

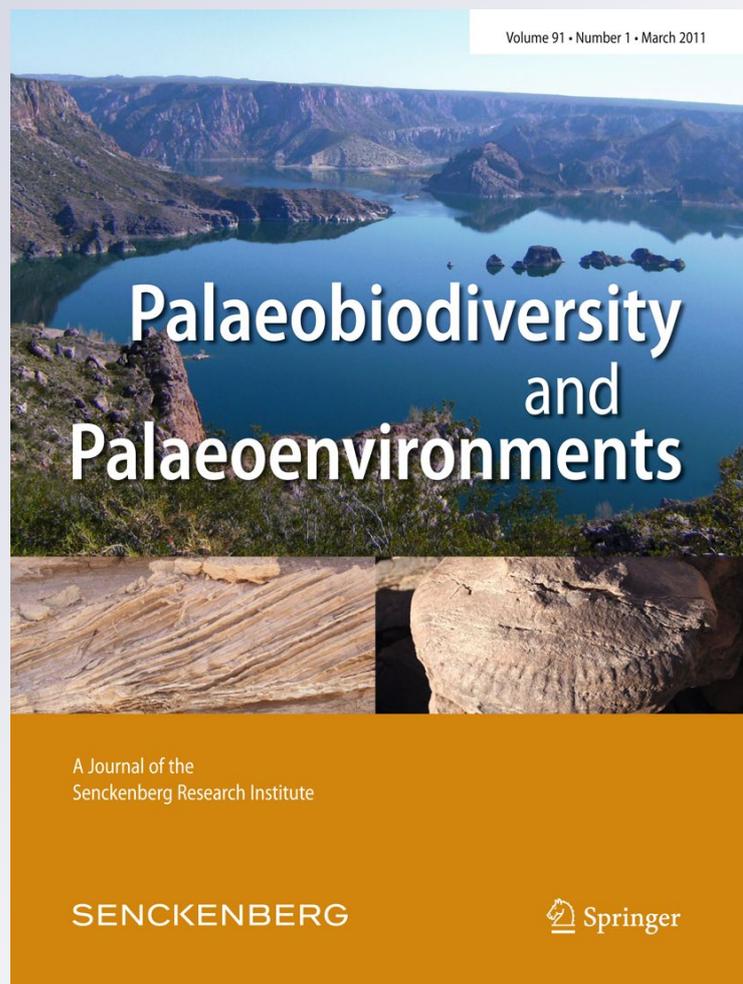
Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura)

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Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura)

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Abstract A small palaeobatrachid from the Late Eocene of Kučlín, Czech Republic is described and compared with Middle Eocene palaeobatrachids from Messel, described here as *Palaeobatrachus tobieni* (Sanchiz 1998) comb. nov., and with Middle Eocene palaeobatrachids from Geiseltal. *P. tobieni* is the earliest palaeobatrachid documented by articulated skeletons. The description of the Eocene palaeobatrachids from Messel and Kučlín necessitated a revision of all palaeobatrachid genera. In order to correctly assess taxonomic variation within the Palaeobatrachidae, we studied variation in the

frontoparietal, one of the most frequently preserved skeletal elements in the palaeobatrachids, in a sample of *Palaeobatrachus grandipes* from Bechlejovice, Czech Republic. It was found that other genera in which the frontoparietal is known (*Pliobatrachus*, *Albionbatrachus*) basically fit into the range of variation seen in *Palaeobatrachus*. Therefore, the differences that can be observed (e.g., sculpture in *Albionbatrachus*) may be interspecific in nature, rather than intergeneric. Moreover, some of the diagnostic characters of these genera are already used to diagnose the palaeobatrachid family (e.g., synsacrum in *Pliobatrachus*). Accordingly, it is proposed that these genera be synonymized with *Palaeobatrachus*, and that variations among the currently recognised genera be considered diagnostic at the species level only. The distribution of Eocene palaeobatrachids, encompassing only western and central Europe, contrasts with the distribution of palaeobatrachids in post-Eocene times. This suggests a shift in their distribution between the Late Cretaceous and Palaeocene (western Europe) and the Pliocene and Pleistocene (eastern Europe). The last palaeobatrachids were recorded from the Muchkap interglacial (621–568 Ka) in Russia. This implies that palaeobatrachids, as obligate water-dwellers, did not survive the Oka glaciation (474–425 Ka). They were probably “trapped” between a periglacial zone with temperatures below freezing in the north and a dry steppe zone in the south.

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Introduction

The earliest record tentatively assigned to the Palaeobatrachidae is a poorly preserved fragment of maxilla with peculiar lingual knobs between alveoli, recovered from the Late

Barremian of Spain (Buscalioni et al. 2008). The oldest doubtless representative of the Palaeobatrachidae is an isolated fragmentary frontoparietal from the Lower Campanian of the locality Villeveyrac in southern France (Buffetaut et al. 1996). Indeterminate palaeobatrachids, represented by disarticulated angulars, one presacral vertebra, distal humeri, and numerous ilia, have been reported from the Late Campanian or Early Maastrichtian of Spain (Astibia et al. 1990; Duffaud and Rage 1999), and another indeterminate palaeobatrachid was reported from the latest Maastrichtian of Spain (Blain et al. 2010). Furthermore, Estes and Sanchiz (1982) described *Palaeobatrachus occidentalis* on the basis of three ilia from the Late Maastrichtian of North America, although Sanchiz (1998) later doubted the generic assignment of this species. This was supposedly the first palaeobatrachid known outside Europe. Recently, another palaeobatrachid-like fragment (fused V1+V2) has been reported from the Late Maastrichtian or Early Pliocene of North America by Gardner (2008), and a partial ilium and not sufficiently prepared urostyle from the Early Maastrichtian of Alberta, Canada by Larson et al. (2010). Moreover, a recent taxonomic revision of *Neusibatrachus wilfertii* Seiffert, 1972 from the Late Berriasian–Early Valanginian of Spain revealed that all its taxonomic characters were either typical of *Palaeobatrachus* or in agreement with the expected ancestral primitive morphotype from which palaeobatrachids supposedly evolved (Báez and Sanchiz 2007). This would point to *Neusibatrachus* as a possible ancestral form of the Palaeobatrachidae.

Perhaps the earliest Cenozoic record of the Palaeobatrachidae is a small specimen of *Palaeobatrachus* from the late Palaeocene of Cernay, France, comprising a synsacrum, ilium, and humerus (Vergnaud-Grazzini and Hoffstetter 1972). A humerus from the late Palaeocene of Hainin, Belgium, may also be referable to Palaeobatrachidae (Groessens-Van Dyck 1981). Additional palaeobatrachid material from Hainin is mentioned by Folie (2006). The Eocene record is substantially richer. In Belgium, indeterminate palaeobatrachids are known from the Lower Eocene of Dornaal (Godinot et al. 1978), and Duffaud (2000) assigned fragmentary frontoparietals from Boutersem to *Palaeobatrachus* cf. *grandipes*. Several articulated but poorly preserved skeletons are known from the Middle Eocene of Geiseltal, and were assigned by Špinar (1972) to *Palaeobatrachus grandipes*. Similar skeletons are known from Messel, Germany (Wuttke 1988). Recently, additional material was recovered in Messel, tentatively assigned to a “small species of the Xenopidae” (Morlo et al. 2004), but obviously belonging to the Palaeobatrachidae. Disarticulated palaeobatrachid elements were reported from the Late Eocene of the Isle of Wight and Hordle Cliff, England, by Rage and Ford (1980) and Milner et al. (1982). Among them were a frontoparietal and some associated elements, which

were subsequently described as *Albionbatrachus wightensis* (Meszoely et al. 1984). However, Hossini and Rage (2000) questioned the generic status of this species, and considered it to belong to *Palaeobatrachus*. The only Late Eocene palaeobatrachid from continental Europe (documented by angulars, presacral vertebrae, and humeri) is from Grissoles, France (Duffaud 2000).

Frontoparietals similar to that of *Albionbatrachus* were later recovered from the Early Oligocene of Hoogbutsel, Belgium (Duffaud 2000), from the Late Oligocene (MP 30) of Oberleichtersbach, Germany (Böhme 2008), and from the Early Miocene (Agenian) of Laugnac, France (Hossini and Rage 2000). The frontoparietals from Hoogbutsel and from Laugnac were assigned to *Palaeobatrachus* (the latter as *P. robustus*), with the implication that *Albionbatrachus* can be considered a synonym of *Palaeobatrachus*.

The post-Eocene history of palaeobatrachid frogs is documented by numerous finds that have been, however, mostly restricted to central and eastern Europe (roughly east of the Rhine and north Italy). They are completely absent from Oligocene localities in France, but have been recorded in Belgium, Germany, and Switzerland. In the Miocene, palaeobatrachids are also unknown in central European localities, although they are abundant in localities of the same age (e.g., Gritsev) in eastern Europe and perhaps even in Turkey (Claessens 1997). This suggests an eastward shift in the distribution of palaeobatrachids (Rage and Roček 2003). The youngest records of the Palaeobatrachidae are from the Middle Pleistocene (Mindel I/Mindel II) of Kozi Grzbiet, Poland (Sanchiz and Szyndlar 1984) and from several localities of approximately the same age (Lower Neopleistocene according to the Russian stratigraphic scale) in the basin of the Don River (Ratnikov 1993, 1996, 1997, 2002a, b, 2003). Palaeobatrachids have not been found in younger anuran assemblages (Ratnikov 2002a, 2005), which suggests that they became extinct approximately 0.5 Ma ago.

Except for the few finds mentioned above as belonging to *Albionbatrachus*, all palaeobatrachids that date to the Miocene or older have been assigned to *Palaeobatrachus*, whereas those from the Pliocene and Pleistocene have been assigned to *Pliobatrachus* (Ivanov 2007). However, the latter genus was mainly based on a disarticulated synsacrum when first erected (Fejérváry 1917). Only much later did Sanchiz and Młynarski (1979) assign additional specimens to this taxon.

The main aim of this paper is to formally describe palaeobatrachids from the Middle Eocene of Messel, Germany and from the Late Eocene of Kučlín, Czech Republic, and to compare them with previously known Eocene palaeobatrachids from Geiseltal, Germany. In order to assess taxonomic diversity within the Palaeobatrachidae, we decided to perform a case study of individual and developmental variation in the frontoparietal in a sample

Table 1 Comparisons between the diagnostic features of the Family Palaeobatrachidae and those of previously recognised individual palaeobatrachid genera

Palaeobatrachidae	Palaeobatrachus	Pliobatrachus	Albionatrachus
<p>Maxilla with 15–18 teeth (Vergnaud-Grazzini and Hoffstetter 1972: 162).</p> <p>Frontoparietal azygous (Špinar 1972: 35).</p> <p>Parasphenoid slender and dagger-shaped (Špinar 1972: 35); parasphenoid long, markedly extended beyond anterior border of sphenethmoid (Hossini and Rage 2000: 225).</p> <p>Angular with tubercular coronoid process (Rage and Ford 1980: 49; Hossini and Rage 2000: 226); same as in <i>Pliobatrachus</i> (Vergnaud Grazzini and Mlynarski 1969: 2401–2402). Sphenethmoid same as in <i>Pliobatrachus</i> (Vergnaud Grazzini and Mlynarski 1969: 2401; Sanchiz and Mlynarski 1979: 166).</p> <p>8 procoelous, imbricate presacral vertebrae (Špinar 1972: 35); dorsoventrally</p>	<p>Premaxilla bears 6 teeth (Špinar 1972: 55).</p> <p>Maxilla without zygomatico-maxillary process (Špinar 1972, text-fig. 14); with 17 teeth (Špinar 1972: 55); 15–18 (Vergnaud-Grazzini and Hoffstetter 1972: 162); <i>P. grandipes</i> 8–17 (Hodrová 1982: 40).</p> <p>Frontoparietal of the same width anteriorly and posteriorly (Špinar 1972: 98); pineal foramen opens on the ventral face, but not on the dorsal face (Rage and Ford 1980: 48); dorsal surface covered by sculpture up to anterior margin of bone (Rage and Ford 1980, pl. 1, fig. 1).</p>	<p>Premaxilla toothed (Sanchiz and Mlynarski 1979: 169).</p> <p>Maxilla with both the frontal and zygomatico-maxillary processes (Vergnaud Grazzini and Mlynarski 1969: 2401); number of teeth 1–8 (Mlynarski 1977: 23); about 8 (Sanchiz and Mlynarski 1979: 169); 8–12 (Hodrová 1982: 40); anterior part of maxilla is toothed (Mlynarski 1977: 23); anterior diastema (Sanchiz and Mlynarski 1979: 169); anterior diastema (Hodrová 1982: 40); teeth supported by osseous knobs (Sanchiz and Mlynarski 1979: 165).</p> <p>Frontoparietal strongly convex, without sculpture (Sanchiz and Mlynarski 1979: 169); dorsal surface depressed anteriorly, anterior U-shaped depression well delimited; two parallel cristae in the middle part; pineal canal opens ventrally but not dorsally (Sanchiz and Mlynarski 1979: 165, fig. 6); flat area delimited by ridge on dorsal surface, from where the bone slants down towards its margins (Ratnikov 1997: 72).</p> <p>Parasphenoid fused to sphenethmoid (Sanchiz and Mlynarski 1979: 166).</p>	<p>Frontoparietal hourglass-shaped, with prominently sculptured (pits and ridges) dorsal surface (Meszoely et al. 1984: 144); prootic processes slender and long, with sculpture continued on them (Meszoely et al. 1984: 144); dorsal surface depressed and smooth anteriorly (termed “nasal depression” in Meszoely et al. 1984, fig. 1A); pineal foramen opens on the ventral face, but not on the dorsal face (Meszoely et al. 1984: 145).</p> <p>Angular with a coronoid process in a form of a tubercle depressed in the middle (Sanchiz and Mlynarski 1979: 166); it has two depressions separated by raised area (Ratnikov 1997: 73).</p> <p>Sphenethmoid very long, with ventral groove for parasphenoid (= “parabasal”), septum nasi very short, fenestra frontoparietalis large (1/2 of the length of the bone) (Vergnaud Grazzini and Mlynarski 1969: 2401); similar to those in other palaeobatrachids (Sanchiz and Mlynarski 1979: 166; Hodrová 1982: 39). Vertebrae procoelous, with large and dorsoventrally compressed centrum.</p>

Table 1 (continued)

