

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

ZBYNĚK ROČEK,^{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 MÁRTON VENCZEL,⁹ MICHAEL WUTTKE,¹⁰ AND TOMÁŠ ZIKMUND¹¹

¹Department of Palaeobiology, Geological Institute, Academy of Sciences of the Czech Republic, Prague, Czech Republic

²Institut International de Paléoprimateologie et de Paléontologie Humaine, UMR 7262 CNRS, Université de Poitiers, Poitiers, France

³Multiscale Group, Laboratoire Navier, UMR8205-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

⁹Țării Crișurilor 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

Abbreviations used: DP FNNSP = Department of Paleontology, Faculty of Natural Sciences, Prague; MCZ = Museum of Comparative Zoology, Harvard University; MDE = Musée des Dinosauriens in Espérazza (Aude); MNHN = Muséum national d'Histoire naturelle Paris; MTC = Țării Crișurilor Museum, Oradea; NMP = National Museum Prague; PW-LS = Landessammlung für Naturkunde/Naturhistorisches Museum Mainz, currently deposited in the Section Geological History of the Earth, Department of Archaeology, General Department of the Cultural Heritage of the Rhineland-Palatinate, Mainz; SVL = snout-vent length, measured from the symphysis of praemaxillae to the tip of urostyle; UBB = Babeş-Bolyai University, Cluj-Napoca.

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

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X-ray high resolution computer tomography (micro-CT). To infer the scope of variation present in the fossil specimens, we also examined developmental and interspecific variation in extant *Xenopus*. In adults of extinct taxa, the internal structure of the frontoparietal bone consists of a superficial and a basal layer of compact bone, with a middle layer of cancellous bone between them, much as in early amphibians. In *Albionbatrachus*, the layer of cancellous bone, consisting of small and large cavities, was connected with the dorsal, sculptured surface of the bone by a system of narrow canals; in *Palaeobatrachus*, the layer of cancellous bone and the canals connecting this layer with the dorsal surface of the frontoparietal were reduced. The situation in *Palaeobatrachus robustus* from the lower Miocene of France is intermediate—while external features support assignment to *Palaeobatrachus*, the inner structure is similar to that in *Albionbatrachus*. It may be hypothesized that sculptured frontoparietals with a well-developed layer of cancellous (i.e., vascularized) bone may indicate adaptation to a more terrestrial way of life, whereas a reduced cancellous layer might indicate a permanent water dweller. *Anat Rec*, 298:1848–1863, 2015. © 2015 Wiley Periodicals, Inc.

Key words: Anura; *Albionbatrachus*; *Palaeobatrachus*; *Xenopus*; Palaeobatrachidae; frontoparietale; development; variation

INTRODUCTION

The holotype of *Palaeobatrachus diluvianus* (Goldfuss, 1831), type species of the genus *Palaeobatrachus*, believed to be lost by Špinar (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., Špinar, 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 *Albionbatrachus 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 *Albionbatrachus* 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 hypothesized 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 *Albionbatrachus* 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

