ON *PELOBATES DECHENI* TROSCHEL, 1861, AND *ZAPHRISSA EURYPELIS* COPE, 1866 (AMPHIBIA: SALIENTIA: PELOBATIDAE) FROM THE EARLY MIOCENE OF ROTT NEAR BONN, WEST GERMANY

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ABSTRACT—The type specimen of *Pelobates decheni* Troschel, 1861, from Rott near Bonn, has been reinvestigated and described. It is shown to be identical with the type (and only) specimen of *Zaphrissa eurypelis* Cope, 1866, described from the same locality. The latter name thus must be regarded as a junior synonym of the former. This also implies the reassignment of *Zaphrissa* from Discoglossidae to Pelobatidae. Some unique plesiomorphic characters of *P. decheni* not known in Recent frogs are pointed out.

INTRODUCTION

In the course of compiling a bibliography of the fauna of the formerly famous paleontological locality Rott near Bonn (Aquitanian), one of us (WB) rediscovered the description of a pelobatid frog by Troschel (1861) under the name *Pelobates decheni*, which had not been included in the comprehensive monograph on the Tertiary frogs of central Europe by Spinar (1972). Troschel's type specimen is deposited in the collection of the Geological-Paleontological Institute of the Rheinische Friedrich-Wilhelms-Universität, Bonn (Inv. no. "Troschel 1"). The original description (Troschel, 1861:56) is extremely brief and insufficient: "Pelobates Decheni, an der Sculptur der Kopfknochen leicht zu erkennen, von dem lebenden P. fuscus durch kleinere Kreuzwirbel-Fortsaetze bestimmt unterschieden." Therefore, we decided to study the fossil in detail and to compare it with Zaphrissa eurypelis Cope, 1866—as according to Cope's (1866) description these sympatric nominal species appear to be very similar.

The geological age of the locality is still a matter of discussion. It was assigned to the early Miocene by e.g. Wolterstorff (1901) and Parker (1929). Afterwards it has also been considered to be middle to late Oligocene, mainly due to the findings of anthracotherian mammals (*Microbunodon*, cf. Stehlin, 1932:319; Westphal, 1958:66; see also bibliography given by Statz, 1939). Rott has been quite recently placed in MN O of the sequence given by Mein (1976).

DESCRIPTION

The type of *P. decheni* is an impression of the dorsal side of an incompletely preserved skeleton (Fig. 1). The ventral side is lacking. With the exception of the

frontoparietal, the left squamosal, three vertebrae, the left humerus and radioulna, three carpal elements of the left forelimb, and some metacarpals and phalanges of the right forelimb, all other bones are disarticulated.

Neural Endocranium

Preserved are a very small part of the right prooticooccipital in the area of the posterior section of the squamosal-frontoparietal suture; impressions of the quadrate bones, which are separated from the quadratojugals by a rather distinct suture; and a very incomplete and indistinct impression of the sphenethmoid. Unfortunately, these endocranial elements do not provide much information.

Neural Exocranium

Nasal—It is a paired, heavily sculptured bone. The sculpture consists of numerous pits of medium size separated from each other by comparatively sharp ridges (Fig. 2), similarly to *Eopelobates* (see e.g. Estes, 1970, fig. 2; Špinar, 1972, pl. 158/1). The general shape of the bone is well apparent in Fig. 4; it is similar to that in *Pelobates cultripes* or *P. syriacus*. In spite of the fact that the bones in question are dislocated, it seems that at least in the extent of the posterior one-quarter of the anteroposterior length the elements were not in mutual contact. From this it can be concluded that the sphenethmoid could have been exposed on the skull surface in that area.

Frontoparietal—A rather large bone whose anterior free ends enclose a narrow cuneiform fontanelle. Posteriorly this fontanelle is transformed into the median suture, which disappears shortly behind the level of the posterior orbital margins. The posterior part is rather damaged by some breaks; however, the median part, close to the posterior mar-

