to its posterior end. The parapineal foramen, which is homologous with the single, anterior foramen in *Xenopus laevis*, is located rather posteriorly, in the interorbital section, where the bone is constricted. The parapineal canal runs posteroventrally, and in the ventral part of the bone turns anteroventrally (Fig. 6—2b). There is no trace of a posterior pineal canal. The bone is compact, with only minute, irregularly distributed cavities, however, in the posterior half of the bone (posteriorly to the single, parapineal canal) it is divided by a sharp, whitish line into a dorsal, lighter layer and a ventral, darker layer (Fig. 6—2d, e), very much like in the young *Xenopus laevis* (Fig. 5—3b, e); the whitish line represents a dense layer of laminar bone. Close to its posterior end the bone is split along the whitish line; this, however, might be an artifact.

**DISCUSSION**

Founding a new taxon on a single, disarticulated bone comes with several obvious risks that act in combination. *Albionbatrachus wightensis*, as a new species of a new genus, was defined on a single, isolated, anteriorly incomplete, three-dimensionally preserved frontoparietal from the late Eocene of England, and diagnosed by an hourglass shape and prominently sculptured dorsal surface, with prominent spurlike paroccipital processes (Meszoly et al., 1984). Based on shared characters (see Wuttke et al., 2012, Table 1), there were no doubts about assigning this frontoparietal to the Palaeobatrachidae. However, most palaeobatrachid species recognized at that time were based on articulated skeletons, often preserved as imprints in matrix, and in many cases with imperfectly preserved frontoparietals. This set bounds to thorough comparisons of disarticulated and articulated skeletal material. Nevertheless, similar (although not identical) hourglass-shaped frontoparietals were found also in large individuals of some Palaeobatrachus species, and the question arose whether *Albionbatrachus* perhaps represents a fully grown stage of *Palaeobatrachus*. Thus, besides difficulties caused by comparisons of articulated and disarticulated fossil material, there are also problems caused by developmental (i.e., age-dependent) or individual variation.

Problems with developmental variation in fossil frogs may be partly eliminated by examination of individuals in terminal stages of development. The easiest way to determine relative age in frogs is to assess the degree of skeletal ossification, especially the degree of epiphyseal ossification of the long bones (e.g., of the femur and tibiofibula). In young individuals, the epiphyses are cartilaginous, thus absent in fossils, whereas they become fully ossified or at least calcified (thus preserved) in adults. However, this simple criterion can only be applied to articulated skeletons, not single, disarticulated frontoparietals.

To characterize developmental stage of the frontoparietal in extinct Palaeobatrachidae, we examined developmental changes of the frontoparietal in the modern pipid frog *Xenopus*, as pipids are generally considered to be most closely related to Palaeobatrachidae (e.g., Goldfuss, 1831; Estes and Reig, 1973; Dong et al., 2013: Fig. 8). We recognize that our study only sampled three growth stages in *Xenopus* and that broad inferences based on this sample size should be taken with caution; however, our results can be used as a first approximation for understanding the influence of development when interpreting palaeobatrachids. Taking this into account, we found that the following features may be characteristic of postmetamorphic development in *Xenopus laevis* (see also Table 2): (1) outlines of the bone, including the posterior median process which is always the most posterior part of the bone, maintain constant shape; (2) in contrast, proportions of the bone change, as evidenced by the fact that in younger individuals it is broader in the posterior part, whereas in older individuals it becomes wider anteriorly and elongated; (3) a single median keel, typical for medium-sized and older individuals, arises from two indistinct parasagittal ridges that laterally delimit the low frontoparietal table of young individuals (Figs. 5—3); (4) the keel of older individuals becomes posteriorly bifurcated and anteriorly spreads in a broad, elevated triangular field which ultimately disappears on the smooth anterior part of the bone; (5) there are two canals (the anterior parapineal canal and the posterior pineal canal) in the midline of the anterior portion of the bone which fuse with one another ventrally in medium-sized individuals. The ventral opening of the anterior parapineal canal is always located in the narrowest portion of the bone (disregarding its relative proportions).

In older individuals, the anterior parapineal and posterior pineal canals become obliterated, first the posterior and later the anterior. The latter canal, however, can be traced even in the oldest individuals, but can be detected only on micro-CT serial sections.
Thus it seems that the frontoparietal of *Xenopus laevis* undergoes significant changes during development (Table 2). For instance, the frontoparietales of young individuals strongly differ from those of fully grown adults by external morphology (they are smooth in young individuals, whereas they have a keel in fully grown individuals). In contrast, general outlines of the bone seem to be stable through the course of development, which may be illustrated by the fact that the posterior median process always represents the most posterior part of the bone, and the paroccipital processes do not extend beyond this level. Similarly, the most anterior extent of the bone is in the midline (thus the anterior margin of the bone is always convex), no matter whether the nasals are separated or fused.