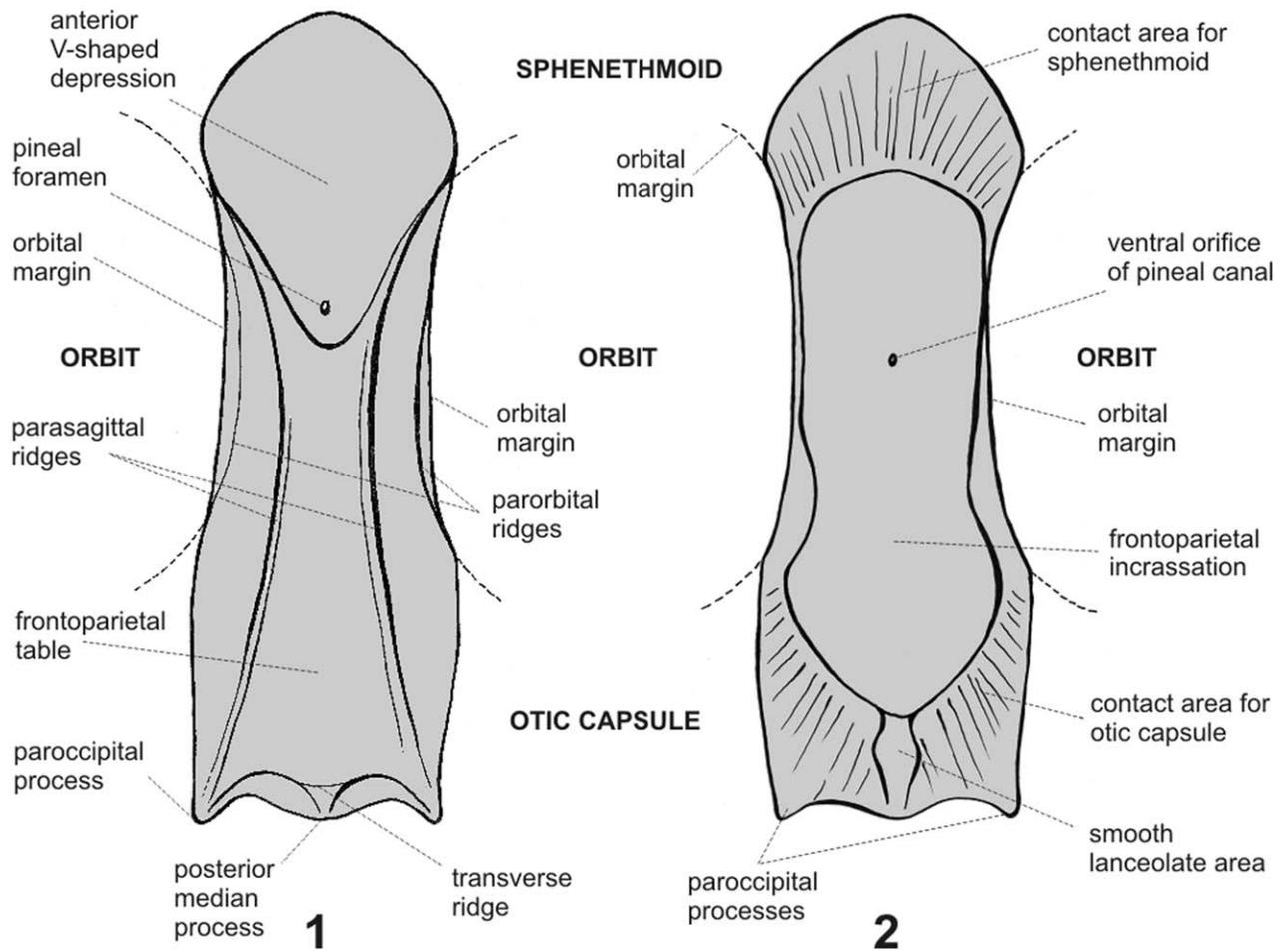


Fig. 1. Descriptive terminology of a generalized palaeobatrachid frontoparietal in dorsal (1) and ventral (2) aspects.

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 (Meszoely et al., 1984); *A. oligocenicus*, UBB V 442, holotype, from the early Oligocene of Suceag, Romania (Venzel et al., 2013); *Palaeobatrachus* sp., PW 2011/5897-LS, from the late Oligocene of Enspel, Germany; *P. robustus*, MNHN.FLAU 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 (Venzel, 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*¹ ♀ (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).

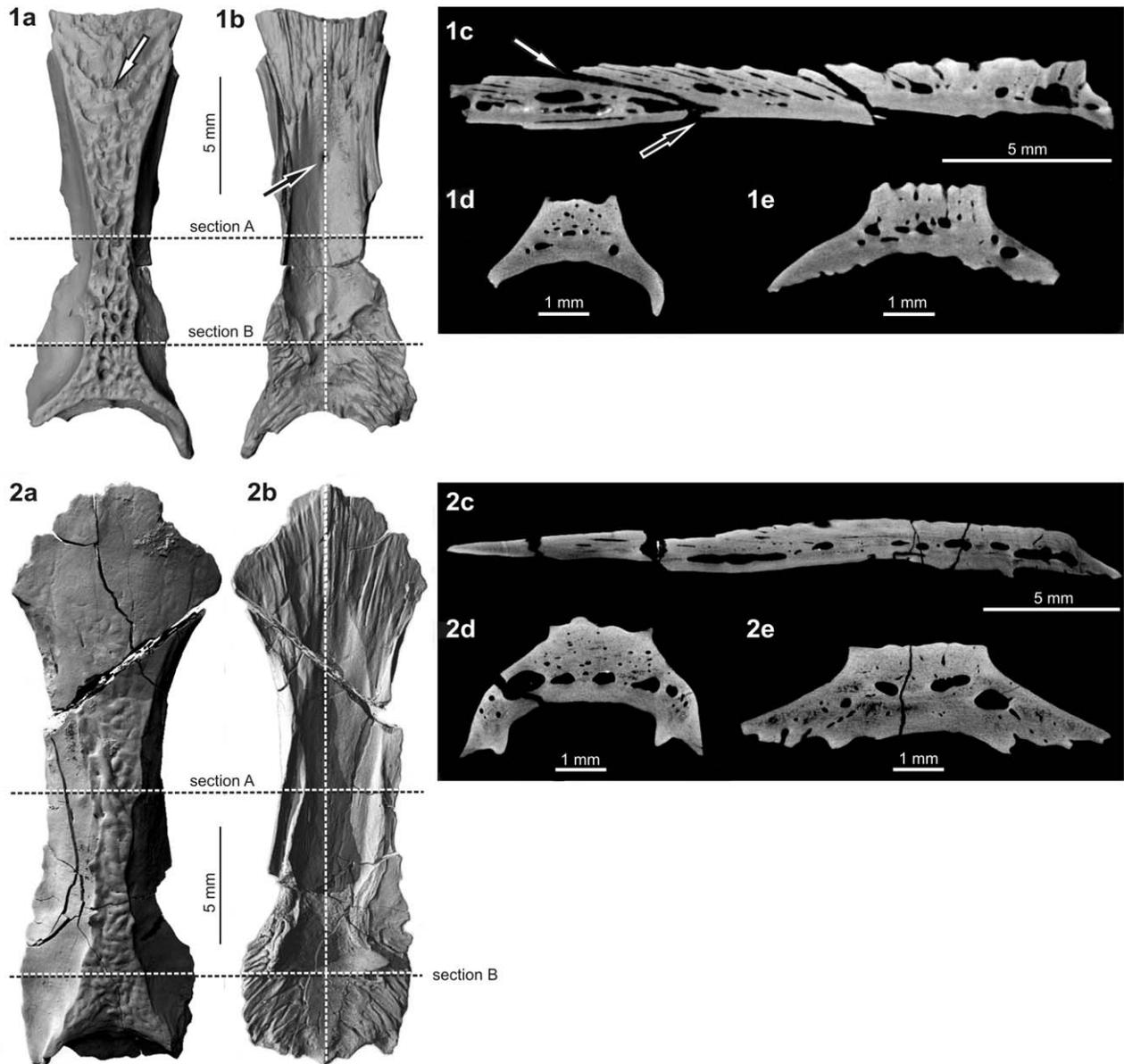


Fig. 2. Frontoparietals of *Albionbatrachus*. 1: *Albionbatrachus wightensis*, holotype (MCZ 8784) from the late Eocene of the Isle of Wight, England, in dorsal (1a) and ventral (1b) views; longitudinal section of the same specimen in the midline (1c), and transverse sections in the narrowest part of 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: *Albionbatra-*

chus 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.

developmental stages of *Xenopus laevis*) were scanned with a GE phoenix vltomelx 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 CEITEC (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 \times 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 datolx 2.0. Images of the 3D volume rendering were made with VGStudio Max 2.2, using the volume

rendering algorithm with two light sources and shadows on.