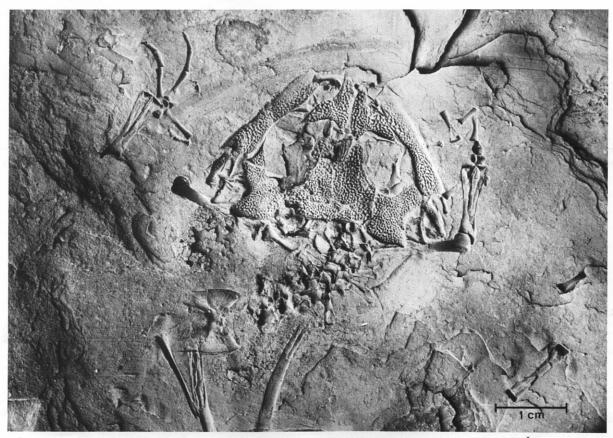


FIGURE 1. Pelobates decheni Troschel, 1861, holotype (GPUBo, "Troschel 1"). Photo by Z. V. Špinar.

gin of the bone, is well preserved and does not show any trace of a suture (Fig. 3). The sculpture is similar to that in the nasal, the only difference being that the pit-like depressions in some parts of the bone are elongate; in the posterior part it forms a nearly reticulate sculpture pattern (Fig. 2). Remarkable is the length of the squamosal–frontoparietal suture, which represents nearly one-half of the length of the anteroposterior bone axis. The posterior margin of the bone is almost straight, with the exception of a small but distinct convexity between the two slender, slightly diverging processus paraoccipitales. These bear a distinct crista on the distal part of their surface.

Premaxilla—Only the impression of a disarticulated fragment of the right premaxilla including its pars facialis is preserved; the general shape of the bone is not clear.

Maxilla—A paired, sculptured, tooth-bearing bone. Its margo orbitalis is slightly concave. The sculpture is very similar to that described above for the frontoparietal and covers evenly the whole surface of the bone except for a cuneiform area in the anteriormost third of the ventral margin. An im-

pression of the slender palatine process is preserved at the border between the anterior and middle thirds of the bone. The general shape of the maxilla is shown in Fig. 4; it resembles that of *P. cultripes* and *P. syriacus*.

Quadratojugal—A paired, elongate bone that is robust in comparison to all Recent members of the genus *Pelobates*. It slightly narrows posteriorly and is remarkable in that its outer surface is sculptured. The sculpture is similar to that of the nasal. It is clearly separated from the quadrate.

Squamosal—A paired bone whose lamella alaris bears a sculpture similar to, but more delicate than, that of the nasal. The ventral margin of this lamella is semicircularly concave; the posterior margin is slightly convex. The course of the squamosal—fronto-parietal suture appears to have been nearly straight. Thus, a wide postorbital exocranial covering of the prooticooccipital was developed in this area. This structure is similar to that in *Pelobates cultripes*. Also the contact between the squamosal and the maxilla was rather long, again similarly to *P. cultripes*. As for the posterolateral processes, the situation is not clear.

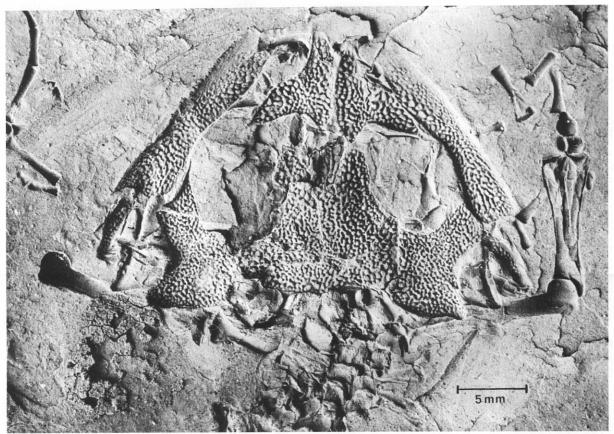


FIGURE 2. The skull of Pelobates decheni, same specimen as in Fig. 1. Photo by Z. V. Špinar.

Between the lamella alaris squamosi, quadratojugal and maxilla there are two structures which could perhaps be interpreted as parts of the pterygoid (Fig. 4).

Vertebral Column

Six presacral vertebrae are well preserved, the first five in articulation. Two more presacrals can be tentatively identified from vague impressions. The spinal processes of the neural arches are posteriorly inclined, so that they overlap the neural arch of the successive vertebra. The fourth, fifth and sixth vertebrae are connected with ribs which seem to be free. The rib of the sixth vertebra is the largest. The sacral vertebra has distinct wing-like expansions composed of four parts; the second part is the largest and represents the transverse process proper (cf. Fejérváry, 1917:151, p. III; Špinar, 1972:65, figs. 18, 19, 20). The remaining accessoric laminae are outgrowths of the pre- and postzygapophyses. The shape of the urostyle is clearly apparent in Fig. 4.

