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"LOST" AND REDISCOVERED:
HOLOTYPE OF *PALAEOBATRACHUS DILUVIANUS* (GOLDFUSS, 1831)

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Abstract: A brief history and notes on the significance of the holotype specimen of *Palaeobatrachus diluvianus* (GOLDFUSS, 1831) are presented, together with a detailed description and illustrations. The specimen was seemingly lost during WW2, but this was caused by the fact that whereas all specimens in the repository of the Goldfuss Museum were catalogued during the 1970s, the holotype was included in a public exhibition of the Museum and thus escaped the catalogization. The specimen is a natural cast of a nearly complete articulated skeleton in the sediment exposed in the dorsal aspect, in which only the distal sections of the hindlimbs were not preserved. Although the original Goldfuss' illustration of the specimen is largely idealized, the original illustration by Meyer (1860) is fairly precise, so the identity of the specimen is beyond doubt. It bears most of diagnostic characters of the genus *Palaeobatrachus* and some additional ones (such as a big skull, contrasting with the comparatively short vertebral column) that can be taken as diagnostic for the species. This makes this specimen a reasonable starting point for all future comparative analyses.

Key words: Anura, Palaeobatrachidae, *Palaeobatrachus diluvianus*, holotype, osteology, Goldfuss, Orsberg

Introduction

As evidenced by their fossil record consisting of articulated skeletons and isolated bones, frogs of the genus *Palaeobatrachus* were common in central and eastern Europe from the Oligocene until the Pliocene. Although their area of distribution was basically restricted to Europe, they were closely related to Gondwanan pipids, both by their anatomy (the only strict difference is the procoelous shape of the vertebral centrum, which is opisthocoelous in pipids) and permanent aquatic life-style. It seems that their permanent water dwelling in close vicinity to the continental glacier could have been the reason why they became extinct relatively recently, about 500 thousand years ago (Wuttke et al. 2012), but was also the reason for their extreme morphological uniformity. Although a comparatively large number of taxa were described especially during the 19th century, some authors later expressed doubts about their validity and argued that at least some of them could have been just juveniles or extremely old individuals.

This ambiguity lead to the necessity for a taxonomic revision of the genus *Palaeobatrachus* TSCHUDI, 1838 less than 30 years after the first specimen (Text-figs 1–3), found in open cast mines near Orsberg and deposited in the Friedrich-Wilhelms University in Bonn Poppelsdorf, was published as *Rana diluviana* by Goldfuss (1831), and then named *Palaeobatrachus diluvianus* by Tschudi (1838). The first confusion was caused by the fact that Tschudi used the species name *goldfussi* for this specimen instead of the original name *diluvianus*. Further confusions followed: another specimen from Orsberg, deposited in Senckenberg Museum in Frankfurt a. M., was assigned by Rüppel (1845) to the same species as was Goldfuss's specimen previously deposited in Bonn, but in accordance with Tschudi's (1838) definition under the name *Palaeobatrachus goldfussi*. However, the counterpart of the Senckenberg Museum specimen, now deposited in the Museum of Mineralogy and Geology in Dresden (former Dresdener Hof-Mineralien-Cabinet), was assigned by Giebel (1851) to the genus *Palaeophrynos*, as *Palaeophrynos grandipes.* The genus *Palaeophrynos* was established by Tschudi (1838) for a fossil frog named *Palaeophrynos gessneri* from the late Miocene of Öhningen. The fossil frog from Dresden was transferred to *Palaeobatrachus* by Meyer (1860), who was aware that the Senckenberg specimen and Dresdner specimen were in fact ventral and dorsal parts of the same individual, and assigned them to *Palaeobatrachus diluvianus* (literally to "*Palaeobatrachus Goldfussi*"). Wolterstorff, nearly 30 years later (1887), confirmed that *Palaeobatrachus grandipes* is a separate species.