Palaeobatrachidae	Palaeobatrachus	Pliobatrachus	Albionbatrachus
<p>compressed centrum, condyle and cotyle tend to be crescentic (Vergnaud Grazzini and Mlynarski 1969: 2399); transverse processes never inclined anteriorly (Vergnaud Grazzini and Mlynarski 1969: 2399).</p> <p>V1+V2 always fused (Špinar 1972: 35).</p> <p>V3–V6</p>		<p>cotyle semilunar (ends directed dorso-laterally), transverse processes never inclined anteriorly (Vergnaud Grazzini and Mlynarski 1969: 2399).</p> <p>V1 fuses at least to V2 (Sanchiz and Mlynarski 1979: 167).</p> <p>Resemble bufonids, but with centra compressed dorso-ventrally (Sanchiz and Mlynarski 1979: 167); fully consistent with the Palaeobatrachidae (Hodrová 1982: 41).</p> <p>Synsacrum consists of 2 presacral and 1 sacral vertebra (Fejérváry 1917: 149–150); Centra fused completely, leaving no sutures (Hodrová 1982, pl. II, fig. 1; Ratnikov 1997: 73); same as in other palaeobatrachids (Sanchiz and Mlynarski 1979: 167).</p> <p>Sacrum with 2 posterior condyles (Vergnaud Grazzini and Mlynarski 1969: 2399); intercondylar process of urostyle may leave corresponding depression on ventral surface of sacrum (Ratnikov 1997: 73).</p> <p>Urostyle without spina urostyli, with transverse processes as small extensions (Fejérváry 1917: 151); urostyle without dorsal crista (Sanchiz and Mlynarski 1979: 167); crista dorsalis can be well developed (Ratnikov 1997: 73); intercondylar process may protrude anteriorly from ventral part of intercotylar partition (Ratnikov 1997: 73).</p> <p>Scapula short, uncleft, well-developed crista on margo anterior (Sanchiz and Mlynarski 1979: 169).</p> <p>Coracoid similar to that in all Palaeobatrachidae (Vergnaud Grazzini and Mlynarski 1969: 2400).</p> <p>Humerus almost symmetrical (both epicondylar are of the same size) (Vergnaud Grazzini and Mlynarski 1969: 2401).</p>	<p>Vertebrae procoelous, compressed dorsoventrally (Meszoely et al. 1984: 145).</p> <p>V1 fused to V2 with no trace of fusion (Rage and Ford 1980: 49); V1 not fused to V2 (Meszoely et al. 1984: 145).</p> <p>Synsacrum consists of 2 presacrals and 1 sacral vertebra (Meszoely et al. 1984: 145).</p> <p>Sacro-urostylar articulation bicondylar (Meszoely et al. 1984: 145).</p>
<p>V8+V9 or V7+V8+V9, including their transverse processes, may fuse, thus forming a synsacrum (Špinar 1972: 35); synsacrum consists of 3 vertebrae (Tschudi 1838: 42–43).</p> <p>Sacro-urostylar articulation bicondylar (Špinar 1972: 35).</p>	<p>Shape and morphology of synsacrum vary (Špinar 1972: 98).</p> <p>Urostyle short, broad, stake-shaped (Špinar 1972: 98).</p>		
<p>Urostyle in all Palaeobatrachidae is the same as in the holotype of <i>Pliobatrachus langhae</i>, 2 anterior cotyles, dorsal crest very indistinct (Vergnaud Grazzini and Mlynarski 1969: 2400).</p> <p>Scapula short, uncleft, i.e., without an incisure between pars acromialis and pars glenoidalis (Špinar 1972: 35; Hodrová 1982: 43).</p> <p>Coracoid with processus rostriformis sensu Špinar 1972 (Špinar 1972: 35, 80).</p> <p>Humerus without cubital fossa and ventral crest (Vergnaud Grazzini and Mlynarski 1969: 2401).</p>	<p>Humerus asymmetrical (epicondylus ulnaris slightly larger than epicondylus radialis) (Vergnaud Grazzini and Mlynarski 1969: 2401).</p>		

Table 1 (continued)

Palaeobatrachidae	Palaeobatrachus	Pliobatrachus	Albionatrachus
Acetabular portion of the ilium large (about 2/3 of complete acetabulum), symphyseal area strongly convex (Vergnaud Grazzini and Mlynarski 1969: 2401); prominent convexity on the inner surface of the acetabular portion (Vergnaud-Grazzini and Hoffstetter 1972: 164).	Dorsal tubercle of the ilium mostly bears 2 impressions separated by an oblique crista (Vergnaud Grazzini and Mlynarski 1969: 2401).	Ilium with a single dorsal tubercle, not subdivided by crests (Sanchiz and Mlynarski 1979: 169; Mlynarski et al. 1984: 213); dorsal tubercle not separated (Vergnaud Grazzini and Mlynarski 1969: 2401); usually undivided [...] divided in some ilia (Hodrová 1982: 46); no well-developed preacetabular fossa (Mlynarski et al. 1984: 213); iliac synchondrosis somewhat stronger (Mlynarski et al. 1984: 213).	

of several tens of *Palaeobatrachus* specimens from a single locality (Bechlejovice, Czech Republic). Finally, all known Cenozoic occurrences of palaeobatrachids are summarized in this paper. This makes it possible to assess changes in the distribution of palaeobatrachids from the Palaeocene to the Middle Pleistocene, to infer reasons for these changes and, finally, to consider the reasons for the extinction of this group.

Abbreviations. Ba – Collection Bastelberger, Munich; Fle – Collection Flegel, Hamburg; GM – Geiseltalmuseum Halle (Saale); HLMD-Me Hessisches Landesmuseum, Darmstadt, collection Messel; Kel – Collection Keller, Frankfurt a.M.; Kess. – Collection Kessler, Darmstadt; Pb – Collection of palaeobatrachids, National Museum Prague; Po – Collection Pohl, Thermopolis, Wyoming; SMF-Me – Senckenbergmuseum Frankfurt am Main, collection Messel; So – Collection Sommer, Michelstadt; UDB-Kuc – Bilina Coal Mines, collection Kučlín; We – Collection Weiss, Fischbach i.T.

Anatomical abbreviation. SVL – snout-vent length, measured from the symphysis of the premaxillae to the posterior margin of the ischia.

Generic diversity

Historical

The genus *Palaeobatrachus* was established by Tschudi in 1838, on the basis of “*Rana diluviana*” of Goldfuss (= *Palaeobatrachus diluvianus* Tschudi, 1838) from the uppermost Oligocene (MP 30) of the locality Orsberg near Bonn in Germany. Tschudi correctly recognised that this species did not belong to *Rana* (the synsacrum was clearly mentioned by Tschudi on p. 42, which contains a quote from the original description by Goldfuss). The first thorough account of the genus (including tadpoles) was given by von Meyer (1860), and includes a description of the synsacrum in the holotype and various other specimens (von Meyer 1860: 150). The family Palaeobatrachidae was erected by Cope in 1865, and the first review of the Palaeobatrachidae (still consisting of a single genus) was published in two parts by Wolterstorff (1886, 1887).

In 1917, Fejérváry described an isolated fragmentary synsacrum consisting of three vertebrae and a separate urostyle from the early Pleistocene (Biharian) of the locality Püspökfördö (now Betfia in Romania) as *Pliobatrachus langhae*, and associated one angular from the same locality with them. At that time, the locality was considered to be of Pliocene age, explaining the generic name (the species name was derived from Aranka M. Lángh, Fejérváry's fiancée). Although palaeobatrachids were comparatively well known at that time, Fejérváry (1917) rather surprisingly related *Pliobatrachus* to the extinct genus *Platosphus* De l'Isle, 1877, which has a synsacrum consisting of two vertebrae

and belongs to the family Bufonidae (it has since been synonymized with *Bufo*; Dubois and Bour 2010). Subsequently, similar synsacra and urostyles were recovered by Młynarski (1960, 1961, 1962) from the Polish Pliocene localities of Wąże I and Rębielice Królewskie, and some of these specimens were described as the new species *Bufo tarloi* Młynarski, 1961. However, comparisons with the type material of *Pliobatrachus* Fejérváry, 1917 revealed that the holotype of *Bufo tarloi* (a urostyle) belongs to *Pliobatrachus* (as *P. tarloi*), and that *P. tarloi* is most probably a synonym of *P. langhae* in any case (Vergnaud Grazzini and Młynarski 1969). Vergnaud Grazzini and Młynarski (1969) were also the first to suggest a close relationship between *Pliobatrachus* and *Palaeobatrachus*. Extensive excavations in other Pliocene and early Pleistocene localities (Wąże I, Rębielice Królewskie I and II, Sanchiz and Młynarski 1979; Hajnáčka, Ivanovce, Hodrová 1981, 1982; Wąże II, Młynarski et al. 1984; Kozi Grzbiet, Sanchiz and Szyndlar 1984; Apastovo, Veretie, Koziy Ovrage, Korotoyak, Liventsovka V, Staraya Kalitva I and II, Uryv I and Yablonovets, Ratnikov 1997) revealed other disarticulated bones, which were related with synsacra and urostyles attributed to *Pliobatrachus* on the basis of the stratigraphic ages of the localities. Variation in this material, however, led to considerable taxonomic uncertainty at the species level, leading Sanchiz and Szyndlar (1984) to suggest that all material not recovered from the type locality should be referred to *Pliobatrachus* cf. *langhae*. More recently, Ratnikov (1997) questioned the validity of *Pliobatrachus* based on the presence of rather high morphological variation within this genus, as well as the strong resemblance between *Pliobatrachus* and *Palaeobatrachus*.

In 1941, Kuhn described the genus *Halleobatrachus* from the Middle Eocene of Geiseltal, Germany, and tentatively assigned it to the Palaeobatrachidae. He considered *Halleobatrachus* distinct from *Palaeobatrachus* because the synsacrum of the former supposedly consisted only of the sacral vertebra and the most posterior presacral, rather than of three vertebrae as in other palaeobatrachids, and because the sacral diapophyses were large (see, however, comments on Geiseltal palaeobatrachids below).

A further palaeobatrachid, this time represented by three-dimensionally preserved isolated bones, was recovered from the Late Eocene of southern England. Meszoely et al. (1984) noted the presence among this material of a domed frontoparietal with horizontal, sculptured table, which they considered so distinctive that they erected the genus *Albionbatrachus* for these English specimens. This was, however, strongly criticized by Hossini and Rage (2000), who questioned the validity of *Albionbatrachus*.

From Messel, another middle Eocene locality, Wuttke described in his PhD thesis (1988) nine incomplete palaeobatrachid skeletons under the generic name *Messelobatrachus*. The most important diagnostic characters are a frontoparietal

that is wider posteriorly than anteriorly, and a synsacrum that comprises three vertebrae (V7–V9) but bears well-developed diapophyses only on the sacral (V9). The diapophyses of V7 and V8 are either absent or vestigial. This material is revised and formally described below.

To complete the list of hitherto recognised palaeobatrachid genera it should be added that another genus, *Lithobatrachus*, was established by Parker (1929) on the basis of a poorly preserved specimen originally described as *Hyla europaea* by Noble (1928). The specimen was collected from the Late Oligocene locality Rott near Bonn, and deposited in the Natural History Museum, London. Parker assigned it to the Palaeobatrachidae (which was disputed by Noble 1930), but his diagnosis was rather vague. Personal examination of the specimen by one of us (Z.R. in 1994) revealed that most of the diagnostic characters given by each author are too unclear to be interpreted unambiguously. One of the few that can be properly assessed (a lateral beak-like projection on the coracoid; note that both coracoids are represented by well-preserved imprints) seems to be absent (although this seems to be the norm in Eocene palaeobatrachids; see below). Thus, assignment of this late Oligocene specimen to the Palaeobatrachidae is doubtful.

Diagnosis of Palaeobatrachidae

The family Palaeobatrachidae is now readily distinguishable from other anuran families. This strongly contrasts with the situation 50 years ago, when Palaeobatrachidae was considered merely “a waste basket for difficult specimens” (Hecht 1963: 24). However, the diagnostic features of the individual genera included in the Palaeobatrachidae are less clear, as they often overlap with the diagnostic features of the family (Table 1) and do not take into account individual and developmental variation. Therefore, we present below a list of the diagnostic characters of the family, which may not be used in diagnoses at lower taxonomic levels. Please note that presence of the rostriform process of the coracoid and the cubital fossa of the humerus most probably do not apply for Eocene taxa, so these two characters can potentially be removed from the diagnosis.

Maxilla without, or with strongly reduced, zygomatico-maxillary process (Špinar 1972, text fig. 14; Vergnaud Grazzini and Młynarski 1969, pl. I, figs. 9, 10). Quadratojugal absent (posterior process of maxilla terminates without contacting any other bone). Nasals narrow and crescent-like (Špinar 1972, text fig. 13). Frontoparietal azygous, with dorsal surface flat or domed. Parasphenoid without lateral alae, extremely long and slender (“dagger-shaped”), with anterior tip extending beyond anterior border of sphenethmoid. Angular with coronoid process either smooth or bearing muscle scars on dorsal surface (Vergnaud Grazzini and Młynarski 1969, pl. I, figs. 25, 26; Młynarski 1977, pl. VI, fig. 5; Hossini and Rage 2000, figs. 1–2, 3). Sphenethmoid long, with frontoparietal fenestra more than

half total length of bone (Sanchíz and Młynarski 1979, fig. 8-2), with two parallel ridges delimiting articulation area of parasphenoid on ventral surface (Vergnaud Grazzini and Młynarski 1969, pl. 1, fig. 24; Sanchíz and Młynarski 1979, fig. 8-1), and with septum nasi and lateral processes (= ossified parts of postnasal walls) very short (Sanchíz and Młynarski 1979, fig. 8-1). Mentomandibular ossified, fused to dentary (Špinar 1972: 35). Vertebral centra procoelous, strongly compressed dorsoventrally, with condyle and cotyle typically crescentic (Vergnaud Grazzini and Młynarski 1969, pl. 1, figs. 5, 6; Špinar 1972, text fig. 17; Sanchíz and Młynarski 1979, fig. 5-6). V1 and V2 fused in adults. V7, V8 and sacral vertebra (V9) fused to form synsacrum (Roček and Rage 2000, fig. 9). V2–V5 bear free ribs in juveniles, but ribs are coalesced to diapophyses in adults (consequently, diapophyses appear long). Urostyle without diapophyses, with dorsal crest poorly developed or entirely absent (Sanchíz and Młynarski 1979, figs. 5-7, 8; Hodrová 1982, pl. I, figs. 3, 4). Clavicle with long, straight scapular process (sensu Špinar 1972) on lateral end (Špinar 1972, text fig. 32). Coracoid with beak-like rostriform process (sensu Špinar 1972) on anterior margin of lateral end (Špinar 1972, text fig. 31; Sanchíz and Młynarski 1979, fig. 7-6); rostriform process probably absent in Eocene taxa. In articulated skeletons, processes on clavicle and coracoid contribute to formation of glenoid fossa (Špinar 1972, text fig. 30B). Scapula short, with anterior margin straight, and acromial and glenoidal portions not separated by incisure (Sanchíz and Młynarski 1979, figs. 7-1, 4; Hodrová 1982, pl. II, figs. 4–6). Humerus without cubital fossa (except for Eocene taxa), with caput humeri comparatively small and located on or near long axis of bone, and with epicondyles similar in size (Vergnaud Grazzini and Młynarski 1969, pl. 1, figs. 20–22; Sanchíz and Młynarski 1979, figs. 6-6, 7). Metacarpals markedly elongated. Ilium with massive ascending part, large acetabulum extending anteroventrally beyond margin of main body of bone (concealing descending part), and symphyseal area strongly protruding; dorsal tubercle protrudes only slightly in dorsal direction, but is laterally prominent and bears muscle scars on lateral surface; distinct horizontal depression on inner surface of iliac shaft, ventral margin of which continues onto dorsal margin of ascending part (Vergnaud Grazzini and Młynarski 1969, pl. I, figs. 17–19). Pubes ossified. Proximal tarsals (tibiale and fibulare) not fused.

Variation

In order to assess developmental and intraspecific variation, we studied the development of the frontoparietal in *Palaeobatrachus* from Bechlejovice (Late Oligocene). The number of specimens from this locality in which the frontoparietal is preserved, either as bone or as an imprint in the sediment, is about 80. The frontoparietal was chosen because both articulated and isolated examples are known, because the

holotypes of *Albionbatrachus wightensis* and *Palaeobatrachus robustus* are frontoparietals, and because in *Pliobatrachus* frontoparietal morphology is used as a diagnostic character (Sanchíz and Młynarski 1979).

A thorough examination of all specimens in which the frontoparietal was preserved revealed two principal types of frontoparietal in adults (identified based on ossified epiphyses of the long bones). Frontoparietals of the first type (Fig. 1, upper row) are long and distinctly waisted in the middle (interorbital) section, with two symmetrical arched crests on the dorsal surface that join in the middle of their length to produce a distinct median crest that bifurcates both anteriorly and posteriorly. The part of the bone delimited by the dorsal crests is dome-like and protrudes above the moderately convex basal areas lying farther anteriorly and posteriorly (marked by dark gray in the diagram in Fig. 1). Palaeobatrachid frontoparietals of the second type that occurs at Bechlejovice (Fig. 1, right lower part) are thin, smooth and dorsally flat. They are narrower anteriorly than posteriorly, and are not constricted in the middle. If symmetrical ridges occur on the dorsal surface, they are low and rounded (Fig. 1t, ii, jj).