Shoulder Girdle

Clavicle—A narrow element covering the first vertebra could be interpreted as this part of the shoulder girdle.

Coracoid—A short and stout bone similar to that in *Eopelobates*. The details of its shape cannot be discerned from the incomplete impression.

Cleithrum and Suprascapula—The general shape, excluding the part overlapped by the humerus, is given in Fig. 4.

A deep impression close to the proximal end of the right coracoid can be regarded as the sternum.

Forelimb

Both humeri are preserved, the right one still retaining its natural articulation with the coracoid. The distal parts of both radioulnae are clearly divided. Three carpal elements are preserved in the left forelimb in their original position. They are the ulnare, the centrale II and probably the radiale. Moreover, the prepollex is preserved in the right forelimb. The elements of the metacarpus and the phalanges are also partly preserved, but they are of no help in characterizing the specimen.

Pelvic Girdle and Hindlimb

Only the anterior parts of both ilia, a fragment of the femur, and an isolated bone that could be inter-



FIGURE 3. Frontoparietal bone of *Pelobates decheni*, same specimen as in Fig. 1. Photo by J. Krhovský.

preted as one of the tarsal elements, and one of the phalanges, are preserved. Again, these elements have little significance.

DISCUSSION

Individual Age of the Specimen

Before making any conclusions about the systematic position of the specimen, it is necessary to consider its individual age. Because the medial margins of both nasals diverge posteriorly (see description above and Fig. 4), thus leaving space for the exposed sphenethmoid (a criterion for the relative individual age according to Basoğlu and Zaloğlu, 1964:239), and because the anterior part of the frontoparietal is still divided by a cuneiform fontanelle, it can be judged that the specimen is an adult, but not yet fully grown. This is supported also by the presence of sutures in the wings of the sacral vertebrae.

Generic Assignment

The following combination of characters allows assignment of the specimen to the genus *Pelobates*:

1. The posterior part of the frontoparietal is com-

pact, without a median suture, which suggests that a median element arising above the tectum synoticum takes part in the origin of this bone complex. This is considered to be an important character of the family Pelobatidae as redefined by Roček (1981), i. e. containing only the genera *Pelobates* and *Eopelobates*.

2. The general shape of the frontoparietal is different from that found in the genus *Eopelobates* (Špinar, 1972, fig. 82; Roček, 1981, fig. 49c; Estes, 1970, figs. 12B, 21A), but it is rather similar to the condition observed in the four Recent species of *Pelobates* (Roček 1981, fig. 57; Estes 1970, figs. 21B, 23B).

3. The general shape of the nasals corresponds quite well to that found in the four Recent species of *Pelobates*, while it differs from that in *Eopelobates*. In *Eopelobates* the anterolateral margin is always nearly straight (Spinar, 1972, figs. 81, 82; Estes, 1970, figs. 12B, 21A), while it is always concave in *Pelobates*, as it takes part in formation of the margins of fenestra exonarina.

4. The shape of the squamosal of *P. decheni* resembles closely that of the Recent *P. cultripes* (Estes, 1970, fig. 18d), while it differs from that in *Eopelobates* (Spinar, 1972, fig. 83; Roček, 1981, fig. 49b).

5. The maxilla, the neural arches of the vertebrae, and the wings of the sacral vertebra are shaped as in *Pelobates*. The combination of these characters is

typical of Pelobates.

From the above characters it can be seen that Pelobates decheni clearly differs from Eopelobates anthracinus Parker, 1929, whereas its relation to Zaphrissa eurypelis Cope, 1866, also from Rott like the two preceding taxa, remains to be clarified. The only reference stating that Z. eurypelis perhaps could be identical with P. decheni is that of Wolterstorff (1866:9, 10), who, however, provides no argument for his assumption which is expressed with a question mark. Estes (1970:333) believed that Zaphrissa is a discoglossid; however, recently he stated that he changed his opinion (Estes, in litt.). Otherwise, Z. eurypelis was believed to be a monotypic genus close to the discoglossid Latonia (Cope, 1866:77; Friant, 1960:133 f.; Baird, 1970:385). A direct comparison carried out by us on the basis of Cope's original description, a photograph of the type (Fig. 5), and a cast of the type specimen (Princeton University Museum of Natural History cat. no. 11953) convinced us that this taxon is in fact identical with P. decheni. The reasons for this opinion are:

(1) the robust and sculptured quadratojugal,

(2) the identical shape of the nasal,

(3) the general shape and proportions of the maxilla,

(4) the very broad postorbital bridge,

(5) the type of sculpture,

- (6) the shape of the lateral expansions of the sacral vertebra,
- (7) the shape of the urostyle, and

(8) the presence of free ribs.