Albionbatrachus wightensis was scanned using a Sky-Scan 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 $2,240 \times 2,240$ 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 frontoparietals, 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 frontoparietals, 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

Sample	System	Isotropic voxel size (μm)	Acceleration voltage (kVp)	X-ray tube current (μA)	Filter	Integration time (ms)	No. projections per 360°
<i>Albionbatrachus wightensis</i> MCZ 8784	SkyScan 1173	9.59573	127	61	1 mm Al	590	1,200
<i>Albionbatrachus oligocentrus</i> UBB V 442	GE phoenix v tome x L240	15	70	140	1 mm Al	500	1,800
<i>Palaeobatrachus robustus</i> MNHN.F.LAU 7	RX solutions UltraTom	7.95	100	80	1 mm Cu	333	1,440
<i>Palaeobatrachus</i> sp. Subpiatra MTC 23195	GE phoenix v tome x L240	10	70	140	1 mm Al	500	1,800
<i>Palaeobatrachus</i> sp. Enspel PW 2011/5897-LS	GE phoenix v tome x L240	39	80	80		667	1,000
Palaeobatrachidae indet. Villeveyrac MDE-Vil-16	RX solutions EasyTom XL Duo	12.79	60	166	1 mm	83	992
<i>Xenopus laevis</i> NMP 6d-24/2014/1	GE phoenix v tome x L240	8	60	140	0.5 mm Al	400	2,000
<i>Xenopus laevis</i> ♀ DP FNSP 6331	GE phoenix v tome x L240	8	60	150	0.5 mm Al	400	2,000
<i>Xenopus laevis</i> ♀ NMP 6d-24/2014/2	GE phoenix v tome x L240	12	60	170	0.5 mm Al	400	2,000
<i>Xenopus muelleri</i> ♂ DP FNSP 6541	GE phoenix v tome x L240	5.5	60	200	0.1 mm Al	700	2,000
<i>Xenopus tropicalis</i> DP FNSP 6542	GE phoenix v tome x L240	5	60	200	0.2 mm Al	500	1,800

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

***Albionbatrachus wightensis* Meszoely, Špinar 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 incassation (smooth part of the ventral surface, which in an articulated skull fits into the fenestra in the roof of the endochondral braincase; see also Roček, 2003: 1908) is delimited by shallow vertical walls. The posterior part of the parietal portion of the incassation is not preserved and cannot be restored. The anterior and posterior parts of the ventral surface of the bone are striated, and served for attachment to the sphenethmoid and otic capsules. The canal for the pineal complex is preserved along its whole extent (Fig. 2—1c). The inner anatomy is dominated by the middle layer of the bone, consisting of comparatively large cavities sharply separated from the ventral, compact part of the bone; the cavities are interconnected by a net of horizontal canals, and the whole system is connected with the dorsal surface of the bone by canals that open within the sculptural pits and furrows (Fig. 2—1c). On the periphery of the bone, the middle, cancellous layer consists of smaller cavities, but the line along which the cavities are arranged may reach up to the surface.

***Albionbatrachus oligocenicus* Venczel, Codrea et Fărcaș, 2013.** The bone is almost complete; its length is about 25 mm (Fig. 2—2). The size of the bone, along with the obliterated canal for the pineal complex, suggest that it belonged to a fully grown, adult individual. The anterior portion of the bone is flat, smooth, and slightly wider than the posterior portion. The frontoparietal table is flat and moderately ornamented (better posteriorly than anteriorly). The parasagittal ridges take their origin on the lateral margins of the anterior part of the bone, where the bone is widest and where the frontoparietal and the nasal meet one another on the orbital margin. The paroccipital processes seem to be shorter than in *A. wightensis*, but they do extend posteriorly beyond the midline portion of the bone. The frontoparietal incassation is divided by a distinct constriction that separates the region into a larger frontal and a smaller parietal portion; the latter extends posteriorly as a smooth, lanceolate area (which seems to be absent in *A. wightensis*). The ventral surface of the bone outside the incassation is striated as in *A. wightensis*. On each side, a deep groove between the orbital margin of the

bone and the prominent lateral wall of the frontoparietal incassation served as a contact area for the lateral wall of the braincase. Contrary to *A. wightensis*, the canal for the pineal complex of *A. oligocenicus* is obliterated, 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 incassation 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., Subpiatră.** 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