Morphologically, the most similar to the first type of the frontoparietals are those that are smaller and have both crests unfused (Fig. 1e-k). The area between the crests is flat or slightly depressed (Fig. 1f). The rest of the similar frontoparietals, clearly belonging to the first type, show less extensive development of all characteristic features (they are less constricted or not constricted around the midpoint, the crests are not pronounced but are well separated from each other, and the degree of dorsal convexity is slight; Fig. 1l, s, cc). Finally, the first type of frontoparietals may also be considered to include the smallest frontoparietals. These are flat and low, and have rounded crests that can be recognised only anteriorly and posteriorly.

It may be inferred from the shape of the frontoparietals of the first type that the described series is in fact a developmental series. This is supported by the size distribution of the frontoparietals and the less ossified epiphyses of the long bones associated with the purportedly younger frontoparietals. The series begins with small, flat and smooth frontoparietals, and later the two parasagittal crests appear close to the lateral margins of the bone. The crests move closer to one another and ultimately come into contact in the middle of their length. At the same time, the crests become deeper, so that the bone takes on a domed shape. The distinctness of the border between the basal layer of the bone (Fig. 1a-2) and the upper, domed part suggests that the latter could be some sort of exostosis, similar to those in *Ceratophrys* or in casque-headed tropical hylids (Trueb 1970).

At the same time, some developmental stages are represented by several individuals, which illustrate the range of individual variation. For instance, the adult stage is represented by specimens illustrated in Fig. 1a-1, b-d, the

preceding stage in Fig. 1e–k, and the stage before that in Fig. 1l–o. It is obvious that the principal features vary only slightly within each stage.

The situation is not so clear in the second type (flat and smooth frontoparietals illustrated in the right lower part of Fig. 1). We tried to arrange them in a developmental series too, which seems most satisfactory for the specimens depicted in the left and right columns of that part of the figure (Fig. 1ii, dd, t and kk, gg, bb). However, the range of morphological variation in the purportedly most ontogenetically advanced frontoparietals (presumably adult, as evidenced by epiphyses of the associated long bones) also encompasses forms that differ strongly from those illustrated in Fig. 1t and bb. This might suggest the presence of additional taxa among these small forms.

Moreover, the youngest frontoparietals of the first type are similar to the youngest frontoparietals assigned to the second type. In fact, these young specimens can barely be distinguished from each other. The reason may be that, even at the adult stage, small palaeobatrachids would not have attained the large size and extensive degree of ossification seen in large palaeobatrachids. Large palaeobatrachids with domed frontoparietals (mentioned above as the first type) could have evolved from small forms by prolongation of their somatogenesis accompanied by hyperostosis, or vice versa—small, less ossified palaeobatrachids with flat and thin frontoparietals could have evolved from large palaeobatrachids by abbreviation of somatogenesis. The latter alternative is more probable, as suggested by a domed frontoparietal from the early Campanian of Villeveyrac (Buffetaut et al. 1996).

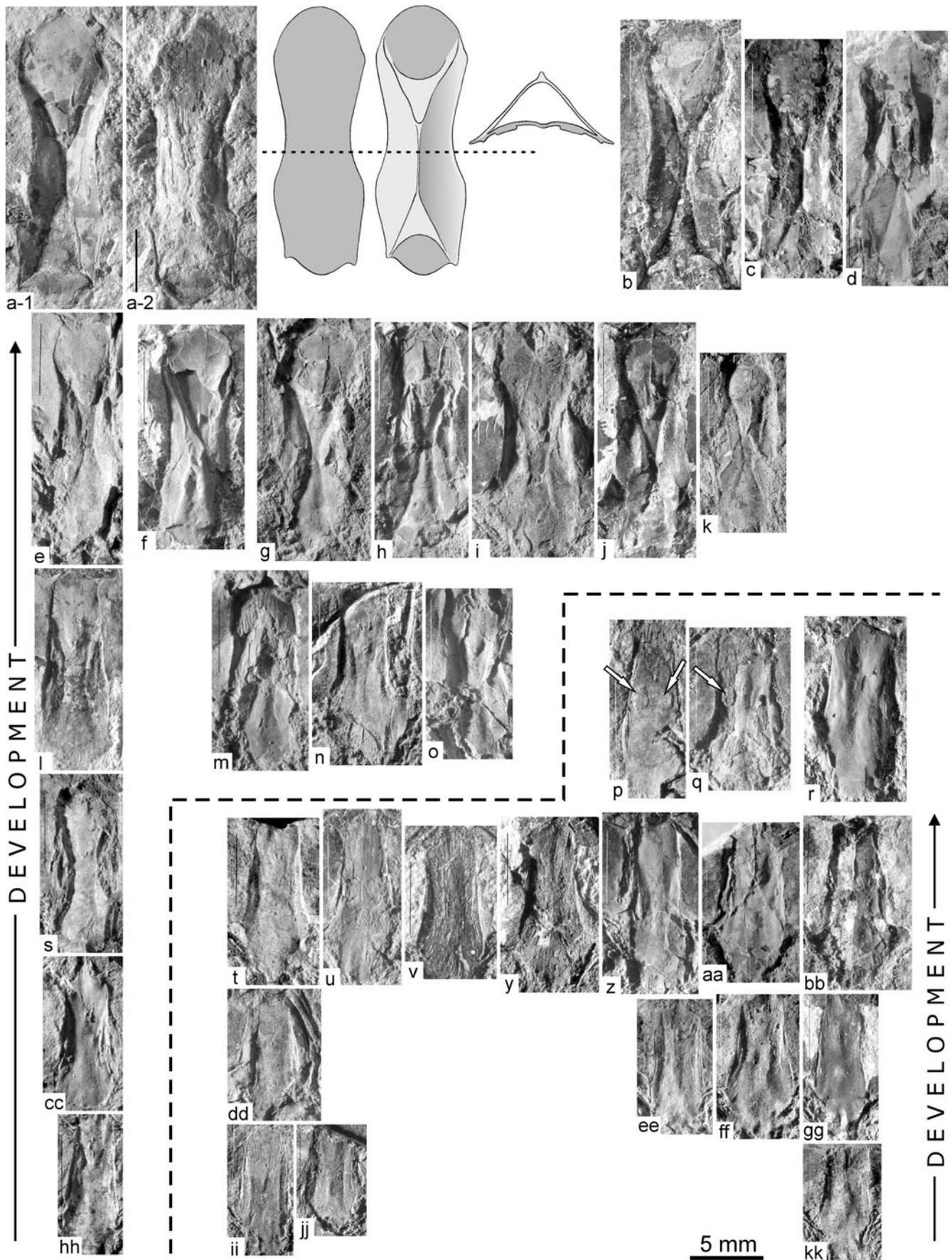
Discussion

As noted above, three (or four; see, e.g., Sanchiz 1998) genera have been recognised within the Palaeobatrachidae. Besides *Palaeobatrachus*, these are *Pliobatrachus*, *Albionbatrachus*, and *Messelobatrachus* (disregarding *Halleobatrachus* and *Lutetibatrachus*, which are generally not regarded as palaeobatrachids). *Palaeobatrachus* is the type genus of the family Palaeobatrachidae, and Tschudi (1838) emphasized the presence in the holotype of his *Palaeobatrachus diluvianus* (“*Rana diluviana*” of Giebel) of, in particular, three (V7–V9) sacral vertebrae fused to each other by their diapophyses (i.e., a synsacrum) and one free caudal vertebra between the last sacral vertebra (V9) and the urostyle. From today's perspective, the synsacrum is a diagnostic character of all Palaeobatrachidae, and the holotype shows an anomalous condition, because in typical specimens V9 articulates directly with a urostyle that incorporates all of the caudal vertebrae (Špinar 1972, text fig. 18B). A more thorough description of the holotype was given by von Meyer (1860), who mentioned the following characters

as being most important: skull longer than vertebral column (measured from craniovertebral articulation to anterior end of urostyle); orbits located anteriorly; otic capsules (“Felsenbeine”) large; six free vertebrae (V1 and V2 fused with each other); synsacrum consisting of V7, V8, and V9; transverse processes of synsacral vertebrae unfused in juveniles, fused into compact lamellae in adults, and partly fused but separated by fenestrae at intermediate stages; urostyle comparatively short, robust, and free from synsacrum; tibiofibula slightly shorter than femur. It is obvious that the definition of the genus *Palaeobatrachus*, as it was established by von Meyer (1860), overlaps extensively with the general features of the Palaeobatrachidae (see above and Table 1).

As noted above, *Pliobatrachus* was erected on the basis of an isolated synsacrum and urostyle, and referred to the Bufonidae. The similar synsacra and urostyles, as well as other isolated bones associated with them, were recovered from the Pliocene of Poland. Vergnaud Grazzini and Młynarski (1969) assigned them to the Palaeobatrachidae. Their list of characters for *Pliobatrachus*, based on the material available at that time, led them to conclude that *Pliobatrachus* and *Palaeobatrachus* (the only palaeobatrachid known at the time) agreed with each other in morphology of the following elements: presacral vertebrae, urostyle, coracoid, clavicle, humerus, maxilla, sphenethmoid, and coronoid process of angular. The only differences involved the structure of the synsacrum (in the Polish material either only one, i.e. V8, is fused to the sacral vertebra, whereas V7 is free, or two, i.e. V7 and V8, are fused to the sacral vertebra), and the shape of the dorsal tubercle of the ilium (compact in Polish material, whereas in

Fig. 1 Individual and ontogenetic variation among palaeobatrachid frontoparietals from the Late Oligocene of Bechlejovice. The *left column* represents a presumed developmental series from the earliest stage (**hh**) to adult (**a-1**), with individual variation displayed horizontally for the three most advanced developmental stages (adult: **a-1**, **b-d**; penultimate stage: **e**, **g-k**; preceding stage: **l-o**). All specimens are sediment impressions of the dorsal surface of the bone, with the following exceptions: **a-2** represents the dorsal side of the basal layer of the bone, and **f** is a remnant of the anterior part of the basal layer combined with an impression of the inner surface of the domed part of the bone. The diagram shows the basal part of the bone (*left*), a reconstructed version with the domed part restored in *light gray* (*middle*), and a hypothesized cross-section at the level marked by the *broken line* (*right*). Individual variation (horizontal series **t-bb**) and presumed ontogenetic variation (vertical series) in thin, flat and smooth frontoparietals is illustrated at the *lower right*. All specimens are sediment impressions of the dorsal surface, except that **p** and **q** are completely or partly preserved bones in ventral aspect (please note the knob-like structures marked by arrows, which supposedly fitted into openings in the roof of the braincase; see also Špinar 1972, plate 11) while **r** is a complete frontoparietal in dorsal aspect. All bones to scale. **a-1** Pb963, **a-2** Pb962, **b** Pb528, **c** Pb552, **d** Pb80, **e** Pb101, **f** Pb1369, **g** Pb105, **h** Pb107, **i** Pb113, **j** Pb804, **k** Pb498, **l** Pb500, **m** Pb93, **n** Pb157, **o** Pb1575, **p** Pb671, **q** Pb166, **r** Pb301, **s** Pb99, **t** Pb537, **u** Pb138, **v** Pb405, **y** Pb1674, **z** Pb156, **aa** Pb304, **bb** Pb1248, **cc** Pb170, **dd** Pb1566, **ee** Pb1537, **ff** Pb148, **gg** Pb592, **hh** Pb 132, **ii** Pb770, **jj** Pb141, **kk** Pb525



typical specimens of *Palaeobatrachus*—but not always—separated into two depressions interpreted as the respective insertion areas of the gluteus muscle and of the iliofemoralis plus the iliofibularis). Špinar (1972), however, found enormous variation in the synsacra within a sample of palaeobatrachids from the single locality of Bechlejovice, and synsacra of *Pliobatrachus* fit into the observed range. The diagnostic value of the dorsal tubercle on the ilium was doubted even by Vergnaud Grazzini and Młynarski (1969). They concluded that "... all characters that distinguish the Palaeobatrachidae from other anurans are present also in *Pliobatrachus*", but "... because of the lack of more precise characters it would be premature to join *Pliobatrachus* to the genus *Palaeobatrachus*". They did not exclude the possibility that the two genera might be united in the future.

Given this situation, attempts were made to recover other, previously unknown elements, which could provide additional characters to be used in a differential diagnosis of *Pliobatrachus*. Młynarski (1977) pointed to a reduced number of maxillary teeth in *Pliobatrachus* (1–8), in contrast to 15–18 in *Palaeobatrachus*. Unfortunately, he did not mention the number of tooth positions, which is more significant than the number of preserved teeth. Nevertheless, it is clear that the posterior part of the bone was toothless in all palaeobatrachids, as illustrated in Špinar (1972, plate 9-2). For the sake of clarity it should be noted that the maxilla is reversed in Młynarski (1977, fig. 1). Sanchiz and Młynarski (1979) also listed the following diagnostic characters for *Pliobatrachus* from Poland: reduced number of teeth, presence of a diastema (although not precisely defined, it can be inferred from p. 23 of Młynarski (1977) that instead of a gap between the dentitions of the premaxilla and maxilla, as the term "diastema" might suggest, this is a toothless interval near the posterior end of the maxilla), "teeth supported lingually by alternating osseous knobs" (which is, however, a common feature of all palaeobatrachids, as indicated by maxillae from the Late Miocene of Gritsev), frontoparietal domed and with two symmetrical crests on the dorsal surface (comparable with one of the intermediate developmental stages of the first type from Bechlejovice; Fig. 1l, e–k), and angular with coronoid process bearing muscle scars on dorsal surface (a feature which was considered by Vergnaud Grazzini and Młynarski 1969 to be common to all palaeobatrachids). Sanchiz and Młynarski (1979) concluded that the sphenethmoid, V1+V2 complex, synsacrum and urostyle, scapula, coracoid, and ilium of the Polish *Pliobatrachus* specimens are similar to those of other palaeobatrachids. It therefore seems that there is no significant support for maintaining *Pliobatrachus* as a separate genus of the Palaeobatrachidae, and that Młynarski's (1977) decision to retain *Pliobatrachus* for the post-Pliocene forms was not justified by the relevant anatomical evidence.

The genus *Albionbatrachus* was established by Meszoely et al. (1984) on the basis of a frontoparietal, V1+V2

complex, synsacrum, procoelous presacral vertebrae and angular. The holotype frontoparietal, now deposited in the Museum of Comparative Zoology, Harvard University (MCZ 8784), was described in the generic diagnosis as "a distinct, hourglass-shaped, with a prominently sculptured dorsal surface". However, other palaeobatrachid frontoparietals of that size (Fig. 1, upper two rows) are also hourglass-shaped. Nevertheless, in contrast to its counterparts in all other palaeobatrachids, including *Palaeobatrachus robustus* (see Hossini and Rage 2000; not correctly illustrated in Vergnaud-Grazzini and Hoffstetter 1972, pl. 1-6a), the dorsal horizontal table of the holotype frontoparietal of *Albionbatrachus* is sculptured with pits and ridges, and the sculpture extends onto the posterolateral processes. It may be inferred that the anterior basal portion of the bone (incorrectly termed the "nasal depression" by Meszoely et al. 1984, fig. 2a) was broken off. The same also holds true for the posterior part, as can be inferred from the very short distance between the "mesencephalic impression" and the preserved margin of the bone. Under this assumption, the general shape of the intact frontoparietal would not have differed substantially from that seen in the Late Oligocene *Palaeobatrachus* from Bechlejovice (Fig. 1e–k). Sculpturing alone, however well developed (Rage and Ford 1980, pl. 1-1), seems insufficient for maintaining *Albionbatrachus* as a separate genus, a conclusion in accordance with the view of Hossini and Rage (2000). We suggest that this taxon be maintained as a species of *Palaeobatrachus*, *P. wightensis*. Therefore all known palaeobatrachids are referred to the single genus *Palaeobatrachus*, as are the fossils described in further text. For discussion of the generic status of the palaeobatrachid from Messel see below.

Systematic palaeontology

Palaeobatrachidae Cope, 1865

Palaeobatrachus Tschudi, 1838

Palaeobatrachus tobieni (Sanchiz, 1998) comb. nov.