Zaphrissa eurypelis differs from P. decheni in:

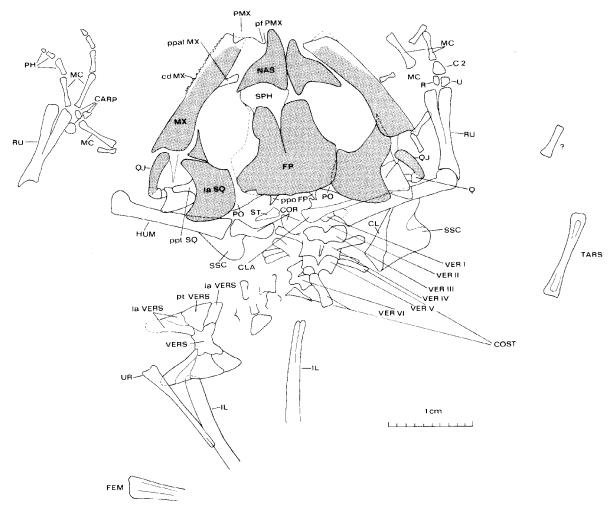


FIGURE 4. Pelobates decheni, drawn after holotype. The broken lines indicate restored parts of the bones. Redrawn by U. Bott after the reconstruction by Z. Roček. Abbreviations: C2, centrale 2; CARP, carpal elements; CL, cleithrum; CLA, clavicula; COR, coracoid; COST, costa; FEM, femur; FP, frontoparietale; ppo FP, processus paraoccipitalis frontoparietalis; HUM, humerus; IL, ilium; MC, metacarpalia; MX maxilla; cd MX, crista dentalis maxillae; ppal MX, processus palatinus maxillae; NAS, nasale; PH, phalanges; PMX, premaxilla; pf PMX, pars facialis praemaxillae; PO, prooticoccipitale; Q, quadratum: QJ, quadratojugale; R, radiale; RU, radioulna; SPH, sphenethmoid; la SQ, lamella alaris squamosi; ppl SQ, processus posterolateralis squamosi; SSC, suprascapula; ST, sternum; TARS, one of the tarsal elements (talus or calcaneus); U, ulnare; UR, urostyle; VER, vertebra; VERS, vertebra sacralis; la VERS, laminae accessoriae vertebrae sacralis; pt VERS, processus transversus vertebrae sacralis.

(1) the absolute size,

(2) the distal fusion of the radioulna, and

(3) the sutures on the wings of the sacral vertebra.

These discrepancies can be interpreted as differences in ontogenetic age of the two specimens. Whereas the type of *P. decheni* is not a fully grown individual, the *Z. eurypelis* type is. Thus, the few differences are inconsequential and the two specimens represent the same species. As *Pelobates decheni* Troschel, 1861, antedates *Zaphrissa eurypelis* Cope, 1866, the latter is to be regarded as a synonym of the former.

Intrageneric Position

There are some characters that distinguish *P. de*cheni from the four Recent species of the genus (cultripes, fuscus, syriacus, varaldii):

1. The rather robust and sculptured quadratojugal is a feature not occurring in the Recent members of the genus and is to be considered as a most interesting plesiomorphic character state (see Roček, 1981:109).

2. The presence of a distinct boundary between the quadrate and the quadratojugal must be also regarded as plesiomorphic.



FIGURE 5. Zaphrissa eurypelis Cope, 1866, holotype (Princeton University Museum of Natural History, PU 11953). From a color slide by D. Baird.

3. The very wide postorbital bridge is shared by *P. cultripes*, in which it is, however, developed to a lesser extent (see Roček, 1981, fig. 57). This feature must also be regarded as plesiomorphic (Roček, 1981:148), in contrast to e.g. the opinion expressed by Estes (1970:298).

4. The ribs do not fuse with the transverse processes of the vertebrae. This is another important plesiomorphic character state.