These two examples of rather complicated history clearly demonstrate how important are comparisons of new specimens with those published previously. A key role in these particular comparisons was played by the holotype of

Text-fig. 1 *Palaeobatrachus diluvianus* (Goldfuss, 1831). Holotype (STIPB-Goldfuss-1343) deposited in Goldfuss Museum, Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Rheinische Friedrich-Wilhelms Universität, Bonn, Germany. Photograph courtesy Steinmann-Institut.

Palaeobatrachus diluvianus which is, at the same time, the name-bearing type of the genus *Palaeobatrachus.* It should be therefore used as a starting point for all comparisons. Wol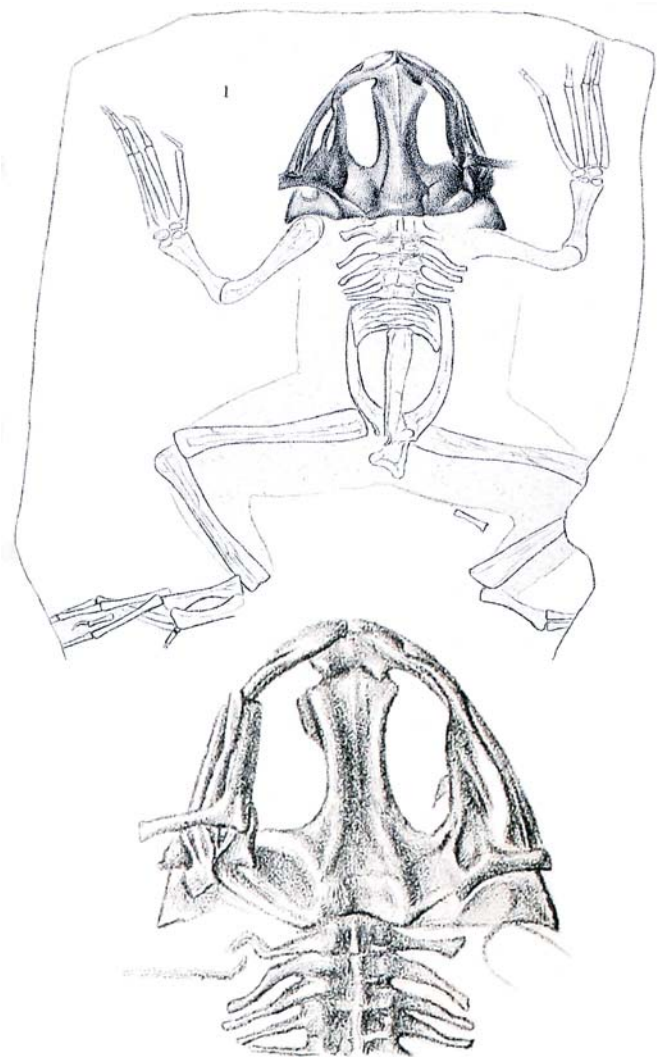terstorff (1886, 1887) adopted this approach, indirectly confirming that the specimen was still deposited in the collections of Bonn University. The subsequent years were a period when only a few authors showed interest in palaeobatrachids. There were two notable events during this
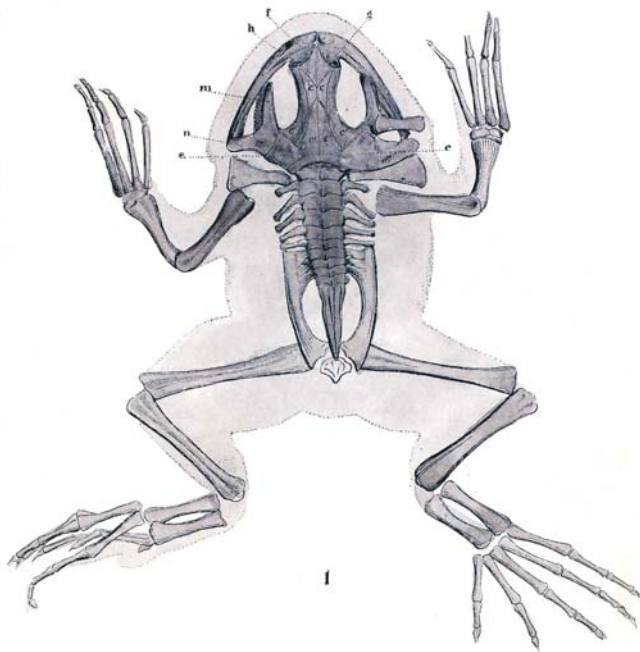
Text-fig. 2 *Palaeobatrachus diluvianus* (*"Rana diluviana"*). **Illustration from Goldfuss (1831: pl. 12, fig. 1). Although the fossil is a natural imprint in matrix, the specimen is illustrated as if the skeleton were preserved in dorsal aspect. Obviously, the drawing was made from a cast, but later was mirror-reversed (see, e.g., toes of hindleg on the left side, which are the same in the fossil and in this illustration). Distal sections of both hindlegs were artificially completed.**