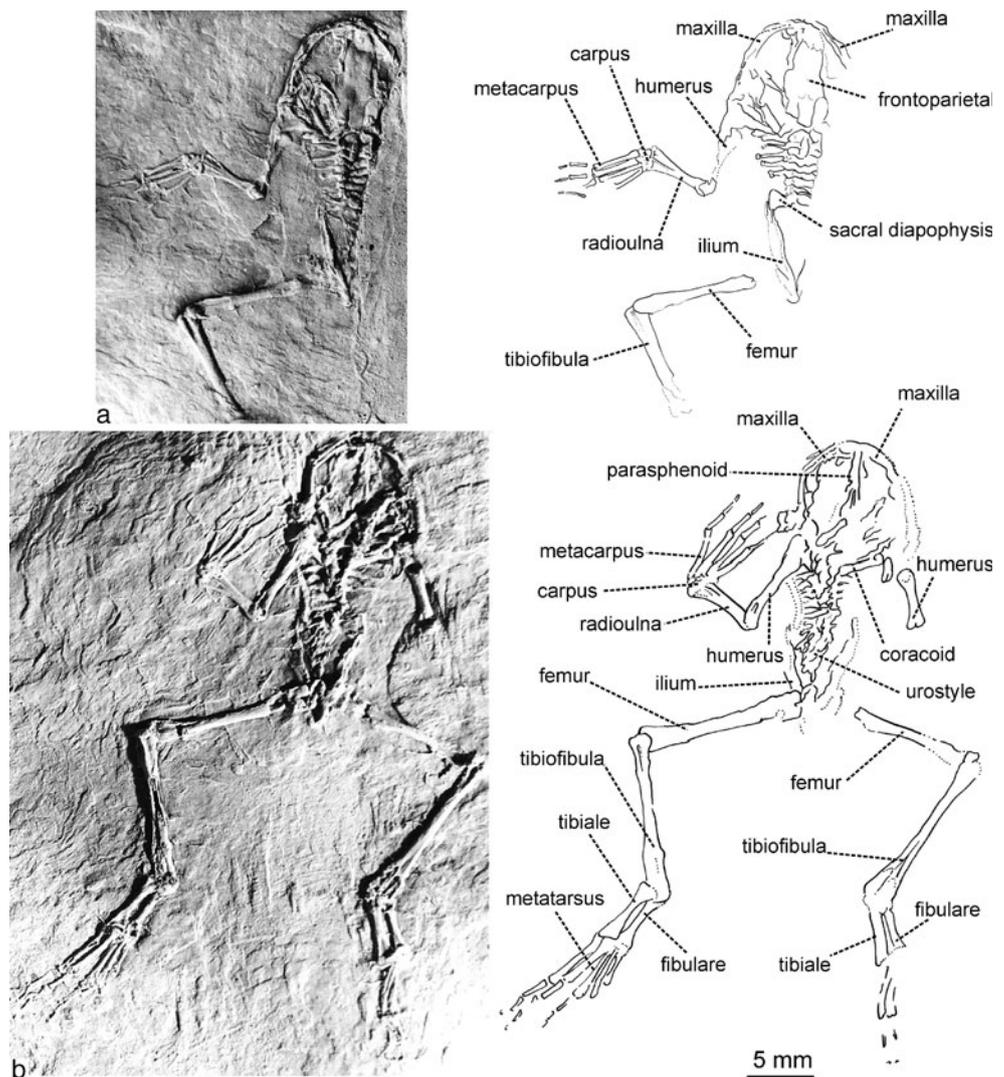
1975 (part) *Propelodytes wagneri* Weitzel, 1938; Klemmer, 1975, p. 196, fig. 4.

1998 *Messelobatrachus tobieni* Wuttke, 1988; Sanchiz, p. 36.

Holotype: SMF-Me 752a+b; incomplete skeleton embedded in two epoxy-resin slabs, representing the main part and counterpart in ventral and dorsal aspects, respectively (Figs. 2 and 3c, f, h).

Type locality and age: "Grube Messel" near Darmstadt, southern Hessen, Germany. Lower Geiselstadium (Franzen and Haubold 1986), Oil-Shale Formation (sensu Weber

Fig. 2 *Palaeobatrachus tobieni* sp. nov., Middle Eocene, Messel, Germany. **a** Skeleton in dorsal view, SMF Me 752b, holotype. **b** Skeleton in ventral view, SMF Me 752a, holotype. Scale bar applies to both specimens



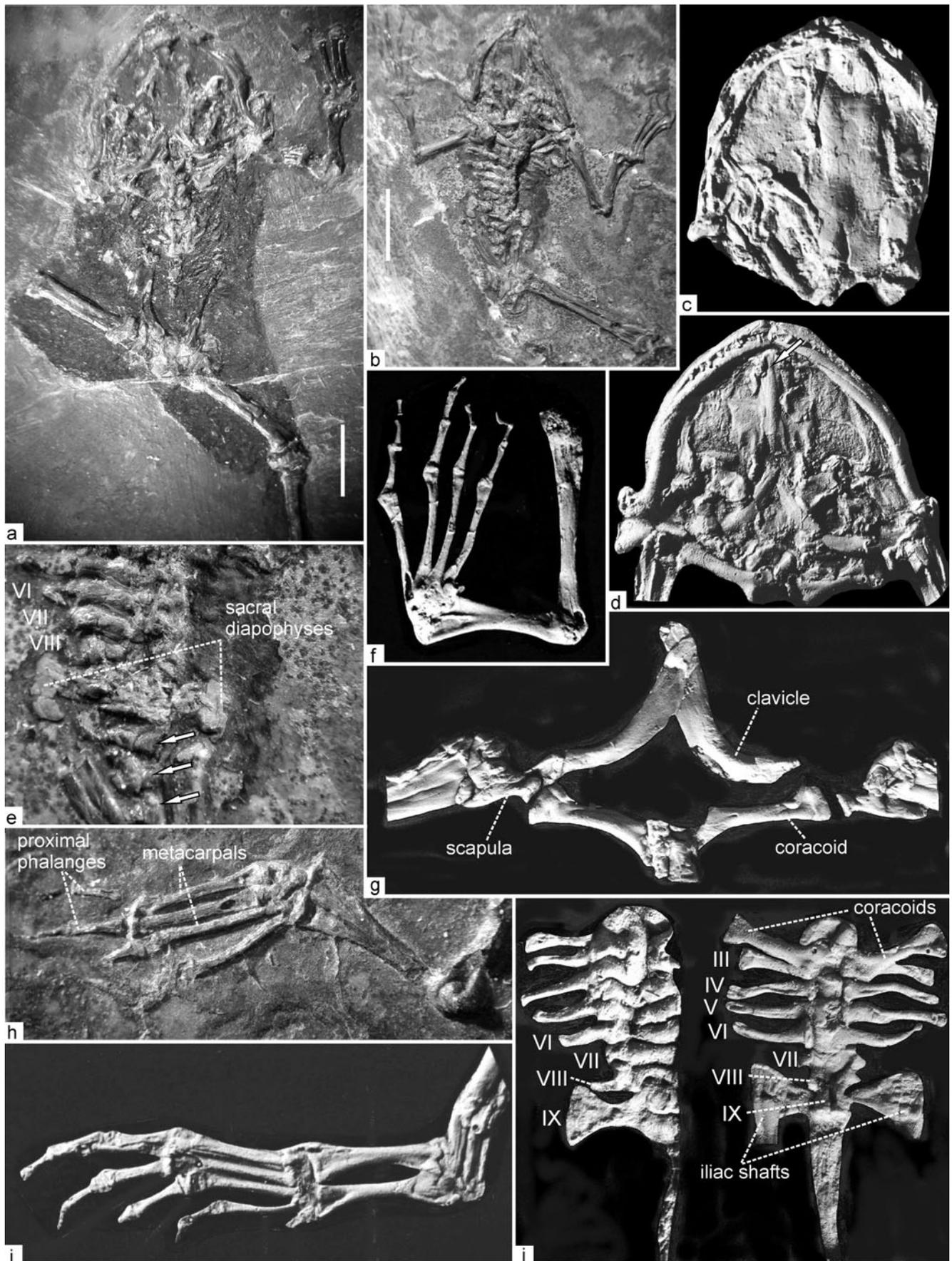
and Hofmann 1982), Middle Eocene (MP 11), 47 Ma (Franzen 2005a; Mertz and Renne 2005).

Paratypes: SMF-Me 1123, incomplete skeleton in ventral aspect embedded in an epoxy-resin slab, showing outlines of soft parts of the body, but without right forelimb and distal parts of hindlimbs (Fig. 3a). SMF-Me 486, incomplete skeleton in ventral aspect, without right hindlimb (Fig. 3b, e). Both specimens are from the same locality and stratum as the holotype.

Differential diagnosis

Palaeobatrachus tobieni differs from following species of *Palaeobatrachus* represented either by articulated skeletons of approximately the same size or by disarticulated bones in having: sphenethmoid partially co-ossified with prootics (contra *P. diluvianus*, *P. grandipes*, *P. laubei*, in which sphenethmoid and prootics are separated from each other);

small process on prootic articulated with medial ramus of pterygoid (contra *P. diluvianus*, *P. grandipes*, *P. laubei*); frontoparietal unsculptured (contra *P. robustus*, in which there are shallow pits on dorsal table, and *P. wightensis*, which is highly sculptured with pits and ridges), broader posteriorly than anteriorly (contra *P. grandipes*, *P. robustus*), not divided into left and right frontoparietal (contra *P. hiri*); dorsal surface of frontoparietal without symmetrical cristae (“parasagittal crests“ of some authors) (contra *P. langhae*; *P. wightensis*; *P. robustus*, *P. hiri*); vertebral complex V1+V2 that bears diapophyses only on V2 (contra *P. diluvianus*, *P. grandipes*, *P. laubei*, in which diapophyses of V1 and V2 are clearly fused with each other); urostyle comparatively thick (contra *P. grandipes*, *P. hiri*); coracoid without hook-like processus rostriformis (contra *P. diluvianus*, *P. grandipes*, *P. laubei*, *P. hiri*); diapophyses on V7 and V8 vestigial or absent, so diapophyses of synsacrum are formed only by diapophyses of sacral vertebra proper (V9) (contra *P. diluvianus*, *P. grandipes*, *P. laubei*); cubital fossa of humerus relatively deep (contra *P. diluvianus*, *P. grandipes*);



◀ **Fig. 3** *Palaeobatrachus tobieni* sp. nov. **a** Skeleton in ventral aspect, SMF Me 1123, paratype. *Scale bar 5 mm.* **b** Skeleton in ventral aspect, SMF Me 486, paratype. *Scale bar 5 mm.* **c** Skull in dorsal view, SMF Me 752b, holotype. **d** Skull in ventral view, Kess. 1. Anterior part of parasphenoid marked by arrow. **e** Posterior part of vertebral column, SMF Me 486. Presacral vertebrae marked by *Roman numerals*, segmentation of urostyle marked by *arrows*. **f** Right anterior forelimb in ventral view, SMF Me 752a, holotype. **g** Pectoral girdle in ventral view, So./Ba. 1. **h** Left anterior forelimb in dorsal view, SMF Me 752b, holotype. Note proportions of metacarpals and digits. **i** Right hindlimb in ventral view, Kess. 1. **j** Vertebral column in dorsal view (*left*), SMF Me 752b, holotype; vertebral column in ventral view (*right*), Kess. 1. Sacral diapophyses are contacted ventrally by anterior portions of iliac shafts. Vertebrae are marked by *Roman numerals*. **c–j** are not to scale

distal part of forelimb relatively short, so metacarpal IV is about two-thirds of ulna (contra *P. diluvianus*, *P. grandipes*, *P. laubei*, in which metacarpal IV is of same length as ulna); femur and tibiofibula about equal in length (contra *P. diluvianus*, *P. grandipes*, *P. laubei*, in which tibiofibula is shorter).

Material

SMF-Me 487; SMF-Me 978; HLMD-Me 7610; Ba. 1; So./Ba. 1; Fle. 1; Kel./We. 1; Kess. 1 (cast); Po. 1 (cast).

Description

(Diagnostic features of the Palaeobatrachidae listed above are mostly omitted). All the dermal roofing bones are smooth, not sculptured. The teeth are reduced in number, and probably monocuspid. Each premaxilla has about six tooth positions. The maxilla is posteriorly free, reaching only the level of the posterior margin of the orbit. It bears about 14 tooth positions, all within the anterior two-thirds of the bone. As in other palaeobatrachids, the quadratojugal is absent, leaving the maxillary arch incomplete. The frontoparietal is elongated, with the caudal portion broader than the anterior, and slightly constricted in the middle of its length. Its dorsal surface is smooth (Fig. 3c). In all specimens, there is a small parietal foramen in the anterior third of the bone. The anterior and posterior margins of the frontoparietal are semicircular. The bone was slightly convex dorsally. The squamosal has no features of particular interest, except that it bears a narrow lamella alaris that is widely separated from the maxilla. The vomers are partially preserved in Kess. 1 (Fig. 3d) and Kel./We. 1, but in both specimens they are represented only by three pointed teeth located lateral to the anterior end of the sphenethmoid. The parasphenoid is dagger-shaped, extends beyond the anterior end of the sphenethmoid (Fig. 3d), and has a convex posterior margin. The pterygoid is modified to compensate for the short maxilla—the pterygoid/maxillary

contact is shifted to the level of the anterior half of the orbit, as is the case with other palaeobatrachids (Špinar 1972, pl. 9), and this is accomplished by elongation of the ramus maxillaris of the pterygoid. The medial ramus of the pterygoid is much shorter, and articulates with a process on the anterior surface of the prootic. The angular is relatively robust, and sigmoid in shape (Fig. 3d). The dentary is not coossified with the mento-mandibular, and the latter bone is in fact absent.

The sphenethmoid is large, but the lateral projections seen in some taxa, which represent ossified portions of the postnasal walls, are completely absent. The anterior median process that represents the ossified portion of the septum nasi is robust (about half the greatest width of the bone). Posteriorly, the sphenethmoid has a narrow contact with the prootic on each side. The floor of the braincase between the sphenethmoid and the otic part of the skull would have been interrupted by a fontanelle bridged by the parasphenoid. The prootics and occipitals are fused together, forming a compact otic capsule. A small anterior process on the prootic articulates with the medial ramus of the pterygoid (Kess. 1; So./Ba. 1). In Kess. 1, there are two ossicles that could be interpreted as a quadrate and articular but are not very distinct from one another. Both elements are often found in the Palaeobatrachidae, although the articular has sometimes been misinterpreted as the “*extremitas articularis*” of the angular (i.e., praearctular; Špinar 1972, text fig. 16).

The vertebral column consists of nine imbricated, stegochordal, procoelous vertebrae, plus the urostyle (Fig. 3e, j). V1 and V2 are fused with one another, leaving no trace of the original intervertebral articulation; the occurrence of fusion can be inferred only from the length of what appears to be a single vertebra at the anterior end of the column. This composite vertebra has only a single pair of transverse processes, representing those of V2. V4 bears the longest transverse processes of any vertebra in the column, and its transverse processes are more or less curved posteriorly (in So./Ba.1, the ends of the processes of V4 even contact the processes of V5). The transverse processes of V5 are typically shorter than those of V4 and slightly inclined anteriorly; those of V6 are bent posteriorly in their proximal section, but anteriorly in their distal section. The centra of V7–V9 are fused, forming a synsacrum. The sacral diapophyses, however, are formed only by the transverse processes of V9 (SMF-Me 752b may be an exception; see below); the transverse processes of V7 are clearly shorter than those of V6. In V8, the transverse processes are either entirely absent or very short, except in SMF-Me 752. In this specimen, the left transverse process is well developed, and its distal half was probably connected by cartilage to the sacral diapophysis of V9 (Fig. 3j, left). A bicondylar articulation connects the sacral to the urostyle. In all specimens except for SMF-Me 486 (Fig. 3e) and Kel./We. 1, in which traces of fusion are recognisable on the transverse processes of V4 and V5

(those of V3 are obscured by the coracoid), the ribs are coalesced with the transverse processes, so it cannot be recognised whether ribs were present on V2–V6 (five pairs) as in other palaeobatrachids, or only on V2–V5 (four pairs). The ribs firmly fused to the transverse processes can be taken as an indication that these specimens are subadults or adults.

