

OLDEST BUFONIDAE (AMPHIBIA, ANURA) FROM THE OLD WORLD: A BUFONID FROM THE PALEOCENE OF FRANCE

JEAN-CLAUDE RAGE, Laboratoire de paléontologie, UMR CNRS 8569, Muséum national d'Histoire naturelle, 8 rue Buffon, 75005 Paris, France, jcrage@mnhn.fr.

The Bufonidae, a neobatrachian frog family, are a successful group of anuran Amphibia. The family is cosmopolitan, except for Madagascar and territories (including Australia) east of Wallace's Line. Fossil bufonids are common in Neogene and Pleistocene localities, but pre-Neogene reports are rare and all but one record from the Paleocene of Brazil are erroneous or questionable. Here the earliest member of the Bufonidae from the Old World is reported. It was recovered from the Paleocene of France and represents one of the two earliest bufonids.

RECORDS OF ANTE-MIOCENE BUFONIDAE

Estes (1970) identified bufonids from the Paleocene of Brazil (i.e., implicitly from the Middle Paleocene of Itaboraí and confirmed by Estes and Báez, 1985). Representatives of two living species groups of *Bufo* have been recognized in this locality (Estes, 1970), but this material remains undescribed.

Bufonid frogs were reported from the Oligocene and Eocene of Europe, Asia, and the Americas, but apart from two doubtful reports (see below), these identifications are all in error (Sanchíz, 1998; Báez, 2000; Roček and Rage, 2000). Patton (1969) and Chkhikvadze (1985) provided lists of fossils from the early or middle Oligocene of the U.S.A. and Kazakhstan, respectively, but the bufonids that appear in these lists are without comments or descriptions and their identifications cannot be substantiated.

Therefore, pre-Miocene bufonids are known only in the Paleocene of Brazil and France, and perhaps in the middle Oligocene of the U.S.A. and Kazakhstan. The Brazilian specimens and those described below are the only known Bufonidae from the Paleocene and are the earliest representatives of the family.

THE LOCALITY

The Bufonidae described herein come from Cernay, northern France. Cernay is late Paleocene (Thanetian) in age and is placed in the last standard level (MP 6) of the Paleocene (Schmidt-Kittler, 1987). Cernay produced a rich and diverse fauna of mammals (Russell, 1964) but anurans are rare. Estes et al. (1967) identified an indeterminate Discoglossidae and an indeterminate Neobatrachia. Subsequently, Vergnaud-Grazzini and Hoffstetter (1972) stated that the discoglossid was actually a palaeobatrachid and they referred it to the genus *Palaeobatrachus*. The latter assignment is accurate (Duffaud, 2000; Roček and Rage, 2000). An additional assemblage includes a few anuran bones. Among them, two ilia and perhaps a pterygoid belong to the Bufonidae. These fossils are housed in the Muséum national d'Histoire naturelle (MNHN), Paris, France.

THE BUFONIDAE FROM CERNAY

MNHN CR 16016 is a nearly complete right ilium, missing the anterior-most part of the shaft (Fig. 1A, B). The supracetabular expansion (pars ascendens) is small, without a supracetabular fossa. There is no elongate ischiatic process. The tuber superius comprises a low and elongate dorsal prominence that bears a somewhat globular dorsal protuberance (sensu Tyler, 1976). The protuberance is located above the anterior margin of the acetabulum. The subacetabular expansion (pars descendens) is developed but not broad and it lacks a preacetabular fossa. The acetabulum is relatively small. The ilial shaft is compressed laterally. A dorsal crest or even a dorsal ridge is absent. A low and blunt

ridge runs along the ventral part of the lateral face of the shaft. Posteriorly, it merges with the anterior part of the acetabular rim. This ridge is reminiscent of the "calamita" ridge (sensu Sanchíz, 1977), a morphological trait present in the living European *Bufo calamita*. The ridge is present also, but less prominent, in some species of the 'calamita group' from Europe and North America (Tihen, 1962). As in *B. calamita*, the ridge is not strongly marked in the fossil from Cernay. The ventral border of the shaft forms an open angle with respect to the pars descendens. A groove runs along the dorsal part of the medial face and it grows deeper anteriorly. The medial face of the acetabulum lacks an interiliac tubercle.

Another ilium (MNHN CR 16017) probably belongs to the same taxon but it cannot be definitely ruled out that it represents another species. The posterior part of the acetabular area is missing (Fig. 1C). It slightly differs from CR 16016 in having a more prominent calamita ridge and a vertical groove on the dorsal protuberance. Such a groove is frequent in bufonids.

A fragmentary pterygoid (MNHN CR 16018) might belong to this bufonid. It is represented by the anterior branch and the bases of the medial and posterolateral branches (Fig. 1D). The medial margin forms a regular curve, which differs from that of Palaeobatrachidae, the only other family identified in the locality. In Palaeobatrachidae, the central part of the medial margin slightly protrudes medially, rendering this margin somewhat sinuous (Špinar, 1972). In the Discoglossidae, the only other family identified in the Paleocene of Europe, the medial margin is straight or almost straight. This fragmentary pterygoid, especially the curve of the medial margin, best compares with the Bufonidae. Obviously, in view of the state of preservation of this specimen, its assignment to the Bufonidae is only tentative.