Text-fig. 3 **Reconstruction of** *Palaeobatrachus diluvianus* (*"Palaeobatrachus Goldfussi"*) **holotype by Meyer (1860: pl. 18, figs 1, 2). Small bone close to right hindlimb and other details are clear evidences that this specimen and the specimen in Text-fig. 1 are the same. The drawing above was made from the original imprint in sediment (although the skull is drawn as if it were a real skeleton in dorsal view), but the drawing below depicts the cast made of bread, i.e., real anatomical situation (note that both drawings are mirror-reversed).**

time: Féjérváry (1917) erected a new genus *Pliobatrachus*, based principally on the synsacrum and urostyle with diapophyses (Féjérváry 1917: 148, pl. 1, figs 2–5), although these features were mentioned by Goldfuss as early as 1831 in connection with *Palaeobatrachus diluvianus* (*"Rana diluviana"*); and in 1941, Kuhn described some palaeo-batrachid material from the Eocene of Geiseltal, but without comparisons with the type species of *Palaeobatrachus*.

After the World War 2, a major revision was made by Zdeněk V. Špinar based on a substantial amount of material which he and his students excavated from a new locality in Bechlejovice in northern Bohemia, the Czech Republic. This locality yielded a large number of palaeobatrachid frogs preserved as articulated skeletons, although dorso-ventrally compressed, and a complete developmental series of their tadpoles. Excavations were carried out from the beginning of the 1950s until the mid-1960s, and Špinar also included in his analysis older material deposited in the National Museum Prague and an older palaeobatrachid collection from the former Carl-Ferdinand University in Prague. At that time, the political regime in the former Czechoslovakia cast severe restrictions on traveling abroad, so he could only study palaeobatrachid collections in East Berlin, Halle and Dresden. He was allowed to travel to Bonn only in May 1968 during "Prague Spring", shortly before Soviet occupation of Czechoslovakia, but he was not able to find the holotype of *Palaeobatrachus diluvianus* in the collections of Bonn University. According to Prof. Heinrich Karl Erben, Head of the Institut für Paläontologie at the University at that time, this specimen was lost probably during WW2 (Špinar 1972:

99). Špinar therefore selected another specimen from the type series as the lectotype (No.8/9, now STIPB Ro 4028; Text-fig. 4).

Only much later, in June 2014, it turned out that the holotype specimen of *Palaeobatrachus diluvianus* had been in a public exhibition at the Goldfuss Museum all the time. The museum then belonged to the Steinmann-Institut für Geologie, Mineralogie und Paläontologie at Rheinische Friedrich-Wilhelms University in Bonn. The holotype had stayed uncatalogued as part of the regional Rott collection and therefore unnoticed until recently when it was lent to scientists abroad for investigations not related to taxonomic study. It was safely returned to Bonn in November 2014.