The medial part of the clavicle is compressed dorsoventrally, more strongly along the margins than in the middle (Fig. 3g). The lateral end of the clavicle extends to form a process that, together with the scapula, takes part in formation of the glenoid cavity, as is the case in other palaeobatrachids. The coracoid seems to differ from those of other palaeobatrachids in lacking a hook-like process (*processus rostriformis sensu Špinar 1972*) on the lateral end of the bone (Fig. 3g). The scapula is known only in ventral aspect, because in all specimens its dorsal side is covered by the suprascapula. It is comparatively short and broad. The suprascapula bears a thickened calcified lamina along its posterior margin, which tapers distally and is visible only from the inner side. The cleithrum is absent (this is a dermal bone that usually invests the anterior edge of the suprascapula; see Špinar 1972, text fig. 28, in which it is termed the “lamina recurvata”). The ilium bears a large acetabulum that covers about two-thirds of the acetabular portion of the bone. The iliac shaft is oval in cross-section. The ischia are fused, and provide no significant information. The pubic bones are not preserved.

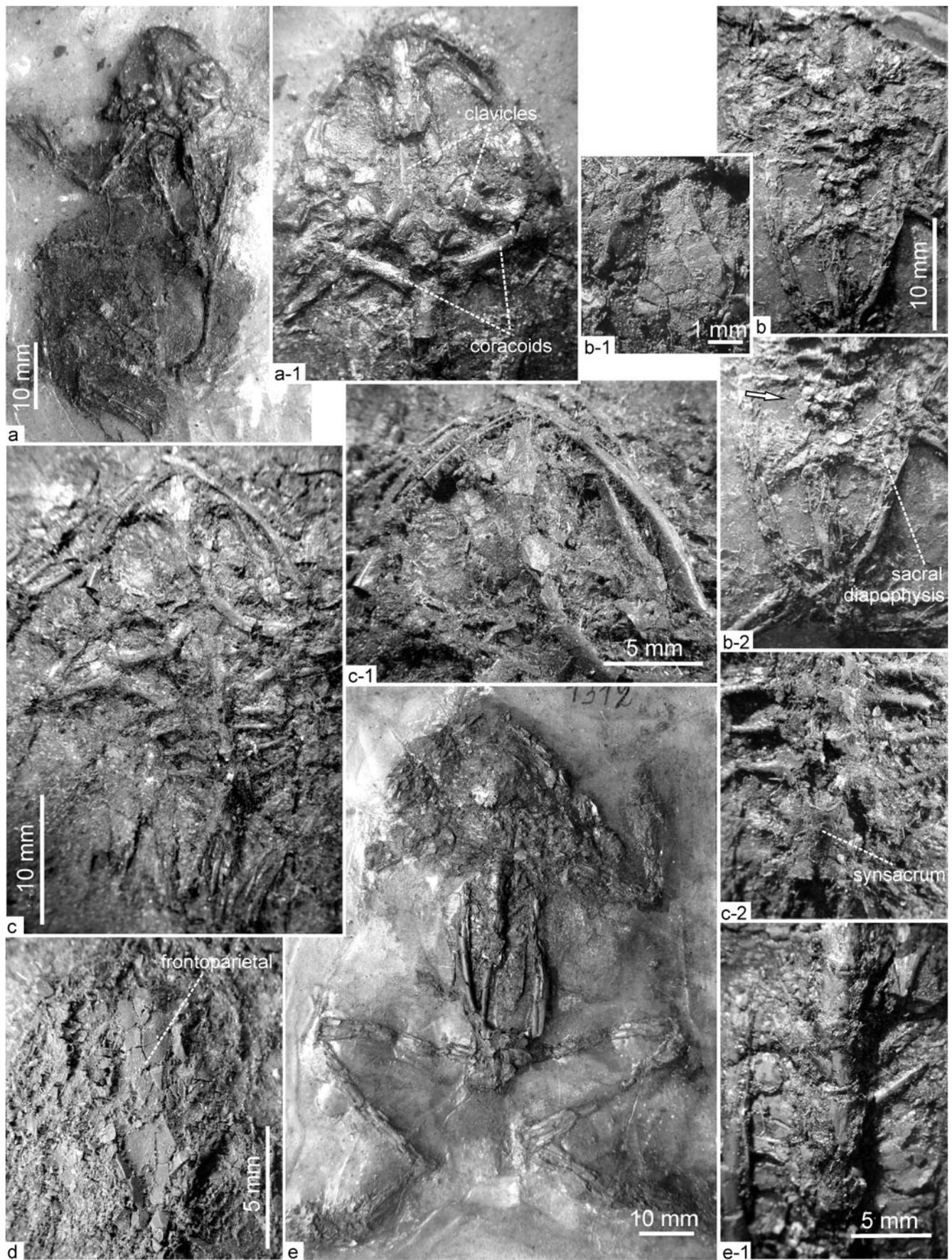
A thin and prominent crista ventralis is present on the proximal third of the humerus. The epicondyles are about equal in size. The cubital fossa, in contrast to those of other palaeobatrachids, is relatively deep. The radioulna provides no significant information. The carpals are not preserved in their original positions which makes them difficult to identify. The distal part of the forelimb is relatively short (metacarpal IV is about two-thirds as long as the ulna, and the proximal phalanx of the 4th digit is about half as long as metacarpal IV; Fig. 3f, h). The phalangeal formula is 2-2-3-3. The femur is only slightly sigmoid in shape, and bears no crista femoris on its proximal part. The tibiofibula is only slightly shorter than the femur (F/TF is 1.08 in HLMD-Me 7610). The tibiale and fibulare are not fused (Fig. 3i). The phalangeal formula of the hindlimb is 2-2-3-4-?3. The prehallux is absent.

Discussion: Although the oldest known palaeobatrachids are Late Campanian (Buffetaut et al. 1996), *Palaeobatrachus tobieni* from the Middle Eocene (MP 11) is the earliest palaeobatrachid represented by articulated skeletal material. Moreover, some specimens (e.g., SMF-Me 486) represent juveniles, as can be inferred from their segmented urostyles and from the presence of free ribs that are not yet fused to the corresponding diapophyses. This allows comparisons with articulated palaeobatrachid skeletons from the Oligocene, in turn making it possible to infer evolutionary trends

within this group of anurans. One of the most remarkable is adaptation to permanent life in water, as indicated by elongation of the distal portion of the forelimb (the metacarpals are still comparatively short, about two-thirds of the length of the ulnar portion of the radioulna, in *Palaeobatrachus tobieni*, whereas they are approximately the same length as the ulnar portion in *P. grandipes*; Špinar 1972: 86, text fig. 37). Similarly, the synsacral diapophyses are still formed only by the transverse processes of the sacral vertebra (V9) in *P. tobieni*, whereas in fully grown adults of Oligocene *Palaeobatrachus* they may be formed by long horizontal laminae that consist of the fused diapophyses of all three vertebrae (V7, V8, and V9). Such enlarged sacral diapophyses undoubtedly represent an adaptation for swimming. They provide support for a sliding articulation between the iliac shafts and the sacral vertebra, allowing fore-and-aft movements of the pelvis during swimming (Van Dijk 2002). It thus seems that palaeobatrachids, which most probably evolved from Gondwanan pipoids during the Early Cretaceous (see below), took up a permanent life in water only during the Eocene.

Remarks: Palaeobatrachids from Messel were informally described as *Messelobatrachus tobieni* in a PhD thesis by Wuttke (1988). As the PhD thesis does not meet the criteria of Art. 8 and 9 of the International Code of Zoological Nomenclature (ICZN), the name was made available only by Sanchiz (1998). Because direct comparisons with *Halleobatrachus* from Geiseltal, the only other fossil frog of a similar age that was assigned to the Palaeobatrachidae even tentatively (Kuhn 1941), were not possible at that time, the generic status of the taxon could not be confirmed. Comparisons with the holotype of *Halleobatrachus* were made only recently, but it turned out that *Halleobatrachus* cannot be assigned to the Palaeobatrachidae (see Fig. 4e). Furthermore, Špinar (1972: 123, text fig. 65c) was able to briefly inspect the anuran material in the Geiseltalmuseum and suggested that some additional

Fig. 4 Palaeobatrachidae indet. 1, Middle Eocene, Geiseltal, Germany. **a** Skeleton in ventral aspect, GM 4962, Leichenfeld 2, Grube Cecilie; holotype of *Quinquevertebron germanicum* (see also Kuhn 1941, pl. V, fig. 1, which is, however, reversed). **a-1** Skull and pectoral girdle of same specimen in ventral view, GM 4962. **b** Skeleton in dorsal view, GM 4985, Leichenfeld 2, Grube Cecilie. **b-1** Posterior part of frontoparietal of same specimen, GM 4985. **b-2** Posterior part of vertebral column of same specimen, GM 4985. *Arrow* marks two presacral vertebrae with reduced diapophyses. **c** Skeleton in ventral view, GM 6691, Trichter NO, Grube Cecilie; holotype of *Pelobatinopsis hinschei* (see also Kuhn 1941, pl. III, fig. 3; Špinar 1972, text-fig. 65c). **c-1** Skull of same specimen in ventral view, GM 6691. **c-2** Posterior part of vertebral column of same specimen, with posteriorly bicondylar synsacrum. **d** Frontoparietal in dorsal view, GM 6726, Leichenfeld 2, Grube Cecilie. **e** Skeleton in ventral view, GM 1312, Leichenfeld 2, Grube Cecilie; holotype of *Halleobatrachus hinschei* (see also Kuhn 1941, pl. I, fig. 1). Obviously not a palaeobatrachid, shown here only for comparison. Specimens are not to scale



specimens, originally described as *Quinquevertebron germanicum* and *Pelobatinopsis hinschei* by Kuhn (1941), actually belong to *Palaeobatrachus*. This confusing situation was resolved only recently, when direct comparisons of the type material from Messel with the aforementioned fossils from Geiseltal and with a newly recovered palaeobatrachid material from Kučlín (see below) could be made. It was discovered that the Eocene palaeobatrachids from Messel, Geiseltal, and Kučlín fit well, on the basis of their preserved characters, into the range of variation seen in the Oligocene palaeobatrachids and even in the genus *Palaeobatrachus*. Nevertheless, the specimens from Messel, though imperfectly preserved, can be differentiated from other Eocene palaeobatrachids. This justifies their status as a separate species. This is why we propose the new combination *Palaeobatrachus tobieni*.

Palaeobatrachidae indet. 1

1941 *Quinquevertebron germanicum*; Kuhn, p. 354, pl. V, fig. 1.

1941 *Pelobatinopsis hinschei*; Kuhn, p. 365, pl. III, fig. 3.

1972 (part) *Palaeobatrachus grandipes* (Giebel, 1851); Špínar, p. 123, text fig. 65c.

Locality and age: Geiseltal near Halle (Saale), southern Saxony-Anhalt, Germany (Haubold and Hellmund 1998, figs. 1, 2). Lower Geiseltalium (Franzen and Haubold 1986), “Obere Mittelkohle” (Haubold and Hellmund 1998, fig. 4), Middle Eocene (MP13), ca. 44 Ma (Escarguel et al. 1997; Franzen 2005b).

Material and preservation: Presence of palaeobatrachids at Geiseltal was confirmed by Špínar (1972), who put the holotypes of *Quinquevertebron germanicum* Kuhn, 1941 (GM 4962; Fig. 4a, a-1; the illustration is reversed in Kuhn 1941, pl. V, fig. 1) and *Pelobatinopsis hinschei* Kuhn, 1941 (GM 6691; Fig. 4c, c-1, c-2), in the synonymy of *Palaeobatrachus grandipes* (Giebel, 1851). Both are preserved in ventral aspect. A cursory inspection of the collections in the Geiseltalmuseum revealed two additional palaeobatrachid specimens (GM 4985 and 6726), though both are so fragmentary that precise taxonomic assignment is not possible. These are preserved in dorsal aspect. A composite description of all four specimens is given below.

Description: In GM 4962 and GM 6691, the premaxilla and maxilla are preserved in ventral aspect, but the ventral margin of the bone is broken away so that it is only possible to observe the teeth. The teeth are small, and the tooth row continues from the premaxilla onto the maxilla without any diastema (GM 4962, GM 6691). In GM 4962, the posterior part of the maxilla is obscured by sediment or possibly broken away, so it cannot be determined whether the most posterior preserved teeth actually represent the posterior termination of the tooth row (Fig. 4a-1). However, the

situation in GM 6691 (Fig. 4c-1) suggests that the most posterior maxillary teeth are at the level of the anterior part of the orbit. There appears to be a row of preserved teeth on the vomer in GM 4962, though the shape of the bone itself is difficult to assess (Fig. 4a-1). The parasphenoid is slender in its anterior section, extending anteriorly to the level of the symphysis of the lower jaws (GM 6691; Fig. 4c-1). The angular and dentary form a regular arch, which is only moderately sigmoid posteriorly (GM 6691; Fig. 4c-1). The frontoparietal is complete in GM 6726 (Fig. 4d), although largely crushed. It is long and smooth, moderately constricted in the middle of its length, and widely rounded anteriorly. It tapers posteriorly, but the precise shape of this part of the bone cannot be restored. It seems that there are two low, arch-like crests on its dorsal surface, which delimit a slightly convex dorsal table. In GM 4985, only the posterior part of the frontoparietal (Fig. 4b-1) is preserved, but it seems to differ in being wide posteriorly, in extending onto the otic capsules, in having dorsal, arch-like crests close to the margins, and in having the dorsal table depressed in the midline.

The total number of vertebrae cannot be determined with certainty, but some anterior vertebrae seem to be coalesced with each other (GM 4962; Fig. 4a-1). The synsacrum is also fully coalesced in some individuals (GM 6691; Fig. 4c-2) but not in others (GM 4985; Fig. 4b-2). The latter specimen is preserved in dorsal aspect, so the degree of fusion of the vertebral centra is not observable. In contrast, the sacro-ostylar articulation is well documented by a disarticulated synsacrum in GM 6691 (Fig. 4c-2). It also seems that the two most posterior presacrals in GM 4985 have strongly reduced diapophyses (Fig. 4b-2), similar to the condition in *Palaeobatrachus tobieni* (Fig. 2a). In general, the diapophyses of the anterior presacrals are long, stout, and perpendicular to the vertebral column (Fig. 4c, c-2).

The clavicles are robust (Fig. 4a-1, c-1), and the same holds for the coracoids. The coracoids seem to lack rostriform processes, but this could be due to poor preservation. The pelvis is exposed only in dorsal and ventral views, and the wide interiliac angle (Fig. 4b-2) suggests that a prominent symphyseal area is present on the medial surface of the ilium.

Discussion: Skeletons from Geiseltal are preserved in lignite, in which the proportion of interstitial water was originally nearly 50% (Haubold and Hellmund 1998). During subsequent evaporation, the lignite and its fossil contents disintegrated into aggregations of loose crumbs. In order to harden the skeletons and prevent their total decay, the specimens were treated in situ, immediately after they were originally collected, with cellulose lacquer, which covered the fossil by a translucent film. It is clear that this conservation method, particularly when applied to fragmented, darkly colored bones, does not allow preservation of delicate morphological features of anuran skeletons and examination of their details. This is why taxonomic assessments

were generally possible only at the family level. The only exception is specimen GM 4985, in which the sacral diapophyses are formed only by the sacral vertebra, and the two posteriormost presacrals have their diapophyses strongly reduced (Fig. 4b-2) as in *Palaeobatrachus tobieni*. It should be emphasized that assignment of this specimen to the Palaeobatrachidae was based on the shape of the frontoparietal. A close relationship between the Messel and Geiseltal palaeobatrachids is not impossible, because the stratigraphic distance between them corresponds to only about 3 million years.