This is paralleled by changes in the inner structure of the bone (Table 2). In young individuals, the bone is compact, devoid of any cavities, except for the two canals of the pineal complex. The bone is thin, divided horizontally by a single whitish line, better pronounced posteriorly than anteriorly (Fig. 5—3b-e). This can be explained by the fact that in early development, the frontoparietales first coalesce together by their parietal portions, and later in their frontal portions (Trueb and Hanken, 1992).

<table>
<thead>
<tr>
<th>Phylogenetically diagnostic traits</th>
<th>Developmentally dependent traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Frontoparietal of adult thin and flat, or thick and domed (Palaeobatrachidae)</td>
<td>Frontoparietal thin, smooth and flat in juvenile, thick and domed in adult (<em>Xenopus</em>, probably Palaeobatrachidae; Wuttke et al., 2012)</td>
</tr>
<tr>
<td>2. Anterior part of frontoparietal broader, narrower, or same as posterior part in adult (Palaeobatrachidae)</td>
<td>Anterior part of frontoparietal narrower in juvenile, broader than posterior part in adult (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>3. Parasagittal ridges originate on dorsal surface of bone (some <em>Xenopus</em>, some Palaeobatrachidae), or on its orbital margin (some Palaeobatrachidae)</td>
<td>Parasagittal ridges indistinct in juvenile, low or prominent in adult (<em>Xenopus</em>, probably Palaeobatrachidae)</td>
</tr>
<tr>
<td>4. Dorsal surface of frontoparietal table flat or concave (Palaeobatrachidae)</td>
<td>Median keel on dorsal surface indistinct in juvenile, prominent in adult (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>5. Median keel on dorsal surface in adult present (some <em>Xenopus</em>) or absent (Palaeobatrachidae)</td>
<td>Median keel on dorsal surface becomes wider anteriorly, similar to frontoparietal table, in adult (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>6. Frontoparietal table flat and ornamented (<em>Albionbatrachus</em>) or depressed along midline and smooth (Palaeobatrachus)</td>
<td>Frontoparietal compact, devoid of any cavities in juvenile, but with dark, less dense line delimiting superficial, compact layer of bone both ventrally and dorsally in medium-sized individuals (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>7. Paroccipital processes extend (<em>Albionbatrachus</em>), or do not extend (Palaeobatrachus, <em>Xenopus</em>), beyond level of posterior median process</td>
<td>Dividing layer of cancellous bone with larger cavities in medium-sized individuals, the cavities are absent in fully grown adults (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>8. Paroccipital processes may be present or absent in adult (<em>Xenopus</em>)</td>
<td>Dorsal part of bone displays successive superimposed growth layers which terminate on ventral surface of bone anteriorly and posteriorly; this may suggest that the bone is resorbed on ventral side (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>9. Frontoparietal table posteriorly delimited, or not delimited, by transverse ridge (Palaeobatrachidae)</td>
<td>Superficial layers below the keel are thick, and deeper layers more regular, suggesting appositional growth on surface (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>10. Parietal portion of frontoparietal table extended laterally, or not extended, in an obtuse process on each side (Palaeobatrachidae)</td>
<td>Canal for pineal complex open or obliterated to various degree (correlated with foramen for pineal complex) (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>11. Parorbital ridges present, or absent (Palaeobatrachidae)</td>
<td>Canal for pineal nerve open or obliterated to various degree (correlated with parapineal foramen) (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>12. Frontoparietal incassation divided, or not divided, into frontal portion and parietal portion (Palaeobatrachidae)</td>
<td>Canal for pineal tract open or obliterated to various degree (correlated with pineal foramen) (<em>Xenopus</em>)</td>
</tr>
<tr>
<td>13. Frontoparietal incassation extends posteriorly as smooth, lanceolate area, or the area is absent (Palaeobatrachidae)</td>
<td></td>
</tr>
<tr>
<td>14. Middle layer of bone consists of large cavities (<em>Albionbatrachus</em>), or is represented by thinner layer of greater density (i.e., with small cavities aggregated horizontally) (Palaeobatrachus)</td>
<td></td>
</tr>
<tr>
<td>15. Middle layer of large cavities is connected with dorsal surface of frontoparietal table by a system of anterously inclined canals (<em>Albionbatrachus</em>), or the thin layer of greater density is not connected with the dorsal surface by canals (Palaeobatrachus)</td>
<td></td>
</tr>
<tr>
<td>16. Foramen and canal for pineal complex present* or obliterated (Palaeobatrachidae)</td>
<td></td>
</tr>
</tbody>
</table>