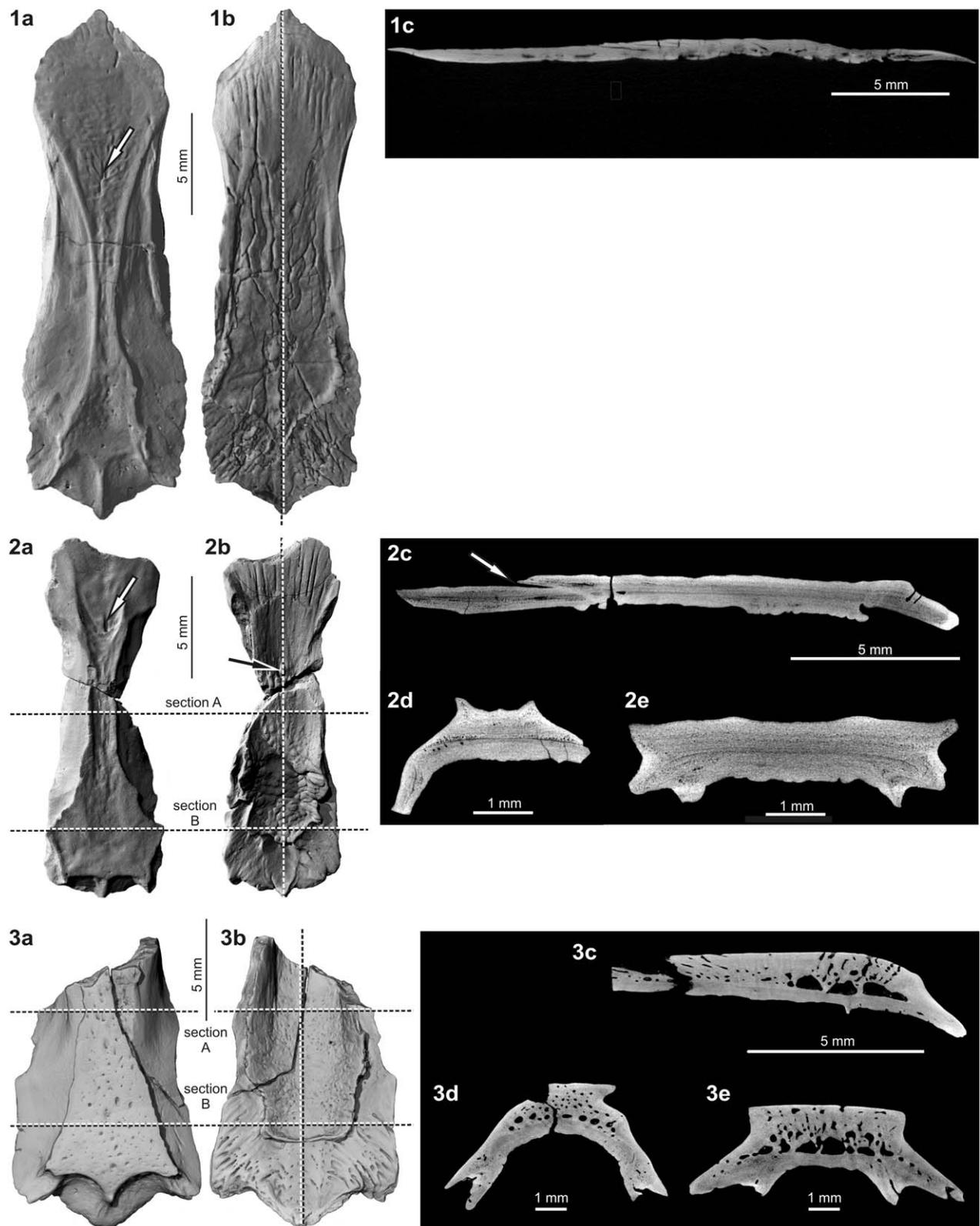


Fig. 3. Frontoparietals of *Palaeobatrachus*. 1: *Palaeobatrachus* sp. (PW 2011/5897-LS) from the late Oligocene of Enspel, Germany. The internal structure of the transverse sections could not be scanned in higher resolution because the specimen was too large due to being embedded in surrounding rock matrix. 2: *Palaeobatrachus* sp. (MTC 23195) from the middle Miocene of Subpiatră, 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).

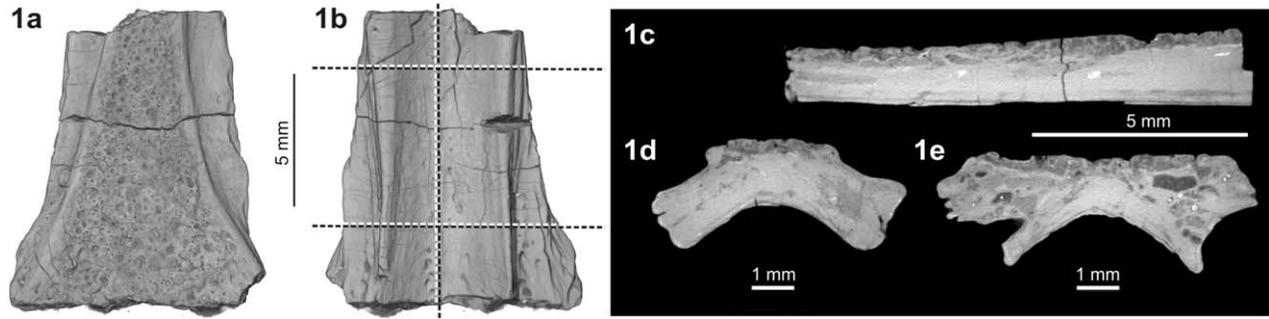


Fig. 4. Posterior part of a palaeobatrachid frontoparietal (MDE VIL 16) from the early Campanian of Villeveyrac, France, the oldest known representative of Palaeobatrachidae. Anterior part of the bone in 1c is to the left. The cross-sections are meant to be at similar levels as in Figs. 2 and 3. The frontoparietal is reversed horizontally if compared with the original publication by Buffetaut et al. (1996, Fig. 3).