COMMENTS

The ilia from Cernay show a combination of characters that point clearly to Bufonidae: pars ascendens short, elongate ischiatic process absent, dorsal crest or ridge absent on top of ilial shaft, tuber superius present and not projecting laterally, pars descendens mid-sized, angle between shaft and pars descendens open, and interiliac tubercle lacking. These ilia are very similar to those of the extant genus *Bufo*. More specifically, the relatively small pars ascendens and pars descendens resemble those of the living European species, and the calamita ridge is reminiscent of some living species of the 'calamita group'. This recalls Estes' statement (1970) that 'present-day species groups of bufonids' are probably present in the Paleocene of Brazil. However, it is not possible to assign these fossils to the genus *Bufo* with confidence on the basis of the available material. Moreover, despite the slight difference in the morphology of the tuber superius of the two ilia, it is presumed that there is only one taxon at Cernay. This difference appears to be within the range of variation of bufonid species, but the presence of two species cannot be definitely rejected.

The assignment of the pterygoid to the Bufonidae is tentative. This allocation rests only on the fact that this bone is consistent with bufonids and that it cannot be referred to one of the other families present in the Paleocene of Europe (i.e., Discoglossidae and Palaeobatrachidae). Moreover, its size is not consistent with that of the small indeterminate neobatrachian from Cernay.

It should be noted that the remains from Cernay, which were referred to an indeterminate family of Neobatrachia, cannot be assigned to the

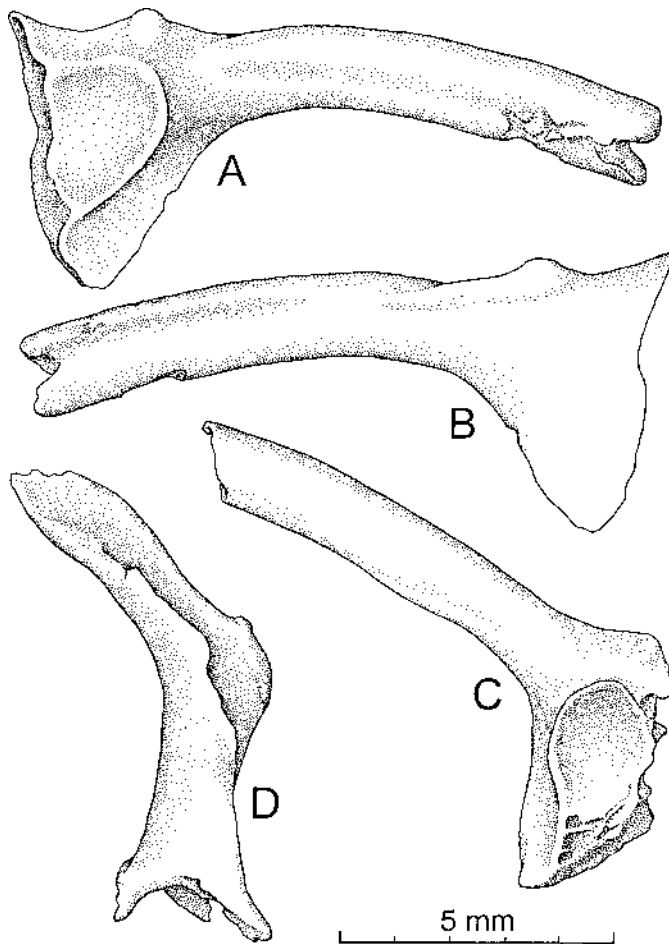


FIGURE 1. Bufonidae from the Paleocene of Cernay. A–B, right ilium (MNHN, CR 16016) (A, lateral view; B, medial view); C, left ilium (MNHN, CR 16017), lateral view; D, right pterygoid (MNHN, CR 16018), dorsal view.

Bufonidae (Estes et al., 1967). Therefore, three anurans are present in the Paleocene of Cernay: *Palaeobatrachus* (Palaeobatrachidae), an indeterminate species of Bufonidae, and an indeterminate neobatrachian family.

Finally, the bufonids from Cernay and Itaboraí represent the earliest known members of the family, Itaboraí (middle Paleocene) being slightly older than Cernay (late Paleocene). This disjunct distribution of the oldest representatives of the family is astonishing but it is not the only example of that kind. Indeed, it is reminiscent of the presence of some vertebrates with South American affinities in the Early Tertiary of Europe: ceratophryine leptodactylid frogs, rheiform birds, and perhaps myrmecophagid mammals. These groups, which are characteristic of South America, are present in the Early Tertiary (Eocene) of Europe

but, as for the bufonids, they are absent in the Early Tertiary (and in older levels) of the geographically intervening landmasses, i.e., North America and Africa (Rage, 1999). This distribution remains unexplained.

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