Therefore, the main aim of this paper is to provide an up-to-date description and illustrations with regard to anatomical characters preserved in other specimens
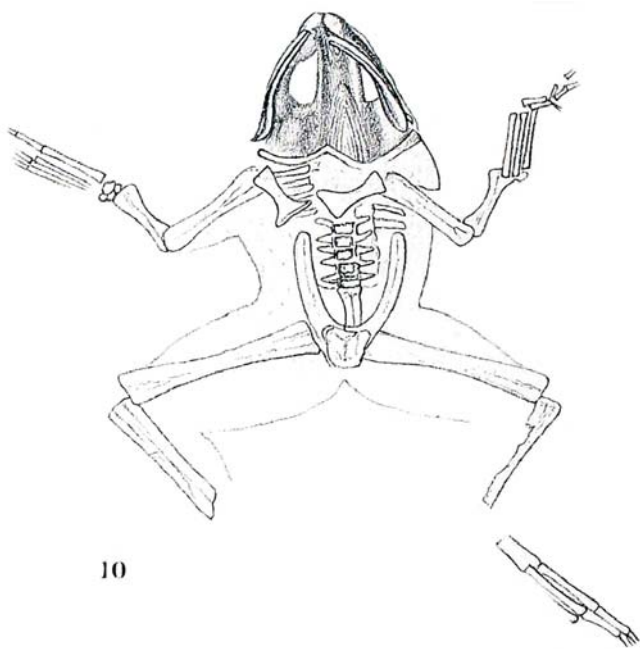
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Text-fig. 4 *Palaeobatrachus diluvianus* (Goldfuss, 1831). **Specimen STIPB Ro 4028 (formerly No. 8/9), one of syntypes, designated by Špinar (1972: 99) as the lectotype, because it was believed at that time that the holotype was lost. The skeleton is preserved in ventral aspect, thus providing additional information to the holotype. The line drawing is by Meyer (1860: pl. 20, fig. 10). Scale bar in bottom picture is 10 mm.**

of *Palaeobatrachus*, which will make possible future comparative analyses.

Redescription of the holotype of *Palaeobatrachus diluvianus* (Goldfuss, 1831)

The holotype specimen is a natural cast of the dorsal side of an almost complete, articulated skeleton of an adult (Text-fig. 1; see also Goldfuss 1831: pl. 12, fig. 1; Meyer 1860: pl. 18, figs 1, 2), which is now deposited in the type collection of Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Friedrich-Wilhelms-Universität,

Text-fig. 5 Locality Orsberg near Erpel, Germany. Type locality of *Palaeobatrachus diluvianus* (Goldfuss, 1831). Abandoned open-cast mine, with traces of mining activities. Situation as on June 23rd 2014.

Bonn, Germany, as STIPB-Goldfuss-1343. Since Goldfuss explicitly referred in his description to this particular specimen, and because other specimens from the type series were juveniles or tadpoles, it can be implied that the holotype was fixed by monotypy (ICZN, Art. 73.1.2). It originates from the Late Oligocene (MP30, Neochattium; Mai 1995), from a now-abandoned opencast browncoal mine at Orsberg near Erpel (50°35'23.63"N; 7°14'47.15"E) (Text-fig. 5).

Both premaxillae are preserved as imprints, but details (such as number of tooth positions, shape of pars facialis) cannot be recognized (see also Text-fig. 3, bottom picture). It seems that the maxilla adjoins the posterolateral end of the premaxilla from the outer side. The frontoparietal projects anteriorly as a slender median process, originally inserted between the two nasals. This means that both nasals (neither of them is preserved) were in contact with one another only over a short section anteriorly, whereas their medial margins were divergent posteriorly. Similar, though not so prominent processes project anterolaterally on both sides of the anterior margin of the frontoparietal. Parasagittal ridges (prominent arch-like crests on the dorsal surface of the bone, with a deep antero-posterior depression between them) run posteriorly from each anterolateral process, approaching each other at the interorbital portion of the bone, but diverging again in its parietal portion, and terminating on the paraoccipital processes. The posterior margin of the frontoparietal is widely convex; the paraoccipital processes do not extend beyond the most posterior part of this convexity, which is thus the most posterior part of the bone. Underneath the imprint of the anterior part of the frontoparietal, there is an imprint of the sphenethmoid, which is well delimited posteriorly; the posterior margin of the sphenethmoid extends to the middle of the antero-posterior diameter of the orbit. The ramus maxillaris of the pterygoid is markedly sigmoid in shape, the end of the ramus interior (= medialis) is rounded, and the margin between the ramus interior and ramus posterior is concave. It seems that the coronoid process of the angular is inclined medially.