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 Enspel, 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 Enspel, 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 incassation is similar to that in *Albionbatrachus 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 *Albionbatrachus*. 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 posteroventrally 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-*

trachus. The frontoparietal incassation is well delimited posteriorly and the lanceolate area in the middle of the posterior part of the ventral surface of the bone is lacking. The inner structure of the bone is characterized by the compact ventral layer. The middle layer of cancellous bone consists of large cavities interconnected horizontally and arranged at their bottoms along a single line (Fig. 3—3c, e), much like in *Albionbatrachus*; anteriorly, these cavities are smaller. Also similar to *Albionbatrachus*, the whole system of cavities is connected with the dorsal surface of the frontoparietal table by thin canals, which are moderately inclined posteriorly in the parietal portion of the bone, whereas they are more anteriorly inclined in the anterior portion of the bone (Fig. 3—3c). Thus, the frontoparietal of *P. robustus* displays a mixture of characters typical of both *Palaeobatrachus* and *Albionbatrachus*.

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

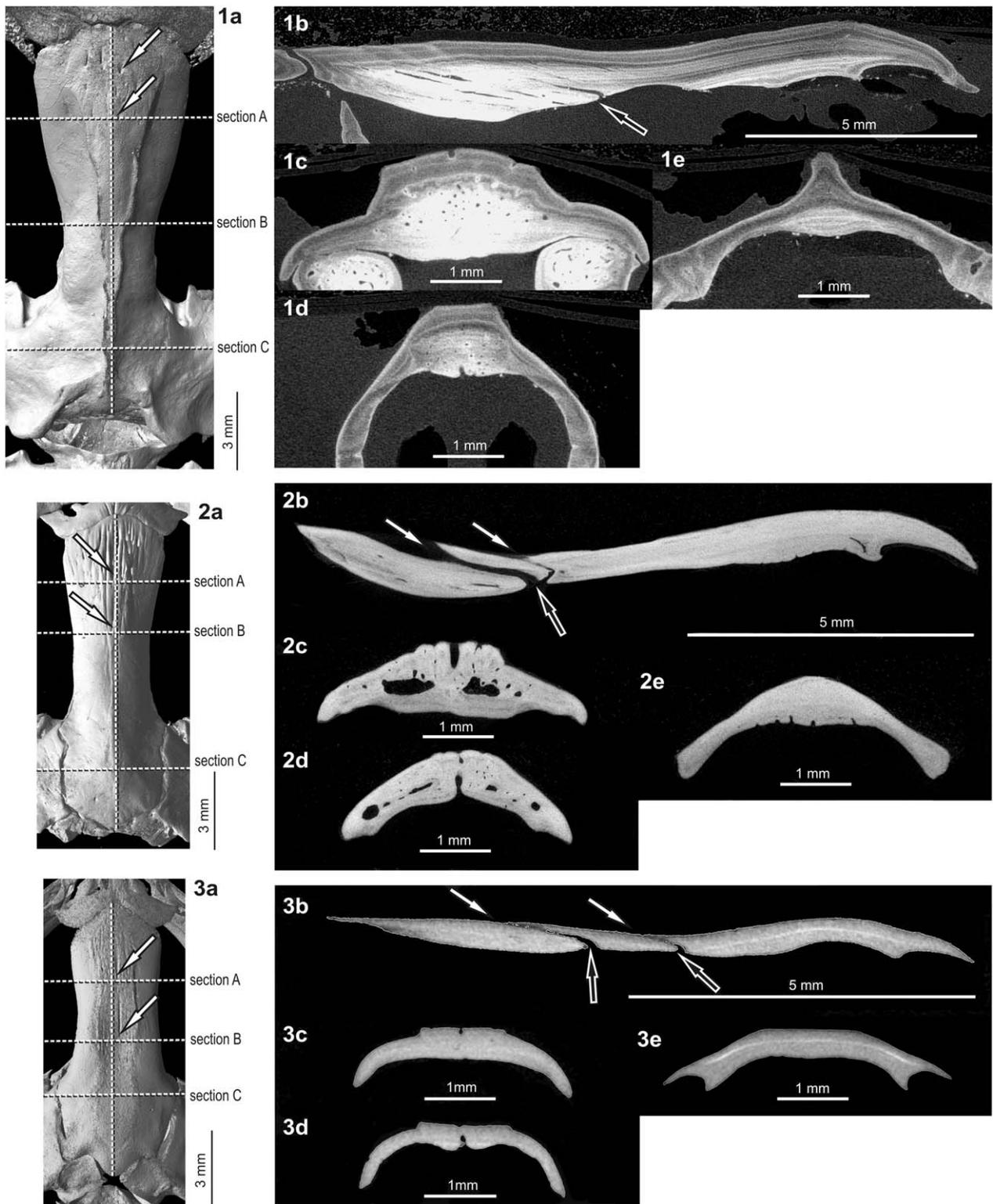


Fig. 5. Developmental changes in the external morphology and inner structure of the frontoparietal bone in *Xenopus laevis* (Pipidae). 1a: Hyperossified, extremely old (min. 12 years) adult (NMP 6d-24/2014/2, ♀), in dorsal view. Note complete fusion with the otic capsules. Parapineal and pineal foramina 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 is 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 FN5P 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.

comparatively thin. Its anterior margin runs out in a prominent median apex. The anterior portion of the bone is only slightly narrower than the parietal portion. The posterior part is the widest on the orbital margin. From here, the parietal portion of the frontoparietal moderately tapers towards the poorly developed paroccipital processes. The most posterior part of the bone is a widely rounded median process. The dorsal surface of the bone is convex and smooth, except for very indistinct and sigmoid parasagittal ridges, which delimit laterally a shallowly depressed table in the middle of the bone. In the midline of the dorsal surface are two foramina—the anterior of them houses the parapineal organ (frontal organ or Stirnorgan of some authors; Eakin, 1961; Korf et al., 1981; Norris, 2007) and continues as a posteroventrally directed canal for the pineal nerve (or frontal organ nerve; Korf et al., 1981), which opens on the ventral surface of the bone. The posterior foramen is located nearly at the level of the anterior margin of the prootics (Fig. 5—3a), and houses the pineal organ proper (i.e., epiphysis); through the canal courses the pineal (or epiphyseal) tract (Korf et al., 1981). The ventral openings of the two canals are separate. The inner structure of the bone is characterized by a horizontal, whitish and not cancellous layer of greater density, which separates the dorsal and ventral compact portions of the bone; the layer is less distinct anteriorly.