Remarks: Among several tens of anuran skeletons (Kuhn 1941: 350–352), mostly fixed on translucent cellulose film, only the holotype and the only specimen of *Halleobatrachus hinschei* (GM 1312; Fig. 4e, e-1) was tentatively assigned to the Palaeobatrachidae by Kuhn. Kuhn based his conclusion on the observation that the synsacrum consisted of two vertebrae (V8+V9), with strongly dilated diapophyses. This, however, could not be confirmed by our examination of the specimen. Rather, it seems that the sacral diapophyses are small and rounded (Fig. 4e-1; it should also be noted that Kuhn modified the shape of the sacral diapophyses on the photograph; see Kuhn 1941: 375), that the centrum of the sacral vertebra is clearly separated from that of the most posterior presacral, and that the two most posterior presacrals bear straight and anteriorly inclined diapophyses that clearly differ from those of other palaeobatrachids. *Halleobatrachus* thus cannot be considered a palaeobatrachid, and we illustrate it in Fig. 4e only for comparative purposes.

Quinquevertebron (Fig. 4a) and *Pelobatinopsis* (Fig. 4c) are each represented by only one incomplete individual. These fossils are not sufficiently informative, hence insufficient to permit recognition of these genera. Therefore, we consider them nomina dubia.

Palaeobatrachidae indet. 2

Locality and age: Kučlín near the town of Bílina, Czech Republic (50°32'16.86"N, 13°48'0.59"E); Late Eocene, 38.3±0.9 Ma (Bellon et al. 1998).

Material and preservation: Slightly disarticulated skeleton preserved on part (UDB-Kuc 387; Fig. 5a) and counterpart (UDB-Kuc 388; Fig. 5b) diatomite slabs. The specimen is split along the ventral surface of the skeleton, so both parts expose its ventral aspect. Some bones are missing, but are documented as imprints in the sediment. A frontoparietal is almost completely preserved in ventral aspect in UDB-Kuc 388 (Figs. 5b and 6b); only a small fragment from the right posterior part of the bone is preserved in UDB-Kuc 387.

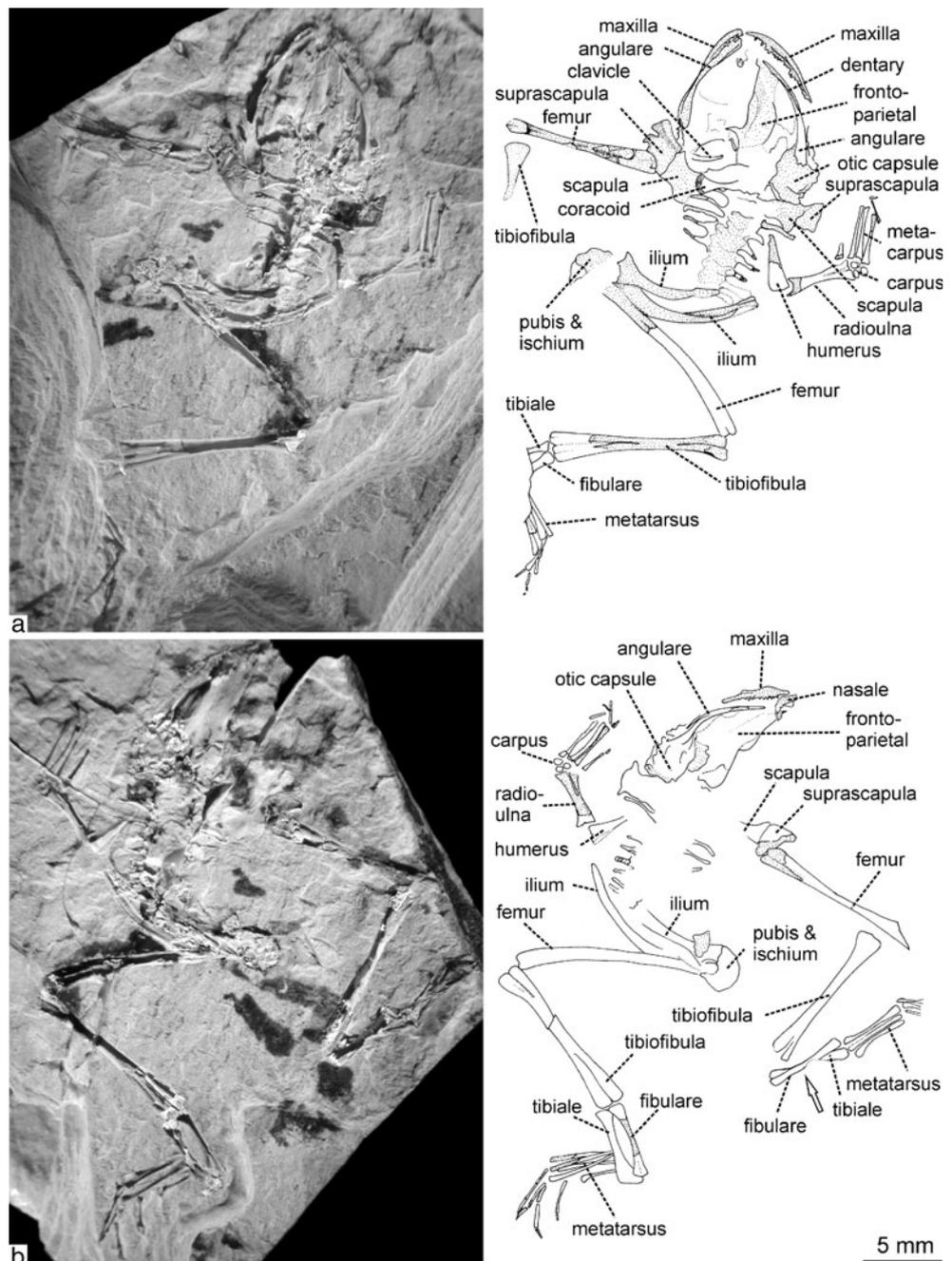
Description: The epiphyses of the long bones (e.g., radius, ulna, femur, both tibiofibulae) are not convex. This implies that they were not fully ossified, so the individual seems to be an early, not yet fully grown adult. Because the skull

(Fig. 6a) is disarticulated, both halves of the lower jaw displaced, and the craniovertebral joint obscured, the proportions of the skull cannot be assessed. The estimated SVL is about 25 mm (the length of the skull plus presacral vertebral column of UDB-Kuc 387 can be estimated with greater precision as 16–17 mm). The tibiofibula is slightly shorter than the femur (F/TF ratio is 1.16).

The premaxillae are obscured by the sediment. The maxilla is preserved as an imprint of the outer surface of the bone in UDB-Kuc 387 (Figs. 5a and 6e-1), revealing some actual teeth that are preserved along with impressions of some others that are missing whereas the anterior portion of the maxilla is preserved in the counterpart slab UDB-Kuc 388. It seems that the short anterior section of the bone is toothless. The anterior teeth are slender whereas those in the middle of the tooth row are more robust and conical, and the tooth row extends comparatively far posteriorly. The frontal process is low and widely rounded, and the zygomaticomaxillary process is poorly developed (Fig. 6e-1, e-2). The quadratojugal is absent. The crescent-like nasal is preserved in UDB-Kuc 388. The frontoparietal (Fig. 6b) is preserved in its ventral aspect in UDB-Kuc 388. It is widest posteriorly, at the level of the otic capsules, and narrower in its middle and anterior parts. It tapers to an obtuse point anteriorly. On the ventral surface, there are two parallel grooves that run along the orbital margins and have a degree of medial convexity. Presumably, they are manifested as crests on the hidden dorsal surface of the bone. The part of the bone between them is moderately convex ventrally, presumably corresponding to a depression on the dorsal surface, and the orbital margins slant steeply downwards. In general, this frontoparietal is rather similar to some of those illustrated in Fig. 1t-bb. A fragment of the posterior part of the frontoparietal is preserved in UDB-Kuc 387. The squamosal is not preserved. The dentary and angular are broken, and partly preserved as imprints in the sediment; they do not provide any information except that the latter bone is sigmoid in shape. The pterygoid is preserved as an imprint in the sediment on the left side in UDB-Kuc 387. It seems that its medial branch was short and had a squared-off end. The ventral part of the braincase is preserved in UDB-Kuc 387. The sphenethmoid appears to extend far posteriorly towards the otic capsules. However, it is unclear whether the sphenethmoid is coalesced with the prootics, because this region is covered by the posterior part of the frontoparietal. The broken outer walls of both otic capsules are preserved. As the capsules are well delimited medially, they probably were still weakly connected to the braincase in the intact skull.

Six procoelous presacral vertebrae are preserved in the vertebral column (Fig. 6c), but the most anterior vertebrae (V1+V2), the synsacrum, and the urostyle are not

Fig. 5 Palaeobatrachidae indet. 2, skeleton in ventral aspect. Late Eocene, Kučlín, Czech Republic. **a** UDB Kuc-387 (main part); **b** UDB Kuc-388 (counterpart). Note that the proximal metatarsals are not coalesced (marked by *arrow* in **b**). Scale bar applies to both specimens



preserved. The transverse processes of five of the six presacral vertebrae bear free ribs (Fig. 6c). The scapula is rectangular and comparatively short, and the coracoid is robust; it cannot be determined whether its lateral end is expanded in a rostriform process. All of the pelvic girdle elements are preserved, though some of them are slightly displaced (Fig. 6d). The ilia are displaced, one being exposed in lateral aspect and one in medial aspect (Fig. 6d). The dorsal tubercle is not recognisable, and most probably was absent. The acetabulum is large. The humerus bears no ventral crista, and the radioulna has a well developed

olecranon. Three carpal elements can be recognised, plus an additional one visible only under polarized light (ulnare, radiale, centrale 2, and unidentified carpal element, Fig. 6f). The metacarpals are about the same length as the radioulna. The femur is straight, without any sigmoid curvature, and is slightly longer than the tibiofibula. As in other palaeobatrachids, the tibiale and fibulare are not fused with one another (Fig. 5b). The phalangeal formula is unknown.

Discussion: Since the specimen is not well preserved and displays few diagnostic characters, it is not possible to assess its relationships with other palaeobatrachids. The only feature



Fig. 6 Palaeobatrachidae indet. 2, Late Eocene, Kučlín, Czech Republic. **a** Skull in ventral aspect; UDB Kuc-387. **b** Frontoparietal in inner (ventral) aspect, UDB Kuc-388. *Arrows* mark medially convex flutes, which correspond to crests on the dorsal surface. **c** Vertebral column in ventral view; UDB Kuc-387. Vertebrae marked by *Roman numerals*. **d** Pelvic girdle in lateral (left) aspect. UDB Kuc-388. *Double-headed arrow* indicates posterior displacement of detached pubis and ischium

posteriorly, *white arrows* mark margins of acetabulum. **e** Left maxilla in normal (**e-1**) and polarized (**e-2**) light; **e-1** from UDB Kuc-387 (reversed for comparison), **e-2** from UDB Kuc-388. Anterior part of the bone is exposed in lateral view, middle and posterior parts are crushed. **f** Right anterior extremity in ventral view, UDB Kuc 388. All *scale bars* are 1 mm

that might be significant in this regard is the F/TF length ratio. The femur is slightly longer than the tibiofibula, whereas in *Palaeobatrachus tobieni* from Messel the femur is slightly

shorter. This specimen also differs from *P. tobieni* in that the metacarpals are about the same length as the radioulna, compared to only two-thirds as long as the radioulna in *P. tobieni*.

Distributional dynamics

The Palaeobatrachidae are restricted to Europe. The possible exception is three ilia from the Late Maastrichtian of North America described as *Palaeobatrachus occidentalis* (Estes and Sanchiz 1982). They display most of the key features of palaeobatrachid ilia, except that “the dorsal border [is] relatively straight along the shaft leading to the supraacetabular expansion (= pars ascendens)”. In palaeobatrachids, by contrast, the ascending part (attachment area of *m. semimembranosus*; Prikryl et al. 2009) protrudes strongly above the dorsal margin of the iliac shaft. It is also necessary to emphasize that the strong interiliac synchondrosis, expressed as a prominent convexity on the inner surface of the bone, is a typical feature of all water-dwelling anurans (not only palaeobatrachids but also pipids and *Barbourula*; Vergnaud-Grazzini and Hoffstetter 1972), and that a similar large acetabulum, not necessarily combined with other palaeobatrachid characters, also occurs in other Late Cretaceous anurans from North America (Roček et al. 2010, 2012). An additional reason for scepticism regarding the assignment of these three ilia to the Palaeobatrachidae is their palaeogeographic location west of the Western Interior Seaway (Niobraran Sea), an inland sea that split the continent of North America into two halves during most of the Early and Mid-Cretaceous Period. Occurrence of palaeobatrachids in this location would suggest that members of the group reached the western part of the continent before the seaway was created, and in this case their fossil distribution should also encompass the eastern part of North America. In spite of these anatomical and palaeogeographical facts that raise some doubts about palaeobatrachid identity of the mentioned ilia, another skeletal fragment, which looks very like a palaeobatrachid one (fused V1+V2), was recently reported from, possibly, the early Palaeocene of Montana (Gardner 2008). Gardner was cautious about this material and pointed to the fact that fusion of the atlas and first trunk vertebra also occurs in some pipid taxa (see also Báez and Pugener 2003; Estes 1977; Roček and Van Dijk 2006). However, he explicitly mentioned (Gardner 2008: 222–223) that “the fused atlas+first trunk vertebra ... [has] ... posterior cotyle”, which suggests opisthocoelous centrum of the Pipidae, rather than procoelous centrum of the Palaeobatrachidae (see below).

It is generally agreed that palaeobatrachids are closely related to pipids, which are today restricted to Africa and South America. The only significant difference between palaeobatrachids and ancient pipids living in Gondwana prior to the separation of Africa and South America, such as *Thoraciliacus*, *Cordicephalus* (Nevo 1968) or *Xenopus*-like *Shelania* (Báez 2000; Estes 1975), lies in the structure of the vertebral centra (opisthocoelous in the Pipidae, procoelous in the Palaeobatrachidae). The northernmost fossil pipids are *Thoraciliacus*, *Cordicephalus*, and *Shomronella* from the Early Cretaceous (Barremian and Hauterivian, respectively) of Israel.

Shomronella, which is represented only by tadpoles, displays in the development of its vertebral centrum an intermediate stage with amphicoelous vertebral morphology from which both types can evolve (Estes et al. 1978; Roček and Van Dijk 2006). This can be understood as an evidence of a close relationship between the Pipidae and Palaeobatrachidae. However, palaeobatrachids must have spread to northern continents well before the Early Cretaceous, because Laurasia and Gondwana were completely separate as early as the Late Jurassic. North America and Europe (which was an archipelago rather than a landmass at that time) became separated from each other by shallow seas in the Early Cretaceous. It should be noted that even shallow marine waters are considered uncrossable for recent frogs, because only a few of them can tolerate sea water for brief periods or brackish water for extended periods (Dicker and Elliott 1970). However, rafting has been proposed as a possible mechanism of colonization of islands by amphibians (e.g., Measey et al. 2007). One of the last islands to maintain contact with Gondwana, namely Iberia, was also the first to be separated from North America. For this reason, what is now the Iberian Peninsula represents the most plausible route for the invasion of Laurasia by palaeobatrachids or their ancestors. The invasion must have occurred after the microplate Iberia split away from North America. *Neusibatrachus* from the earliest Cretaceous would fit into this scenario as a possible transitional form with some palaeobatrachid features (Báez and Sanchiz 2007). As evidenced by an early Campanian palaeobatrachid from southern France (Buffetaut et al. 1996), the spread of palaeobatrachids to other parts of Europe occurred in the Late Cretaceous, when terrestrial connections within Europe were established.

The Cretaceous/Tertiary transition had no impact on the palaeobatrachids. They reached northern France (Cernay) by the end of the Palaeocene (Vergnaud-Grazzini and Hoffstetter 1972), and both Britain and the Czech Republic (Kučlín) by the end of the Eocene. The absence of Eocene localities in eastern Europe is undoubtedly due to the fact that the main part of the continent was in western Europe, whereas present east Europe was covered by epicontinental seas, with scattered small islands well isolated from the European mainland in the west (Rögl 1999, fig. 1). This is why further expansion of the palaeobatrachids to the east was not possible at that time.