Altogether nine vertebrae can be recognized. All are short and broad, hence the presacral vertebral column is comparatively short. The neural arches are imbricate and bear a median crest on their dorsal surface, not extending onto adjacent posterior vertebra. V1 and V2 are fused, V2 bears a pair of transverse processes which are thick proximally and slightly inclined posteriorly (see, however, Text-fig. 3, bottom picture). Transverse processes of V3 and V4 are the longest, and markedly inclined posteriorly (those of V3 are cranked posteriorly in the middle of their length, those of V4 are straight). Transverse processes of V5 are also inclined posteriorly, but moderately bent anteriorly, and those of V6 are straight, perpendicular to the body axis, and directed to the ends of the processes of V5. Transverse processes of V7 are rudimentary and, as Goldfuss (1831) already noted, they lean against the anterior margin of the sacral wings, but it cannot be decided with certainty if they are fused with the sacral wings. V8 and V9, including their transverse processes, are fused with each other, however, proximal parts of the processes remain separated, so there are openings between them. The lateral margin of the sacral wings is slightly concave. The urostyle is stout and comparatively short. There is no evidence that there was a postsacral vertebra on the urostyle with a pair of short transverse processes as Goldfuss (1831) believed.

The anterior and lateral margins of the scapula meet at a right angle, the anterior margin could probably be straight or even moderately convex. The posterior margin of the scapula is distinctly concave. The suprascapula (preserved as a faint imprint on the right side of the specimen) has a distal margin only moderately concave and nearly symmetrical (not extending in two processes of different size). The humerus seems to have a prominent ventral crista in its anterior third, and the distal end of the radioulna seems to be broad. The only preserved elements of the carpus are the ulnare, radiale, and the centrale 2. Other carpal elements were probably still cartilaginous, although the holotype specimen was obviously adult (judging by the ossified epiphyses of the femur and tibiofibula). The phalangeal formula is 2-2-3-3, and all fingers were of approximately the same length (see the right fore limb).

The ilia are disarticulated from one another and twisted along the axis of their shaft, so they display their lateral side with a large acetabulum. The iliac shaft was regularly bent along the whole of its length. The ischia were disarticulated from the ilia, but coalesced with one another. The femur is slightly sigmoid in shape. The tibiale and fibulare are not fused with one another. The phalangeal formula cannot be reconstructed, but the prehallux is preserved.

Measurements: Snout-vent length (SVL, measured from the anterior end of the suture between the two premaxillae to the tip of the urostyle) 53.2 mm; humerus (H) 17.0 mm; metacarpal 2 (Mc2) 11.0 mm; femur (F) 26.0 mm; tibiofibula (TF) 22.7 mm; fibulare (Fb) 11.2 mm. Ratios: SVL:H 3.13; SVL:H+Mc^2 1.9; F:TF 1.15; SVL:F+TF+Tb 0.89.

Description of STIPB Ro 4028 (Špinar's lectotype)

(Text-fig. 4)

As mentioned above, the holotype of *Palaeobatrachus diluvianus* is fixed by monotypy, i.e., it is based on a single specimen from the type series. The type series contains, as inferred from the original publication by Goldfuss (1831), in addition to the holotype specimen, also an incomplete postmetamorphic individual (Goldfuss 1831: pl. 12, fig. 5) which was probably used for the simplified illustration of Ro 4028 also in Meyer (1860: pl. 20, fig. 10), plus three other adults from which only the skulls were illustrated (Goldfuss 1831: pl. 12, figs 2–4). The skull in Goldfuss's pl. 12, fig. 3 belongs to Ro 4113 (according to the original label on the specimen), which is a plaster cast of Ro 4048, the latter illustrated in Meyer (1860: pl. 18, fig. 8). Due to the absence of the left part of the skull it can only be hypothesized that the skull in Goldfuss's pl. 12, fig. 2 was illustrated based on the plaster cast of Ro 4049, which was thus mirror-reversed and is preserved in the collections of Bonn university as Ro 4114. The skull illustrated in Goldfuss's pl. 12, fig. 4 seems not to be a palaeobatrachid, as evidenced by its prominent occipital part of the braincase and shape of the nasals. All other individuals illustrated in Goldfuss (1831: pl. 12, figs 6–9 and pl. 13, figs 1–3) are premetamorphic tadpoles or tadpoles before the end of metamorphosis, some of which probably belong to *Eopelobates* PARKER, 1929 (judging by shape and proportions of the parasphenoid).