The frontoparietal in the medium-sized individual (female) is 12 mm long (Fig. 5—2a) and, compared with the younger individual, is thicker but remains narrower anteriorly than posteriorly. Since the postcranial skeleton of this individual was disarticulated, its SVL is unknown. The frontoparietal is still completely separated from the surrounding skeletal elements by sutures, but the processes on the posterior margin of the bone are less prominent, so this part of the bone is almost rounded. In its parietal portion, there is a sign of a single, indistinct median keel that develops from the table; it is bifurcated posteriorly towards the paroccipital processes (much less prominent, if compared with the youngest studied individual; compare Fig. 5—2a and 3a). Anteriorly, the median keel seems to be divided in two divergent ridges, delimiting a triangular field with anteroposteriorly oriented ridges and furrows. Within the anterior moiety of the bone is a system of small and larger vacuities arranged along the horizontal line dividing the dorsal and ventral parts of the bone (Fig. 5—2c, d) and thus representing the layer of cancellous bone; however, this system is absent in the posterior part of the bone where only a vestigial whitish line (of a dense layer) can be recognized (Fig. 5—2e). The large cavities in the anterior part of the bone are connected with the dorsal surface of the bone by anteriorly inclined canals (Fig. 5—2c) which open in the grooves surrounding the anterior, parapineal foramen and narrower posterior, pineal foramen. Although the posterior pineal canal (for the pineal tract) still pierces the bone, its ventral termination joins the ventral opening of the anterior parapineal canal (Fig. 5—2b).

A moderately larger individual (DP FNSP 6331b; not illustrated) was examined from a dry skeleton only, but it is described here because it is an intermediate stage between the previous one and the fully developed, terminal stage. The frontoparietal is 13.5 mm long, but its median keel is well developed, especially in its posterior

half, and almost reaches the posterior end of the bone. Both ridges running onto the paroccipital processes are well pronounced, but lower than the median keel. In contrast with the previous stage, the paroccipital processes are almost pointed and separated from the median process, which is widely rounded. As in both younger stages, this median process represents the most posterior part of the bone. In the interorbital part of the bone, the median keel is thicker and its dorsal surface is sculptured. The anterior parapineal foramen is located almost at the level where the suture between the frontoparietal and nasal 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 ventral surface of the anterior and posterior part of the bone (Fig. 5—1b), the original frontoparietal of the young animal was partly resorbed. There are anteriorly inclined canals piercing the ventral surface of the bone and ending blindly below the dorsal superficial layer of compact bone (Fig. 5—1b, c). It should be added that this anatomy of the frontoparietal in a fully grown adult is probably not definitive, as the oldest recorded *Xenopus laevis* reared in laboratory conditions was 23 years old (Deuchar, 1975).

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*.