In central Europe, palaeobatrachids seem not to have been seriously affected by the Eocene/Oligocene transition. This can be inferred from both the density of palaeobatrachid localities in the Oligocene of Europe and the relatively rapid spread of palaeobatrachids to the eastern part of the continent. In contrast, the number of post-Eocene localities yielding palaeobatrachids in western Europe is surprisingly low. It seems that the geographic boundary between the eastern and central European region of palaeobatrachid abundance and the western European region of rare, probably relictual, distribution was the Rhine Graben, the central segment of a rift system

which traversed western Europe from the North Sea to the Mediterranean (Illies 1972, 1977). The rifting started in the Middle Eocene and continued until the Middle Miocene. Although the seaway was shallow, it had a constant width of 33–38 km, thus completely separating the western and eastern parts of the continent in the Early Oligocene (Rögl 1999, fig. 2). It would have represented an effective migration barrier for amphibians, and presumably prevented re-immigration of palaeobatrachids to the western part of the continent. This constraint, together with a shift to drying conditions (see below), prevented palaeobatrachids from re-establishing their original pre-Eocene distribution in western Europe, and ensured that their Oligocene and Miocene distribution in the region remained only sparse. It should be noted that palaeobatrachids are completely absent from western Europe from the Pliocene onwards.

In contrast, the majority of Oligocene palaeobatrachid localities fall within central Europe, between the Rhine Graben in the west and the longitude of Zittau and northwest Bohemia in the east; Fig. 7). Palaeobatrachids continued to expand to the east in the Miocene, when they spread to western Romania and Ukraine (Gritsev). As early as the Early Miocene, they also reached Anatolia, presumably via either a relatively narrow strip of land that separated the Paratethys and the Mediterranean (Rögl 1999, fig. 5) or a landbridge that subsequently separated the central and eastern parts of the Paratethys (Rögl 1999, fig. 6). Terrestrial connections of Anatolia with Europe around the Oligocene/Miocene boundary were also confirmed by composition of their ophidian faunas (Szyndlar and Hoşgör 2012). At that time, palaeobatrachids had already become very rare west of the Rhine Graben (being known only from two localities, Issoire and Sansan). In the Pliocene, palaeobatrachids completely disappeared not only from western Europe but also from central Europe. The westernmost Pliocene palaeobatrachid localities are in central Poland and southern Hungary, but during this time their distribution also expanded far to the east. Pliocene occurrences are known in the basin of the Don River, and even at the Apastovo locality in Tatarstan, Russia (Fig. 7; Ratnikov 1997, 2001, 2002c). This distribution remained basically unchanged until the Middle Pleistocene (Early Neopleistocene), when palaeobatrachids died out over a comparatively large area extending from Poland to the eastern part of the European platform.

The apparent eastward shift in the distribution of palaeobatrachids may be explained by palaeogeography. In the Palaeocene and Eocene, Britain was connected with the main part of Europe, so palaeobatrachids could reach its southern part. The late Eocene locality of Kučlín marks the probable easternmost occurrence of palaeobatrachids at that time. A climatic event at the end of the Eocene affected palaeobatrachids (and some other amphibians and reptiles; Rage 1984) in western Europe but not in eastern Europe,

which was changing at the time from an archipelago to a continuous landmass. This made it possible for palaeobatrachids to spread towards the east, whereas the Rhine Graben became established in the Late Eocene and blocked their return to the west. During the Miocene and Pliocene, palaeobatrachids reached the eastern part of the European platform, but this expansion coincided with their decline and disappearance in the west—they probably disappeared first from western Europe, and later also from central Europe.

This sequence of events raises the question of why palaeobatrachids became markedly rare in western Europe during the Oligocene, while apparently flourishing in central Europe. Data from the Paris Basin (Andreasson and Schmitz 1996) suggest that, in the early Middle Eocene, mean winter temperatures were about 14°C and mean summer temperatures about 28°C. Accordingly, the degree of seasonality in this region was approximately the same as it is today, but annual mean temperatures were some 10°C higher. In central Europe, mean annual temperatures are inferred to have been 23–25°C at that time, whereas mean annual precipitation was 1,000–1,600 mm and the mean temperature during the coldest month was 17–21°C (Mosbrugger et al. 2005). In both cases, the data indicate nearly subtropical temperatures, with low seasonality.

At the Eocene–Oligocene transition (33.9 Ma), a sudden climatic deterioration caused by global cooling occurred, accompanied by a shift to drier conditions (Costa et al. 2011). A large terrestrial faunal turnover (termed the Grande Coupure) that occurred due to this climatic change was also triggered in part by dispersal of new species into Europe (e.g., after the closing of the Turgai strait) and, contrary to general belief, affected not only mammals but also small amphibians and reptiles (Rage 1984). Palaeobatrachids vanished completely from some regions, such as Britain (although this statement is based on negative evidence—the microherpetofauna of the Upper Hamstead Beds on the Isle of Wight, which are the only Oligocene beds in Britain, has never been studied, and there are no Miocene deposits in Britain; Milner, personal communication), and became extremely rare in French localities. This strongly contrasts with the situation in central Europe east of the Rhine Graben, where palaeobatrachids remained common until the end of the Miocene. The reasons for their gradual disappearance from the western part of the continent are unclear, but severe drying could have had a negative impact on these obligate water dwellers. The role of drying as a main factor in the decline of the palaeobatrachids in western Europe seems to be confirmed by palaeobotanical studies (Cavagnetto and Anadón 1996) focussing on northeastern Iberia. These have recorded the presence of mangrove swamps, indicating warm climatic conditions, in the middle Bartonian. By contrast, the Priabonian and Early Oligocene vegetation in the area was more open, suggesting a climate with a dry

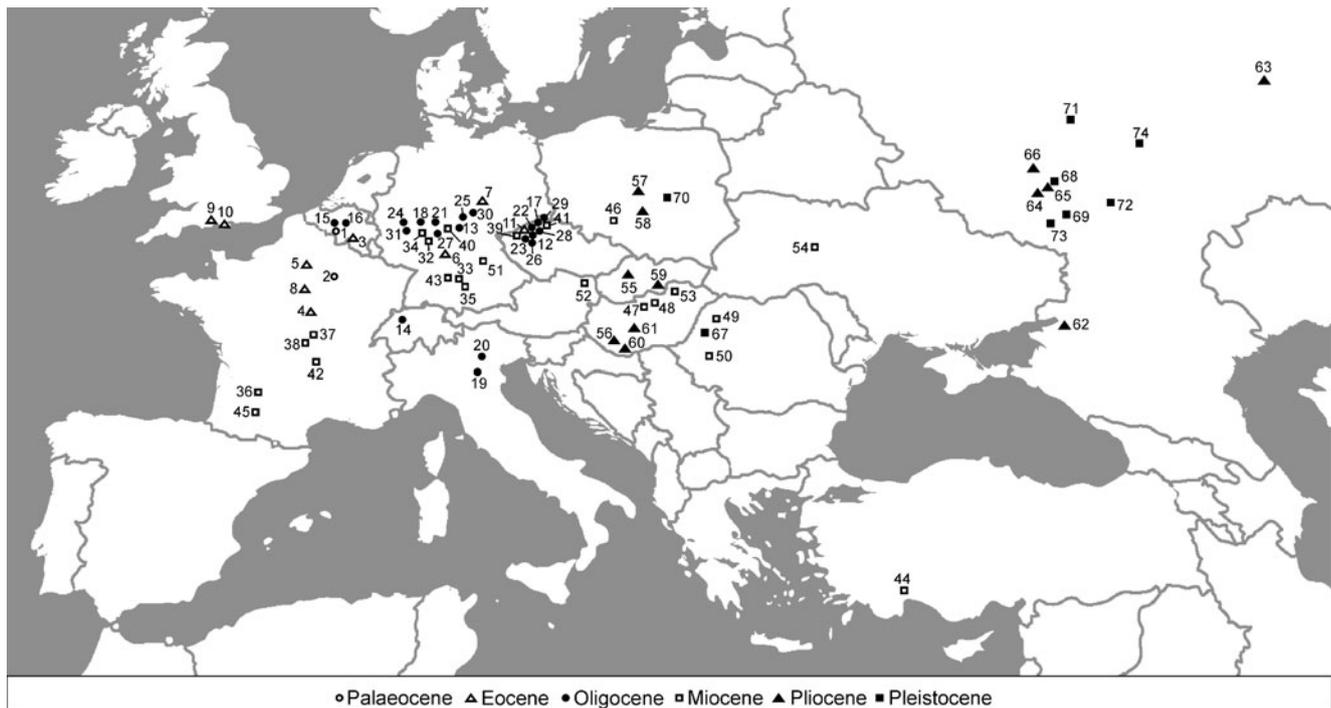


Fig. 7 Occurrences of the Palaeobatrachidae from the Palaeocene to the Pleistocene. 1 Hainin (Middle Palaeocene, MP 1–5) (Groessens-Van Dyck 1981; Folie 2006); 2 Cernay (Late Palaeocene, MP 6) (Vergnaud-Grazzini and Hoffstetter 1972); 3 Dormaal (Early Eocene, MP 7) (Godinot et al. 1978, Duffaud 2000); 4 Condé-en-Brie (Eocene, MP 8–9) (Duffaud 2000); 5 Prémontré (Early Eocene, MP 10) (Augé et al. 1997); 6 Messel (Middle Eocene, MP 11) (Wuttke 1988); 7 Geiseltal (Middle Eocene, MP 13) (Špinar 1967, Vergnaud Grazzini and Młynarski 1969); 8 Grisolles (Late Eocene, MP 16) (Duffaud 2000); 9 Hordle Cliff (Late Eocene, MP 17) (Milner et al. 1982); 10 Isle of White (Late Eocene, MP 20) (Rage and Ford 1980, Meszoely et al. 1984, Holman 1996); 11 Kučlín (Late Eocene) (this paper); 12 Kunderatice (= Kunderatec or Kundratitz) (Early Oligocene, MP 21), Markvartice (= Markersdorf) (Early Oligocene, MP 21), Sulestice (= Sulec or Sulloditz) (Early Oligocene, MP 21) (von Meyer 1860; Bayer 1905; Špinar 1972); 13 Sieblos (Early Oligocene) (Wolterstorff 1887); 14 Soulce (Early Oligocene, MP 21) (Gaudant 1979); 15 Hoogbutsel (Early Oligocene, MP 21) (Hecht and Hoffstetter 1962); 16 Hoeleden (Early Oligocene, MP 21) (Hecht and Hoffstetter 1962); 17 Varnsdorf (Early Oligocene) (Špinar 1972); 18 Moehren 13 (Early Oligocene, MP 22) (Sanchiz et al. 1994); 19 Monte Viale (Early Oligocene, Rupelian) (Vergnaud-Grazzini and Hoffstetter 1972); 20 Laverda (Late Oligocene) (Peters 1877); 21 Enspel (Late Oligocene, MP 28) (Roček and Wuttke 2010); 22 Bechlejovice (Late Oligocene) (Špinar 1972, Bellon et al. 1998); 23 Zálezly (Late Oligocene, Chattian) (Špinar 1972, Vergnaud-Grazzini and Hoffstetter 1972); 24 Stösschen, Orsberg, Rott (Late Oligocene, MP 30) (von Meyer 1860); 25 Oberleichterbach (Late Oligocene) (Böhme 2008); 26 Olešnice, Malečov (Oligocene or Miocene) (Špinar 1972); 27 Herborn (Late Oligocene or Early Miocene) (von Meyer 1860); 28 Odeř, Košťálov (= Koschtialov) near Litoměřice, Vernerice, Kamenice (Oligocene/Miocene boundary, MN 0) (Wolterstorff 1887; Špinar 1972); 30 Hochheim-Floersheim (Oligocene/Miocene boundary, MN 0) (Vergnaud-Grazzini and Hoffstetter 1972); 31 Burgbrohl (Oligocene/Miocene boundary, MN 0) (Vergnaud-Grazzini and Hoffstetter 1972); 32 Weisenau (early Miocene, MN 1) (Wolterstorff 1887); 33 Tomerdingen (Early Miocene, MN 1–2) (Dehm 1935, Sanchiz 1998, Rage and Roček 2003); 34 Am Hambusch (= Dyckerhoff in Mainz-Amöneburg, or Kastel, Amöneburg, Biebrich, Hessler) (Early Miocene, Aquitan to Burdigal, MN 2–3) (Schleich 1988); 35 Haslach bei Ulm (Early Miocene,

MN 2) (Wolterstorff 1887); 36 Laugnac (early Miocene, MN 2) (Vergnaud-Grazzini and Hoffstetter 1972, Hossini and Rage 2000); 37 Poncenat (Early Miocene, MN 2) (Rage and Roček 2003; Hossini and Rage 2000); 38 Saint-Gérard-le-Puy (Early Miocene, MN 1–2) (Rage and Roček 2003); 39 Hájek (= Grassengrün) near Karlovy Vary (Early Miocene) (Špinar 1972); 40 Kaltennordheim (Early Miocene) (Wolterstorff 1887); 41 Skyřice (= Skyritz) (Early Miocene, MN 3) (Špinar 1972); 42 Issoire (Early Miocene, MN 1–5) (Rage and Roček 2003); 43 Randecker Maar (Middle Miocene, MN 5) (Roček et al. 2006); 44 Anatolia (Early Miocene) (Claessens 1997); 45 Sansan (Middle Miocene, MN 6) (Vergnaud-Grazzini and Hoffstetter 1972; Hossini and Rage 2000); 46 Opole (Middle Miocene, MN 7) (Młynarski et al. 1982); 47 Mátraszölös 2 (Middle Miocene, MN 7) (Szentesi and Venczel 2010); 48 Sámsonháza (Middle Miocene, MN 7) (Venczel 2004); 49 Subpiatră 2/2 (Middle Miocene) (Hír and Venczel 2005, Venczel et al. 2005); 50 Tauț (late Middle Miocene, MN 7+8) (Venczel and Știucă 2008); 51 Adelschlag (late Middle Miocene, MN 6–8) (Schlosser 1916); 52 Götzensdorf/Sandberg (Late Miocene, MN 9) (Harzhauser and Tempfer 2004); 53 Rudabánya (late Miocene, MN 9) (Bernor et al. 2004); 54 Gritsev (Late Miocene, MN 9) (Roček, unpublished); 55 Ivanovce (Early Pliocene, MN 15) (Hodrová 1981, 1982); 56 Csarnóta (Early Pliocene, MN 15) (Hodrová 1982); 57 Wąże I, II (Pliocene, MN 15, 16) (Sanchiz and Młynarski 1979); 58 Rębielice Królewskie (Pliocene, MN 16) (Młynarski 1977, Sanchiz and Młynarski 1979); 59 Hajnáčka (Pliocene, MN 16) (Hodrová 1981); 60 Villány 6 (Pliocene, MN 17) (Hodrová 1982); 61 Kisláng (Pliocene, MN 17) (Sanchiz 1998); 62 Liventsovka 5 (Late Pliocene, MN 17) (Ratnikov 1997, 2001, 2002a); 63 Apastovo (Late Pliocene, MN 16) (Ratnikov 1997, 2001, 2002a); 64 Veretie (= Verkhni Ol'shan) (Late Pliocene, MN 16) (Ratnikov 1997, 2001, 2002a); 65 Korotoyak (Late Pliocene, MN 16) (Ratnikov 1997, 2001, 2002a); 66 Uryv I (Late Pliocene, MN 16) (Ratnikov 1997, 2001, 2002a); 67 Betfia 9/B (Early Pleistocene, Biharian) (Hír and Venczel 1997); 68 Koziy Ovrág (Early Neopleistocene) (Ratnikov 1996, 1997, 2002a, c); 69 Staraya Kalitva 1 (Late Pliocene) and Staraya Kalitva 2 (Early Neopleistocene) (Ratnikov 1997, 2002a); 70 Kozi Grzbiet (Early Pleistocene) (Sanchiz and Szyndlar 1984); 71 Yablonsk (Early Neopleistocene) (Ratnikov 1993, 1997, 2002a, c); 72 Ilyinka 2 (Early Neopleistocene) (Ratnikov 2003); 73 Krolatnik (Early Neopleistocene) (Ratnikov 2002a, c); 74 Volnaya Vershina 3 (Early Neopleistocene) (Ratnikov 2002b)

season. Similar drying cannot be recognised in central Europe, where mean annual precipitation was between 1,000 and 1,600 mm during the Eocene and decreased only slightly at the base of the Oligocene (Mosbrugger et al. 2005). However, seasonal fluctuations of climate in the Early Oligocene of central Europe are suggested by lines of arrested growth (LAGs) of the long bones in *Palaeobatrachus* (Sanchiz et al. 1994).