Thus, the type series of *Palaeobatrachus diluvianus* consists of the holotype (STIPB-Goldfuss-1343), Ro 4028, Ro 4048 (and its plaster cast Ro 4113), and most probably Ro 4049 (and its plaster cast Ro 4114). According to ICZN, Art. 72.1.1 and 73.2, all these specimens are syntypes, and collectively they constitute the name-bearing type.

When Špinar (1972: 99) learned that the holotype specimen "was lost probably during World War II", he selected the specimen Ro 4028 as the "paratype" (more correctly, the lectotype or neotype; ICZN, Art. 74 and 75.1). Because in fact it was selected from syntypes of the type series, it was the name-bearing type at that time (ICZN, Art. 72.1.2).

The specimen is a juvenile, with only a moderately developed epiphysis in the femur and with only faint outlines of carpal elements (on the left side). It displays the ventral aspect of the skeleton. The pelvis is markedly shifted anteriorly.

The parasphenoid is narrow and long, with a faint median keel, its tip reaching as far as between the two premaxillae. The posterior part is faintly striated and the posterior margin is medially indented. Clavicles are moderately curved and meet at the midline. The anterior margin of the coracoids is widely concave, with both ends of approximately the same size. The synsacrum consists of fused centra of V8 + V9. The transverse processes of V4 and V3 are sharply cut at their ends, which suggests they were completed by cartilage.

Measurements: SVL ca. 32 mm; H 10.5 mm; Mc2 6.8 mm; radioulna (RU) 7.2 mm; F 18.7 mm. Ratios: SVL:H 3.05; F:H+Mc2 1.85.

Discussion

It may be surprising that Goldfuss, in his first description of the holotype specimen (1831), assigned it to a common European anuran *Rana* LINNAEUS, 1758, in spite of which he correctly recognized its similarities with *Pipa* LAURENTI,

1768. He also recognized that vertebrae in the sacral section are fused with each other as a compound bone. Meyer (1860) already figured out importance of developmental variation, thus he compared individuals of different ages separately (among others, he recognized that the specimen STIPB Ro 4028, designated by Špinar as lectotype, is a juvenile). He also recognized that in adults the sacro-urostylar articulation remains unfused, although within the synsacrum individual vertebrae lost their identity.

This was very important, because with an increasing number of palaeobatrachids from various localities it became obvious that they represent a very uniform group of fossil frogs, in which it is necessary first to recognize characteristic features common to all members of the family Palaeo-batrachidae Cope, 1865 (i.e., diagnostic features of the family) and, similarly, characteristic features common to all members of the genus *Palaeobatrachus* (i.e., diagnostic features of the genus). Only after listing the characters common to all *Palaeobatrachus* individuals, one may begin to search for those characters which are beyond the scope of this list. However, such characters may be of a different kind: they may be characteristic for a species, but they may be only a result of individual and developmental variation. It is crucial to distinguish between species-specific characters and individual and developmental variants within a species. Whereas developmental variation can be comparatively easy to recognize from features indicating individual age (such as degree of ossification of epiphyses of the long bones), individual variation can be assessed only by comparisons with a larger series of individuals of the same size and age (if this can be determined by skeletochronological methods) of related extant taxa. It is also necessary to emphasize that diagnoses should always refer to adult stage, to prevent misunderstandings that could result from comparisons of different developmental stages.