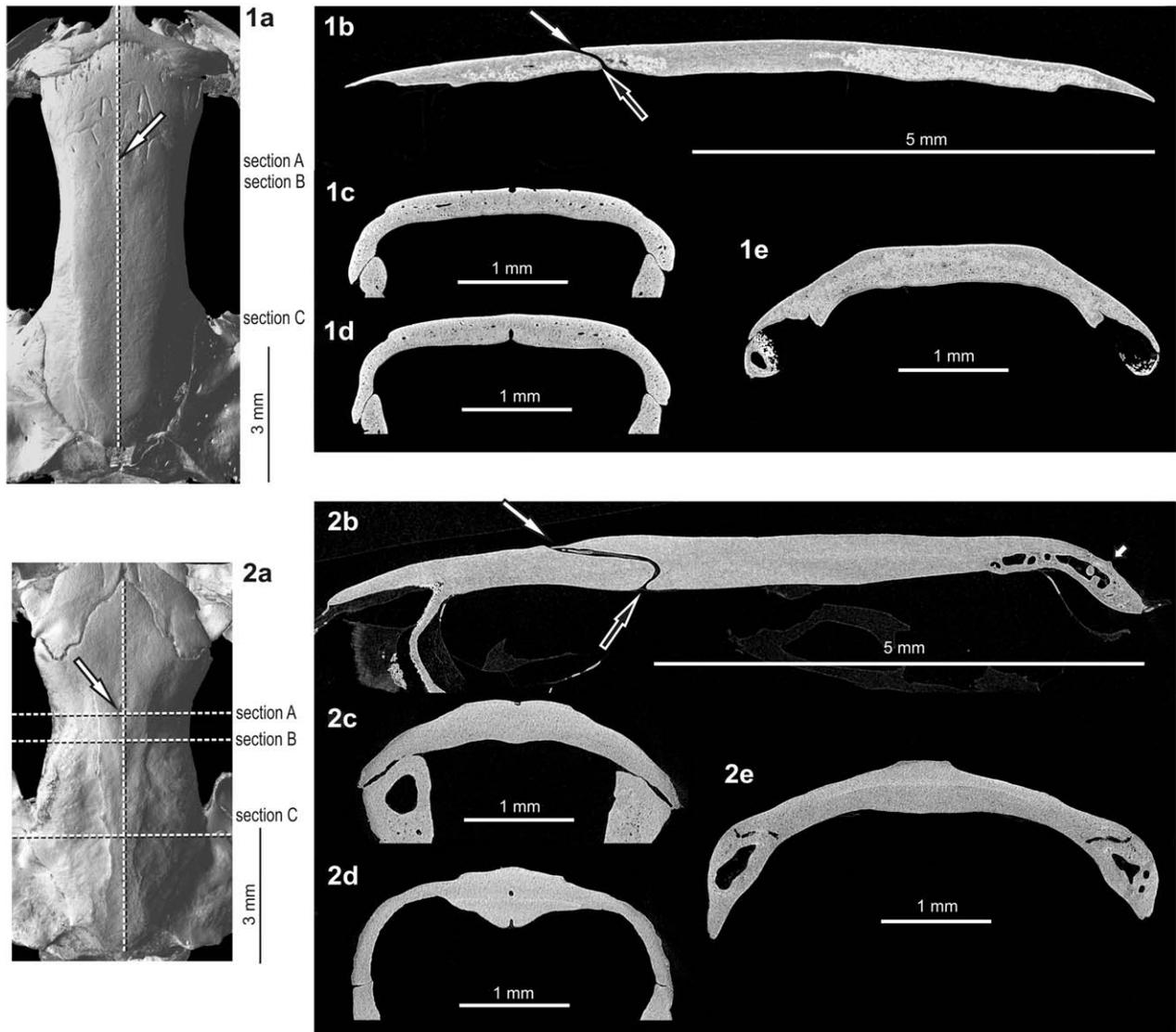


Fig. 6. Interspecific variation of morphology and structure of the frontoparietal bone within the genus *Xenopus* (Pipidae). 1a: *Xenopus muelleri* (DP FNSP 6541, ♂), frontoparietal in dorsal view. Broken lines indicate positions of sections illustrated in 1b–e. 1b: Longitudinal section through the frontoparietal of the same specimen along the midline. 1c–e: Transverse sections A–C, as indicated in 1a. 2a: *Xenopus tropicalis* (DP FNSP 6542, ♀), frontoparietal in dorsal view. Broken lines indicate positions of sections illustrated in 2b–e. 2b: Longitudinal section through the frontoparietal of the same specimen along the mid-

line. Small white arrow on the right side marks the posterior end of the frontoparietal bone, which is firmly coalesced to the ossified tectum synoticum (the part of the synostotic complex which is recognizable by large vacuities). 2c–e: Transverse sections A–C, as indicated in Fig. 2a. White arrows mark the position of the foramen for pineal complex; black arrows mark the ventral orifice of the canal for pineal complex. Longitudinal sections (1b and 2b) are oriented with their anterior ends to the left.

***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 posteromedial 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 posterolateral 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 (Meszoely 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.

TABLE 2. Phylogenetically diagnostic and developmentally dependent traits in the frontoparietal bone of Palaeobatrachidae and *Xenopus*

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

^aNote 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.

Thus it seems that the frontoparietal of *Xenopus laevis* undergoes significant changes during development (Table 2). For instance, the frontoparietals 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 frontoparietals first coalesce together by their parietal portions, and later in their frontal portions (Trueb and Hanken, 1992),

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—2c, 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 epiphyses 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 avascular, very dense bone into the dorsal and ventral portions (Fig. 6—2e) as in the young individual of *X. laevis*. In contrast, despite its larger size, *X. muelleri* was younger, which was evidenced by cartilaginous epiphyses of the long bones, cartilaginous anterior parts of the prootics (Fig. 6—1e), and the frontoparietal separated from all adjacent skeletal elements by sutures. The interior of the bone in its anterior and parietal portions seems to contain signs of cancellous bone, with a thin layer of compact bone on the surface (Fig. 6—1b, e). It can be inferred from the comparisons of the frontoparietals of three developmental stages of *X. laevis* with adult, fully grown *X. tropicalis*, in which the latter corresponds in the degree of the frontoparietal development to young *X. laevis*, that some species of *Xenopus* can be underdeveloped in certain characters, i.e., their adults correspond in certain characters to younger stages of other, closely related species. This may be understood as evidence of paedomorphosis in *Xenopus*.

If the conclusions from our cursory account of *Xenopus laevis* are applied to fossil Palaeobatrachidae, the following may be drawn:

Albionbatrachus and *Palaeobatrachus* differ in general outlines of the frontoparietal, which apparently remain unchanged throughout development. This means the following are of diagnostic value (see also Table 2): (1) the posterior median process of *Albionbatrachus* is short, indistinct, not exceeding the level of the paroccipital processes (whereas this process is always the most posterior part of the bone in *Palaeobatrachus*, and the paroccipital processes are short); (2) the frontoparietal table is horizontal, flat and ornamented in *Albionbatrachus* (whereas it is depressed along the midline, bordered laterally by the prominent parasagittal ridges, and unsculptured in *Palaeobatrachus*, except for *P. robustus*); (3) unless the inner structure of the frontoparietal is a subject of developmental changes, the ventral portion of the bone in *Albionbatrachus* is compact, separated 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 Subpiatră (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 Bechlejovice, 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 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 Subpiatră, 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 frontoparietals are not three-dimensionally preserved, whereas both *Albionbatrachus* species are based on three-dimensionally 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*.