*Note that in pedomorphic taxa (those with abbreviated somatogenesis), features of earlier developmental stages (i.e., juvenile characters) of an ancestral form may become a property of an adult.*
i.e., the whole complex is more “advanced” posteriorly than anteriorly. In medium-sized individuals a dark line of presumably less dense cancellous bone may be recognized which delimits a superficial, compact layer of the bone both ventrally and dorsally (Fig. 5—2e, d). As evidenced on the lateral margin of the bone (Fig. 5—2e), this superficial layer passes without interruption onto its ventral surface, and the bone still maintains its original, juvenile outlines, although it becomes bigger. In old, fully grown individuals (Fig. 5—1b-e), the dorsal part of the bone displays many successive superimposed growth layers, but it seems that these layers terminate anteriorly and posteriorly on the ventral surface of the bone (Fig. 5—1b), which may be explained by resorption of the bone on its ventral side. Moreover, the superficial layers below the keel (Fig. 5—1e) are thick and convex, whereas deeper layers are more regular. This all suggests that the bone of adults is a result of appositional growth on its surface, combined with partial resorption on its ventral surface.

A remarkable feature of the frontoparietal of medium-sized individuals is that in its anterior part, there are larger cavities arranged in a single layer dividing the bone into dorsal and ventral parts (Fig. 5—2c, d), whereas such cavities are absent in the fully grown adult, and there are only irregularly placed small cavities and thin canals (Fig. 5—1c, d). The layer of cancellous bone can thus be interpreted as a temporary phenomenon.

An attempt was made to assess the results of our observations of the development of the frontoparietal of Xenopus laevis in the context of two other species of Xenopus, which externally correspond to young stages in X. laevis, but at least one of them (X. tropicalis; Fig. 6—2) was a fully grown adult. The typical adult size of Xenopus laevis is 45–97 mm in males and 57–147 mm in females (Trueb, 2003), whereas SVL of X. muelleri males is max. 50 mm and females max. 90 mm (Harper et al., 2010), and that of X. tropicalis males is 32–39 mm and females 48–55 mm (Fischberg et al., 1982); thus, both latter species are smaller. A remarkable fact in X. tropicalis was that although its advanced developmental stage was evidenced by almost fully ossified ephyses of the long bones and the frontoparietal coossified with the sphenethmoid, prootics, and opisthotics (Fig. 6—2b, c, e), the frontoparietal was compact and divided by a whitish layer of comparatively large cavities, which are connected from the compact dorsal portion by a horizontal layer of comparatively large cavities, which are connected with the dorsal surface of the frontoparietal table by thin, anteriorly inclined canals. Data on Palaeobatrachus are known only from the specimen from Subpiatra (the taxonomic status of P. robustus is somewhat equivocal; see below) in which the bone is compact and laminar, with only small cavities arranged in a horizontal layer (Fig. 3—2c, d). However, some larger specimens from the late Oligocene locality Bechlejovic, Czech Republic (e.g., DP FNSP Pb 962 and 963; Wuttke et al., 2012), which are split into the dorsal part and ventral counterpart along the horizontal layer of trabecular bone, suggest that such a layer of cancellous bone is present also in Palaeobatrachus. Nevertheless, as can be inferred from the development of the frontoparietal in Xenopus, the horizontal layer of cancellous bone could be a temporary result of formation and remodelling of the bone.

The general pattern of the frontoparietal bone of the Palaeobatrachidae, consisting of dorsal and ventral layers of compact bone separated by a middle layer of cancellous bone, corresponds to a basic structural scheme of dermal bones of early amphibians (Bystrow, 1935; Castanet et al., 2003). It is generally agreed that the cancellous layer is a sign of extensive vascularization, and the thin canals connecting cavities of the trabecular bone with the dorsal surface of the bone and opening within the pits and furrows of the sculpture contained blood vessels that continued onto the bone surface (Vickaryous and Sire, 2009; Witzmann et al., 2010). It has been hypothesized that this system in the bone of early terrestrial tetrapods might have served to relieve excess carbon dioxide from the blood (Janis et al., 2012). If this is correct, Albionbatrachus, with a well developed cancellous layer and sculptured dorsal surface of the frontoparietal, would be more terrestrial than Palaeobatrachus, which not only has a less vascularized frontoparietal with an unsculptured dorsal surface, but also long fingers, indicating a permanent water dweller. Palaeobatrachus robustus from the early Miocene of Laugnac, France (Fig. 3—3), with its frontoparietal morphologically intermediate between Albionbatrachus and Palaeobatrachus, may be interpreted as belonging to Palaeobatrachus (short paroccipital processes not exceeding the posterior median process),
but adapted to a more terrestrial way of life (indicated by the cancellous layer similar to that in *Albionbatrachus*).