Taking this into account, one can first list those charac-ters on the holotype of *Palaeobatrachus diluvianus*, the combination of which is diagnostic to all Palaeobatrachidae (see Wuttke et al. 2013): (1) Frontoparietal azygous; (2) ramus maxillaris of the pterygoid sigmoid-shaped; (3) Eight presacral vertebrae; (4) V1+V2 fused; (5) V8+V9 fused; (6) Sacro-urostylar articulation unfused, bicondylar; (7) Neural arches imbricated; (8) Tibiale and fibulare unfused. There are also other diagnostic features of the family Palaeobatrachidae which, however, cannot be recognised on the holotype, such as parasphenoid slender and long, reaching beyond the anterior margin of the sphenethmoid; quadratojugal absent; angular with tubercular coronoid process; vertebral centra procoelous; scapula "uncleft", i.e. without an incissure between the pars acromialis and pars glenoidalis; coracoid with processus rostriformis; humerus without cubital fossa; prominent convexity on the inner surface of the acetabular portion of the ilium. At present it is not known whether all these characters are also in *Albionbatrachus* Meszoely, Špinar et Ford, 1984 whose identification is based only on the frontoparietal (Meszoely et al. 1984, Roček et al. 2015); other palaeobatrachid bones from the same locality were only indirectly associated with the *Albionbatrachus* frontoparietal and a possibility exists that *Albionbatrachus* may differ from *Palaeobatrachus*, in addition to the shape and structure of the frontoparietal, also in other characters. If this would be

true, then some of the above diagnostic characters would have to be shifted to the generic level.

Diagnostic characters of the genus *Palaeobatrachus* which can be recognized in the holotype are as follows: (1) Lateral processes of sphenethmoid shorter than anterior median process (representing ossified portion of septum nasi); (2) Paraoccipital processes of the frontoparietal do not exceed posteriorly over the level of the posterior margin of the bone in the midline; (3) Transverse processes of V2–V5 long (incorporating larval ribs); (4) V7 with reduced transverse processes; (5) Acetabulum extends beyond the anteroventral margin of the ilium. There are also other diagnostic features of the genus *Palaeobatrachus* which, however, cannot be recognized on the holotype, such as vertebral centra compressed dorso-ventrally, and dorsal tubercle of the ilium with two areas of muscle attachments separated by an oblique crista.

If all characters listed above occur in all *Palaeobatrachus* species, then only a few additional ones could characterize the species *Palaeobatrachus diluvianus*. Included among them are: (1) Shape of the frontoparietal. It is slightly broader posteriorly where it adjoins the prootics than anteriorly where it projects as two pointed anterolateral processes that contribute to the delimitation of the orbit. Anteriorly, there is a distinct median process inserted between the two nasals, and two paraoccipital processes protrude from the bone posterolaterally. A pair of parasagittal crests runs posteriorly from the anterolateral processes onto the paraoccipital processes, approaching one another in the interorbital portion of the bone and diverging again in its parietal portion. A similar, transverse crest, slightly convex anteriorly, connects the posterior ends of both parasagittal crests. The dorsal surface of the frontoparietal between the two parasagittal crests (termed the frontoparietal table; Hossini and Rage 2000, Roček et al. 2015) is depressed. Although it is known that the shape of the frontoparietal and both parasagittal crests change during development in extant pipids (Roček et al. 2015), other frontoparietal features (such as gross morphology of the posterior part) remain stable. Thus, the frontoparietal may be potentially important for species diagnoses. (2) Length of vertebrae. The vertebrae may differ in their length, and because in articulated skeletons they are often articulated with each other, this may initially provide recognition of relatively short vertebral columns in which the vertebrae are short, or long vertebral columns in which they are long. In the *Palaeobatrachus diluvianus* holotype the vertebrae are short, so the tips of the ribs are almost in contact with each other, whereas, for instance, in *Palaeobatrachus gigas* Meyer, 1852 they are long (Meyer 1860). The vertebra length is a character that can also be used in disarticulated vertebrae, but only vertebrae which are extremely different may be reliably distinguished. (3) Synsacrum. All authors who discussed palaeobatrachids focused their attention on this character, but it is very important that only synsacra of adult, fully grown individuals are compared. Clearly, as in the extant *Xenopus* Wagler, 1827, there are also paedomorphic species of *Palaeobatrachus* which retain underdeveloped characters (e.g., incompletely fused vertebrae within the synsacrum) also in adults. In such cases an incompletely fused synsacrum may be a diagnostic character of a species, whereas in those