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LITERATURE CITED

- Buffetaut E, Costa G, Loeuff Martin LJ, Rage M, Valentin J-C, Tong X. H. 1996. An Early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, Southern France). *N Jb Geol Paläont Mh* 1996:1–16.
- Bystrow AP. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. *Acta Zool Stockholm* 16:65–141. doi:10.1111/j.1463-6395.1935.tb00664.x
- Castanet J, Francillon-Vieillot H, de Ricqlès A, Zylberberg L. 2003. The skeletal histology of the Amphibia. In Heatwole H, Davies M, editors. *Amphibian biology—osteology*. Chipping Norton: urrey Beatty & Sons. p 1598–1683.
- Deuchar EM. 1975. *Xenopus*: the South African clawed frog. New York: Wiley.
- Dong L, Roček Z, Wang Y, Jones MEH. 2013. Anurans from the Lower Cretaceous Jehol Group of western Liaoning, China. *PLoS One* 8:e69723.
- Eakin RM. 1961. Photoreceptors in the amphibian frontal organ. *Proc Natl Acad Sci USA* 47:1084–1088.
- Estes R, Reig OA. 1973. The early fossil record of frogs: a review of the evidence. In Vial JL, editor. *Evolutionary biology of the Anurans: contemporary research on major problems*. Columbia: University of Missouri Press. p 11–63.
- Fischberg M, Colombelli B, Picard JJ. 1982. Diagnose préliminaire d'une espèce nouvelle de *Xenopus* du Zaïre. *Alytes* 1:53–55.
- Frost DR. 2014. Amphibian species of the world: an online reference. Version 6.0 (Accessed March 9, 2015). Electronic database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. New York: American Museum of Natural History.
- Goldfuss GA. 1831. Beiträge zur Kenntnis verschiedener Reptilien der Vorwelt. *Nova Acta Physico-Med Acad Caes Leop-Carol Nat Curios* 15:61–128.
- Gray JE. 1864. Notice of a new genus (*Silurana*) of frogs from West Africa. *Ann Mag Nat Hist Ser 3* 14:315–316.
- Harper EB, Measey G J, Patrick D-A, Menegon M, Vonesh J R. 2010. Field guide to amphibians of the eastern arc mountains and coastal forests of Tanzania and Kenya. Nairobi: Camerapix Publishers International.

- Hossini S, Rage JC. 2000. Palaeobatrachid frogs from the earliest Miocene (Agenian) of France, with description of a new species. *Geobios* 33:223–231.
- Janis CM, Devlin K, Warren DE, Witzmann F. 2012. Dermal bone in early tetrapods: a palaeophysiological hypothesis of adaptation for terrestrial acidosis. *Proc R Soc B* 279:3035–3040.
- Korf H-W, Liesner R, Meissl H, Kirk A. 1981. Pineal complex of the Clawed Toad, *Xenopus laevis* Daud.: structure and function. *Cell Tissue Res* 216:113–130.
- Mai DH. 1995. Tertiäre Vegetationsgeschichte Europas. Jena: G. Fischer.
- Meszoely CAM, Špinar ZV, Ford RLE. 1984. A new palaeobatrachid frog from the Eocene of the British Isles. *J Vert Paleontol* 3:143–147.
- Meyer H. 1843. Summarische Uebersicht der fossilen Wirbelthiere des Mainzer Tertiär-Beckens, mit besonderer Rücksicht auf Weisenau. *N Jahrb Miner Geogn Geol Petrefactkde* 1843:379–410.
- Meyer H. 1852. Mittheilungen an Professor Bronn. *N Jahrb Miner Geogn Geol Petrefactkde* 1852:465–468.
- Meyer H. 1860. Frösche aus Tertiär-Gebilden Deutschlands. *Palaeontographica* 7:123–182.
- Norris DO. 2007. Vertebrate endocrinology. Amsterdam: Elsevier Academic Press.
- Peters WCH. 1844. Über einige neue Fische und Amphibien aus Angola und Mozambique. *Monatsber Königl Preuss Akad Wiss Berlin* 1844:32–37.
- Pyron RA. 2014. Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Syst Biol* 63:779–797.
- Roček Z. 2003. Larval development and evolutionary origin of the anuran skull. In Heatwole H, Davies M, editors. *Amphibian biology – osteology*. Chipping Norton: Surrey Beatty & Sons. p 1878–1995.
- Smirnov SV. 1994. Postmaturation skull development in *Xenopus laevis* (Anura, Pipidae): late-appearing bones and their bearing on the pipid ancestral morphology. *Russian J Herpetol* 1:21–29.
- Špinar ZV. 1972. Tertiary frogs from Central Europe. Prague: Academia.
- Trueb L. 2003. Clawed frogs and Surinam toads (Pipidae). In: Hutchins M, Duellman WE, Schlager N, editors. *Grzimek's animal life encyclopedia* 6, amphibians. Farmington Hills, MI: Gale Group. p 99–107.
- Trueb L, Hanken J. 1992. Skeletal development in *Xenopus laevis* (Anura: Pipidae). *J Morphol* 214:1–41.
- Venczel M. 2007. Late Middle Miocene amphibians and reptiles from Subpiatră (Bihor district, Romania). *Nymphaea* 34:39–66.
- Venczel M, Codrea V, Fărcaș C. 2013. A new palaeobatrachid frog from the early Oligocene of Suceag, Romania. *J Syst Palaeontol* 11:179–189.
- Vickaryous MK, Sire JY. 2009. The integumentary skeleton of tetrapods: origin, evolution and development. *J Anat* 214:441–464.
- Witzmann F, Scholz H, Müller J, Kardjilov N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. *Zool J Linn Soc* 160:302–340.
- Wuttke M, Prikryl T, Ratnikov VY, Dvořák Z, Roček Z. 2012. Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). *Palaeobio Palaeoenviron* 92:367–395.