In the Pliocene, however, palaeobatrachids also vanished from central Europe. A possible reason may be that mean coldest month temperatures in this region decreased by nearly 20°C between the Eocene and the Pliocene. Mean annual temperatures and mean warmest month temperatures did not change as significantly over the same time interval, a pattern that implies an increase in seasonality (Mosbrugger et al. 2005). A significant decline in temperature occurred near the end of the Pliocene (Tiglian) and, for the first time, mean coldest month temperatures fell below the freezing point. However, there was also a relatively cool phase in the Late Oligocene (Utescher et al. 2000), during which the coldest month mean dropped to about 5–7°C (Uhl and Herrmann 2010). This obviously did not have a severe impact on the distribution of palaeobatrachids, which remained abundant in the Late Oligocene and Early Miocene. The extirpation of palaeobatrachids in central Europe in the Pliocene coincides with the decrease in coldest month means below the freezing point, and with a significant decrease of about 250 mm in mean annual precipitation during the Zanclean (Mosbrugger et al. 2005). Being obligate water dwellers, palaeobatrachids would have been unable to hibernate when all the water bodies in a given area were frozen. The decreased precipitation presumably caused some water bodies to dry up in any case. These factors may explain their withdrawal from central Europe in the Pliocene.

The Pliocene and Pleistocene were characterized by continuing deterioration of the climate. In addition to decreasing temperatures (in the East European Plain, mean annual temperatures temporarily dropped by up to –6°C in the Late Pleistocene), the deterioration involved climatic fluctuations in which cold periods were interrupted by warmer periods, and dry periods by more humid ones. This was, however, highly variable—for instance, cooling was often associated with aridization (Svitoch 1983). In the Early Neopleistocene, this resulted in the periodic formation of glaciers, rimmed at their periphery by periglacial hyperzones. These glaciations influenced the distribution of forests, and consequently of forest animals (Ratnikov 2009).

In the Pliocene through the Middle Pleistocene, palaeobatrachids were distributed from central Poland and central Hungary, in the west, to the East European Plain (Fig. 7). Their easternmost recorded occurrence is at the Late Pliocene locality Apastovo, Tatarstan, Russia (55°12'15"N, 48°30'16"E) (Ratnikov 1997, 2001, 2002c). Eopleistocene

(Early Pleistocene in global chronostratigraphy) herpetological assemblages are rarely preserved in eastern Europe, but the comparatively thorough record from the Early Neopleistocene suggests that the geographic range of palaeobatrachids contracted at that time, and that their density markedly decreased. The last recorded occurrences are from the Middle Pleistocene (Mindel I/Mindel II, which corresponds to Interglacial II of the Cromerian complex; Lindner and Marks 2008) of Kozi Grzbiet (50°51'N, 20°27'E) near Miedzianka in the Świętokrzyskie Mountains, central Poland (Sanchiz and Szyndlar 1984), and from the localities Ilyinka 2 near the town of Kalach (50°26'N, 41°00'E), southeast of the city of Voronezh (Ratnikov 2003), and Staraya Kalitva 2 near the town of Rossosh (50°08'04"N, 39°45'14"E) and about 160 km south of Voronezh (Ratnikov 1997, 2002a). The Ilyinka 2 and Staraya Kalitva 2 localities belong to the Illynian (=Illinsk) superhorizon of the Early Neopleistocene (Fig. 8). Among the last recorded occurrences, even of younger age, are also the following four localities (Muchkap interglacial of the Early Neopleistocene): Kozii Ovrage near the town of Korotoyak (50°59'11"N, 39°10'30"E), about 75 km south of the city of Voronezh (Ratnikov 1996, 1997, 2002a, c); Krolatnik near the town of Rossosh (50°11'10"N, 39°32'24"E), about 160 km south of Voronezh (Ratnikov 2002a, c); Volnaya Vershina 3 near the town of Muchkapsky in the Tambov region, about 200 km east of Voronezh (Ratnikov 2002b); and Yablonovets near the town of Petrovskoye in the Tambov region (52°27'56"N, 40°27'2"E), about 125 km northeast of Voronezh (Ratnikov 1993, 1997, 2002a, c). All these localities are in the basin of the upper Don River, Russia, and all represent forest or forest-steppe environments. Palaeobatrachids are very rare at these Muchkapan localities, and they are absent from other localities of the same age (Ratnikov 2002a, c). Another warm interval between the Muchkapan and Likhvinian, immediately preceding the Okaian glaciation, was recently recognised (Iosifova et al. 2006, 2009). It is called the Ikoretsian, and its estimated age is 528–474 Ka. The amphibian assemblage of the Ikoretsian is definitively known only from a single locality, Mastyuzhenka (Iosifova et al. 2009), and palaeobatrachids are absent from this site. They are also absent from the locality Nagornoye-1 in Ukraine (Ratnikov and Krokhmal 2005), which is also tentatively estimated to be Ikoretsian in age. Finally, palaeobatrachids do not occur at the younger set of localities dating from the Likhvinian (425–364 Ka; Iosifova et al. 2006), the first interglacial of the Middle Neopleistocene (Ratnikov 2005). Hence, the extinction of the palaeobatrachids can be inferred to have occurred before the Ikoretsian, or during the Oka glaciation at the latest. An important question is why the palaeobatrachids suffered extinction at this time, whereas other anurans, such as *Pelobates*, *Bufo*, *Rana*, and *Bombina*, survived (Ratnikov 2005).

Holocene		Age (Ka)	North West European Stages	East European Plain Stages	Stratigraphic occurrences of last palaeobatrachids	
Pleistocene	Late	100	Weichselian	Valdian (Valdai glaciation)	No palaeobatrachids in anuran fossil assemblages ----- Kozii Ovrage (Ratnikov 1996); Krolatnik (Ratnikov 2002a); Volnaya Vershina 3 (Ratnikov 2002b); Yablonovets (Ratnikov 1993) ----- Kozii Grzbiet (Sanchiz and Szyndlar 1984); Ilyinka 2 (Ratnikov 2003); Staraya Kalitva 2 (Ratnikov 1997)	
		200	Eemian	Mikulinian (Mikulino interglacial)		
	Middle	Saalian	200	Warthe Drenthe		Dnieper (Dnieper glaciation)
			300	Wacken/Dömnitz Fuhne		
		'Cromerian complex'	400	Holsteinian (Holstein intergl.)		Likhvinian (Likhvin interglacial)
			500	Elsterian (Elster glaciation)		Okaian (Oka glaciation)
			600	Interglacial IV		Ikoretsian (Ikorets interglacial)
				Glacial c		Muchkapien (Muchkap intergl.) ←
			700	Interglacial III		Donian (Don glaciation)
				Glacial b		Ilynian (Ilynsk horizon) ←
800	Interglacial II	Pokrovian (Pokrovsk horizon)				
	Glacial a	Petropavlovian (Petropavlovsk horizon)				
Early	900	Dorst				

Fig. 8 Correlation table of east and west European chronostratigraphical stages, showing the latest palaeobatrachid occurrences. Based on the data in Cohen and Gibbard (2011). Data for the Ikoretsian are from Iosifova et al. (2009)

It is likely that palaeobatrachids were severely affected by temperatures below freezing point, because they are thought to have resembled *Xenopus* (Picker 1985) in being obligate water dwellers with only a limited capacity for migrations on dry land. During the Early Pleistocene, cold phases characterized by the southward expansion of ice sheets and permafrost (ground ice) across the East European Plain alternated with warmer intervals when ice sheets and permafrost retreated. Judging by the presence of cryogenious horizons, permafrost appeared in the East European Plain by the end of the Pliocene (2.7–2.1 Ma). During the Early and Middle Pleistocene, cryogenious horizons clearly show increasingly thick permafrost (Velichko 1973). Continuous permafrost reached a latitude of 49°N during the Middle Pleistocene glacial maximum, while discontinuous and sporadic permafrost occurred even further south (Velichko et al. 1996). As mentioned above, palaeobatrachids have been sporadically recovered from localities dating to the Muchkapien interglacial, which followed the Don glaciation. This glaciation reached its southernmost extent on the East European Plain (in the Don basin, the ice sheet advanced well to the south, reaching 50°N; Fig. 9). In spite of the extent of the ice, however, the existence of only limited cryogenic deformation in sediments from this time interval indicates that winter conditions were not very severe. The Muchkapien interglacial (621–568 Ka; Iosifova et al. 2006), which followed the Don glaciation, was characterized

by July mean temperatures of 18–20°C, and January mean temperatures of –3 to 4°C. Annual mean temperatures before the Oka glaciation in the East European Platform are estimated to have been about 8.5°C (Svitoch 1983), so the climate was comparatively warm and humid. Judging by analysis of fossil pollen and spores, the Muchkapien interglacial was the most humid thermochron of the Pleistocene (Bolikhovskaya 1995). In the East European Platform, the Muchkapien interglacial was characterized by large, hydromorphous tracts of forest, and by the highest diversity of Pliocene relic species. It may be supposed that basins along the upper Don River characterized by such humid conditions served as the last refugia for palaeobatrachids during and after the peak of the Don glaciation. Farther south, however, the climate was drier and forest and forest-steppe zones gave way to full steppe, which was too dry for palaeobatrachids. During the Oka glaciation (474–425 Ka; Iosifova et al. 2006), the extent of the ice sheet was much more limited (Fig. 9), but—judging by the palynological evidence from the relevant localities—climatic conditions in the periglacial zones were more severe (Velichko and Wright 2005). During the Likhvin interglacial, palaeobatrachids were already absent from all anuran assemblages (Fig. 8).

Thus, it may be concluded that palaeobatrachids most probably became extinct because mean temperatures during

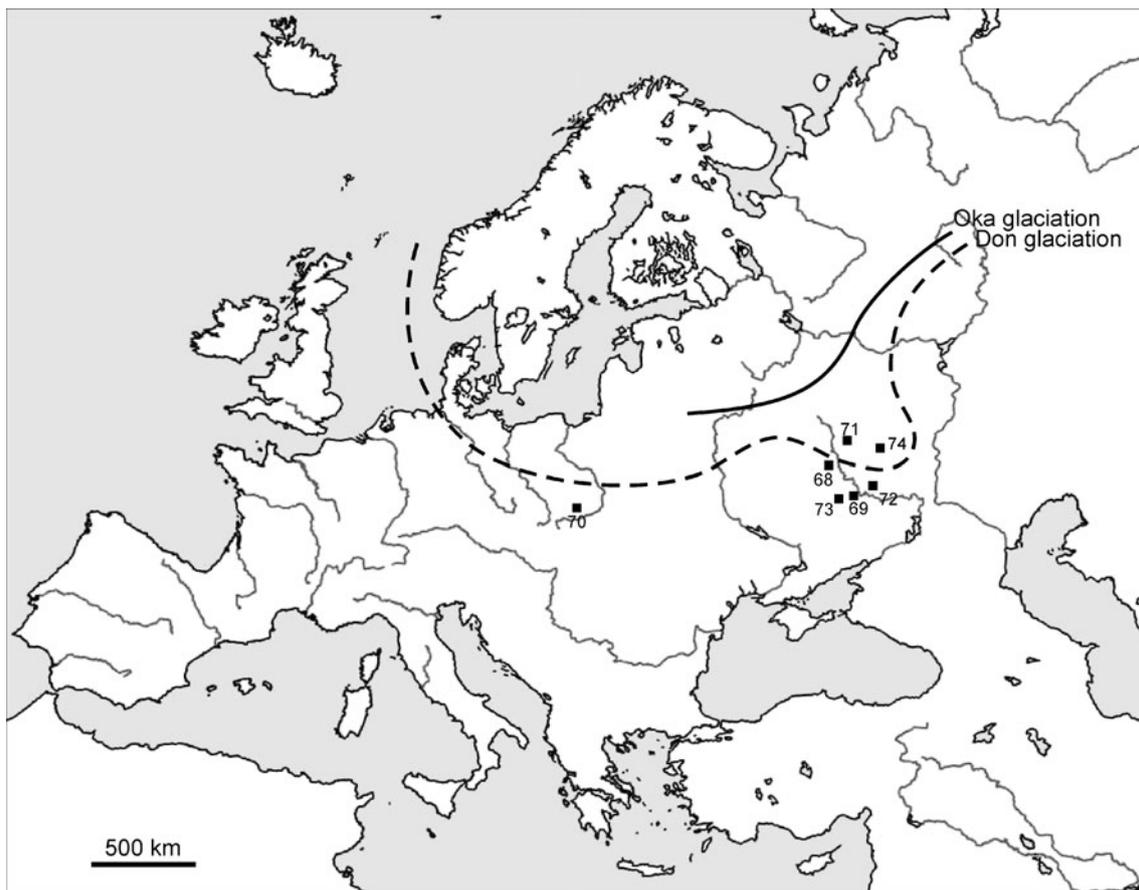


Fig. 9 Reconstruction of the ice sheet extent of the Don and Oka glaciations in the East European Plain and some of the last recorded palaeobatrachids. From Turner (1996) and Shik et al. (2006). For information on the localities see Fig. 7

the coldest month dropped markedly below the freezing point (the same factor explaining their earlier disappearance from central Europe). This can be inferred from the complete absence of thermophilous pollen from the time interval in question, and from the increasing aridity of the climate.

Conclusions

1. Assessment of developmental and individual variation in the frontoparietals of late Oligocene *Palaeobatrachus* specimens from Bechlejovice (Czech Republic) reveals that *Pliobatrachus* and *Albionbatrachus* basically fit into the range of variation seen in *Palaeobatrachus*. They may be retained as distinct taxa at the species level but not at the generic level (as *Palaeobatrachus langhae* and *P. wightensis*, respectively).
2. Palaeobatrachid frogs from the Middle Eocene of Messel (Germany) are described here as *Palaeobatrachus tobieni* comb. nov. This is the earliest palaeobatrachid documented by articulated skeletons. The comparatively short distal part of the forelimb, and the fact that synsacral diapophyses are formed entirely by the transverse processes of the sacral vertebra proper may indicate that *P. tobieni* had become only partly aquatic, rather than an obligate water-dweller.
3. A small, probably early adult palaeobatrachid from the Late Eocene of Kučlín (Czech Republic) described in this paper represents the easternmost known occurrence of Eocene palaeobatrachids.
4. The earliest (Cretaceous) palaeobatrachids are known from Spain and southern France. By contrast, Palaeocene and Eocene palaeobatrachids are found only in western and central Europe, whereas the latest (Pliocene and middle Pleistocene) occurrences of palaeobatrachids are in eastern Europe. Accordingly, the geographic range of these anurans shifted eastward during the period of their existence.
5. Palaeobatrachids probably disappeared from western Europe due to aridization, and subsequently from central Europe due to a decrease of temperatures below freezing in the coldest month of the year. They finally became totally extinct as a result of being trapped, within eastern Europe, between periglacial zones surrounding the continental glacier in the north and a comparatively dry steppe environment in the south.

6. The last known palaeobatrachids are those recorded from the Muchkap interglacial (621–568 Ka), indicating that palaeobatrachids most probably died out during the Oka glaciation (474–425 Ka) or slightly earlier.

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