5. The distal parts of the radioulnae are distinctly separate in subadult specimens; this must also be considered plesiomorphic, as already in the larval stages of all the Recent *Pelobates* species these elements are fused. In the fullgrown specimen of *P. decheni*, however, they are also fused.

Summarizing these characters, *P. decheni* has to be interpreted as a form very close to the stock that gave rise to the modern species, if it is not the ancestor itself. It shows the closest affinities to *P. cultripes*, thus supporting the view that it represents a "basis-

form" (sensu Remane, 1952). From this it also appears that *P. cultripes* is the most conservative species among the living members of the genus (Gislén, 1937; Roček, 1981).

Paleogeographical Aspects

The fossil history of the genus *Pelobates* comprises the Oligocene (Hecht and Hoffstetter, 1962:18–19), the Pliocene (Młynarski, 1961:264–266; 1962:182; 1977:15–16, 19, 21, 25, tables IV/1, IV/2), and the Plio-Pleistocene (Hodrová, 1981). The first work refers to "*Pelobates cultripes*" (see discussion below) from Belgium, the second through fourth (Młynarski) to *P. fuscus* and *P. cf. syriacus* from southern Poland, and the fifth (Hodrová) to *P. cf. fuscus* from Czechoslovakia. This means that in all these instances Recent species are involved. Finally, one of us (ZR) saw fossil remains in the collection of the Université Paris VI, which undoubtedly belong to the genus *Pelobates*; they are from the Miocene of La Grive St. Alban, France.

In conclusion, the genus Pelobates was distributed during the Tertiary throughout western and central Europe. The same can be stated for Eopelobates. E. anthracinus was found in the Aquitanian (early Miocene: see Introduction) of western Germany (Parker, 1929) and in the Oligo-Miocene of Czechoslovakia (Śpinar, 1972:219). E. bayeri is known from the Oligo-Miocene and Miocene of Czechoslovakia (Špinar, 1972:216). Młynarski (1961:261, 1977:25) and Sanchiz and Młynarski (1979:164) mentioned Eopelobates sp. from the Pliocene of Poland. Remains tentatively assigned to this genus were also reported from the late Eocene of England (Rage and Ford, 1980:50). It is necessary to add here that neither E. guthriei nor E. grandis of North America belong to this genus (Roček, 1981:146). The systematic position of E. hinschei from eastern Germany needs further clarification.

As can be seen from this discussion, Pelobates and Eopelobates were well separated already in the early Miocene, and possibly already in the Oligocene. This follows from their coexistence at the locality Rott near Bonn. Their coexistence continued until the Pliocene, as can be seen from the findings of Młynarski (1961, 1977). In this case Eopelobates lived together with a form of Pelobates very close to the modern P. syriacus. However, the Miocene form coexisting with Eopelobates, i.e. P. decheni, is extinct. In this respect the identification of the so-called P. cultripes from the Belgian Oligocene should be reinvestigated. Since the present study indicates that the early Miocene species P. decheni shows some affinities to the modern P. cultripes, it seems much more likely that the material of Hecht and Hoffstetter (1962) is also referable to P. decheni. Evidence for this opinion is afforded by material of a very similar Pelobates from the late Eocene (Tongrian) of Belgium, which was seen by one of us (ZR), and which shows a type of sculpturation virtually identical with

P. decheni (also Hecht, Hoffstetter and Vergnaud-Grazzini, in prep.).

Because of its combination of unique plesiomorphic characters, which is not shared by other pelobatids and by any other member of the Salientia, additional specimens of *Pelobates decheni* would be of high scientific value—the more as the two existing specimens discussed here are incomplete and of different individual age. Further specimens are required for learning more about the extent of variation in this important species. New excavations at Rott, a yielding fossil site in the last century, could provide addi-

tional material.

Acknowledgements—Our thanks are addressed to Prof. Dr. H. K. Erben and Prof. Dr. H. Remy, Geological-Paleontological Institute of the University of Bonn, for the generous loan of the type specimen of *Pelobates decheni*, and to Dr. D. Baird, Princeton University, for the courtesy of supplying us with a cast and color slide of the type of *Zaphrissa eurypelis* Cope. Dr. Baird allowed us to publish a black-and-white reproduction of the slide (Fig. 5). We also thank Dr. J. Krhovský, Department of Paleontology, Charles University, Prague, for photography, and Miss U. Bott, Museum A. Koenig at Bonn, for preparing the final draft of the drawing.

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