species in which the synsacrum is completely fused only in adults it may represent just a developmental stage. It is therefore important to be sure that the synsacrum belongs to an adult, which is not possible in disarticulated bones. Špinar therefore focused his attention not only on the degree of fusion of the vertebrae, but also on how they fuse. Using this approach, he was able to recognize several species-specific ways as to how the sacral vertebra fuse with presacrals. It seems that the sacral diapophyses are incompletely fused at their bases in the adult *Palaeobatrachus diluvianus* holotype and may be considered a diagnostic feature for this species. (4) Morphometrical characteristics may also be useful, but this requires articulated skeletons. One can measure the length of skull (LC, from the anterior end of the suture between both premaxillae, to the posterior margin of the occipital bone) and length of the vertebral column (LVertCol, from the cranio-vertebral articulation to the end of the urostyle), length of the humerus (H), radioulna (RU), and Mc2 (second metacarpal, as a representative indicator of length of fingers). On hindlimbs, one can measure length of the femur (F), tibiofibula (TF), and of the fibulare (Fb). Species-specific may be ratios, mostly calculated as the relationship between these individual body proportions to the snout-vent length (SVL) which is, in the anuran skeleton, the distance between the tip of the snout anteriorly and tip of the urostyle posteriorly (not to the posterior end of the ischia because the pelvic girdle with hindlimbs is a unit which is sliding antero-posteriorly during swimming in many species of frogs (van Dijk 2002), thus the posterior end of the ischia may vary according to fossilization. In the holotype of *Palaeobatrachus diluvianus*, the vertebral column is only slightly longer than the skull. In palaeobatrachids, which are mostly permanent water-dwellers, the front limbs are longer than in other frogs, its relative length may indicate the degree of adaptation to permanent life in water. The whole front limb is preserved on the right side of the holotype specimen. Hindlimbs are also important because their relative length may indicate different locomotor capabilities (e.g., jumping, crawling, burrowing, swimming). In contrast, the skull width (usually measured as the distance between jaw joints) is not a reliable character because the skull, which is a vaulted structure, is always compressed dorsoventrally, which means that the distance between jaw joints is changed. (5) Shape of the nasals also seems to be an important species-specific character, in combination with configuration of the anterior margin of the frontoparietal. The posteromedial margin of the nasals may be divergent so they can be in contact with one another only over a short section anteriorly, or in a long median suture (which corresponds to a short or even absent anterior median process of the frontoparietal). Also their suture with the frontoparietal may be widely rounded or serrated (the latter is typical for *Palaeobatrachus laubei* Bieber, 1881). Unfortunately, the nasals are not preserved in the *Palaeobatrachus diluvianus* holotype, but their approximate shape may be inferred from the contact facets on the roof of the sphenethmoid. (6) Shape of coracoids. This character is also not preserved in the holotype specimen, but as a prominent structure, it can be well preserved in specimens exposed in ventral aspect. The coracoids may vary in their length, relative size of their medial and lateral ends, in relative size of the processus rostriformis, and in shape of their anterior margin (there may be a short process in the middle of their length, or the anterior margin may be concave and smooth. (7) Shape of scapulae. Although both scapulae are only imperfectly imprinted in the holotype specimen (the suprascapula is faintly imprinted on the right side), it seems that the shape of the anterior margin of the scapula (convex, straight, concave) can be significant for species distinction (see also Špinar 1972: text-fig. 30).

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Institutional Abbreviations

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