The Campanian palaeobatrachid from Villeveyrac is rather confusing. It seems that its frontoparietal consists of a ventral layer of compact bone with a few dark lines parallel with the surface, and a darker dorsal layer extending over the surface of the frontoparietal table (Fig. 4—1d, e). The middle portion, extending to the lateral margins of the bone, contains randomly distributed cavities of different size in the parietal part of the bone (Fig. 4—1e), but lacks any cavities more anteriorly (Fig. 4—1d). There is no sign of horizontal stratification similar to *Albionbatrachus* and *Palaeobatrachus*.

**CONCLUSIONS**

1. In *Albionbatrachus wightensis* and *A. oligocenicus*, the inner structure of the frontoparietal shows a dorsal, superficial layer of compact bone ornamented on its external surface, and a compact, basal layer. Both are separated by a middle layer of cancellous bone, with a system of cavities connected with the dorsal surface of the bone by narrow canals which open in pits and furrows of the dorsal surface.

2. In *Palaeobatrachus* sp. from Subpiatrâ, the superficial and basal layers are similar, but the middle layer is represented by a thin layer of bone which contains only small cavities. This seems to be a vestigial layer of cancellous bone.

3. Both superficial and basal layers of compact bone in *Albionbatrachus* and *Palaeobatrachus* show evidence of successive superimposed cycles of deposition.

4. In *Xenopus*, a pipid and thus among the closest extant relatives of Palaeobatrachidae, the frontoparietal undergoes significant changes during development in that it is smooth in young individuals, whereas it has a keel or table in fully grown individuals; in contrast, the general outline of the bone in dorsal or ventral view is stable. Besides, the whitish layer of dense laminar bone which separates the dorsal and ventral compact portions in young individuals is progressively destroyed by external resorption and replaced by cancellous bone in later stages.

5. Although the majority of *Palaeobatrachus* species are based on articulated skeletons in which the frontoparietales are not three-dimensionally preserved, whereas both *Albionbatrachus* species are based on threedimensionally preserved, but isolated frontoparietals, external features of the bone and its internal structure suggest that the distinction between the genera seems to be justified. However, the problem of phylogenetic relationships within the *Palaeobatrachus* (excluding *P. robustus*)—*Albionbatrachus* assemblage cannot be solved in this study, because the inner structure of the frontoparietal alone does not provide enough information.

6. The frontoparietal of *Palaeobatrachus robustus* is intermediate between *Albionbatrachus* and *Palaeobatrachus*. Whereas the external morphology is similar to *Palaeobatrachus*, the internal structure of the bone is more reminiscent of *Albionbatrachus*.

7. The internal structure of the palaeobatrachid frontoparietal from the Campanian of Villeveyrac is rather different, as it is not clearly discernible in three continuous layers.

8. If the system of dorsally extending cavities within the cancellous layer of the bone served to relieve excess carbon dioxide from the blood, as has been hypothesized for early tetrapods, then *Albionbatrachus* was better adapted for terrestrial life than *Palaeobatrachus*, which was a permanent water dweller. In accordance with this, *Palaeobatrachus robustus* would be a palaeobatrachid with a higher degree of adaptation to dry land than most other species of *Palaeobatrachus*.

**ACKNOWLEDGEMENTS**

This research was made possible through the support from Jozef Kaiser, head of the CEITEC's X-ray μCT research group. The authors also thank the team of CeMIM (USM 0504, Departement RDDM, MNHN) for access to their 3D workstation. Thanks are due to Jacques Castanet, formerly Laboratoire d’Anatomie Comparée, Université Paris 7, for his comments on histological development of the frontoparietal in *Xenopus laevis*, Jiri Moravec, National Museum Prague, for the loan of specimen NMP 6d/24/2014/1, and to David Marjanovic and an anonymous reviewer for their critical comments. Figure 1 is by Tomáš Prikryl.

**LITERATURE CITED**


