

MACROPELOBATES OSBORNI NOBLE, 1924
— REDESCRIPTION AND REASSIGNMENT

ZBYNĚK ROČEK

Department of Paleontology, Charles University, Albertov 6, 12843 Praha 2, Czechoslovakia

Abstract: Detailed anatomical analysis which was enabled by the supplementary preparation of hitherto the only known specimen of *Macropelobates osborni* suggests that a form is concerned which has closer relations to the genus *Scaphiopus* than to *Pelobates* and/or European representatives of the genus *Eopelobates*. However, hypothesis that *Macropelobates* is ancestor of European pelobatids should be refused not only for anatomical but also paleogeographical reasons, as Turgai Strait persisted between Europe and Asia until the Oligocene, representing thus important zoogeographical barrier. Hence it seems that *Macropelobates* is rather a form belonging to the lineage of Scaphiopodidae.

INTRODUCTION

Macropelobates osborni was described by NOBLE (1924) from the Oligocene (at about the boundary between the Early and Middle Oligocene after MELLETT 1968) of Mongolia, and considered a representative of the group ancestral to Pelobatidae which comprised according to him (NOBLE op. cit.: 11) genera *Scaphiopus*, *Pelobates*, *Pelodytes* and *Megophrys*. Only three fossil genera considered belonging to Pelobatidae were known in these times (FEJÉRVÁRY 1917: 170): *Protopelobates*, *Pelobates*, and *Pelodytes*, all post-Miocene. *Eopelobates* was described later (PARKER 1929: 277—280). This historical background influenced Noble when he formulated his theory on the evolution of the Pelobatidae (NOBLE 1924: 9—10). He theorized that the Pelobatidae arose from primitive discoglossids of which *Leiopelma* and *Ascapus* are the only surviving representatives. Besides Leiopelmatidae, primitive discoglossids gave rise to the family Pelobatidae. The first stage in the evolution of the pelobatids is represented by *Megophrys*, the second by *Macropelobates*. From the supposed radiation centre in Asia the spadefoots (op. cit.: 10) »have succeeded in migrating westward across favorable sandy areas of Asia to western Europe and eastward across the Bering Strait connection, southward to southern Mexico«.

Some later authors were influenced by Noble's opinions in their evolutionary considerations concerning pelobatids (e. g. PARKER 1929: 281; ŠPINAR 1952: 469, 487; ZWEIFEL 1956: 38; ESTES 1970: 326; however ESTES, op. cit.: 293—294 noted that *Macropelobates* was too late in time to be an ancestor of pelobatines); on the

other hand, some criticism was also expressed (e. g. GISLÉN 1936: 121—122; ZWEIFEL 1956: 15; ROČEK 1981: 151).

The present state of knowledge of palaeogeography, palaeoclimatology, and anatomy of fossil frogs contradicts that part of Noble's theory concerning the origin of European pelobatids. As was pointed out elsewhere (ROČEK 1981: 120—123) there are a great number of characters in which *Macropelobates* differs from them. Factors besides these anatomical discrepancies strongly disfavour Noble's theory. A wide strip of epicontinental sea called Turgai Strait existed from the Jurassic until the Oligocene, and completely separated Europe and Asia. But *Eopelobates*, whose European species are undoubtedly pelobatids, as well as *Pelobates* were already present in Europe in the Eocene (for review of records see BÖHME, ROČEK and ŠPINAR, 1982).

This contradictory situation needs clarification. Therefore, the present study aims to provide additional knowledge of the anatomical structure of the type specimen *Macropelobates* (unfortunately, no other specimen has been found). These anatomical data should supplement those published by NOBLE (1924: 5—6), ESTES (1970: 324—326) and ROČEK (1981: 120—123). On the basis of these data the kinship relations of *Macropelobates* will be discussed.

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DESCRIPTION

Skull: a) Neural endocranium

Sphenethmoid (fig. 3; see also ESTES 1970, figs 4c, 7B). In addition to what was said elsewhere (ROČEK 1981: 120—122) it is possible to state that both canalis olfactorius and canalis pro ramus medialis nervi ophthalmici piercing the postnasal wall are clearly visible, separated by a comparatively thin partition when reaching the nasal cavity (see ESTES op. cit., fig. 4c). It is necessary to point out that the sphenethmoid and the frontoparietal do not maintain their original positional relations. What was designated as ethmoid by NOBLE (1924, fig. 1A) is actually maxilla (see ESTES 1970: 325). It is also worthy of note that fig. 7B given by ESTES (op. cit.) should be explained as restored ventral view (with outline drawn from above). However, the direct examination of the ventral surface of the sphenethmoid is prevented by the conglomerate of bones forced immediately beneath it.

Prooticooccipital (ROČEK 1981, fig. 48). Only dorsal and anterior walls of the left otic capsule are preserved, as well as the dorsolateral section of the foramen magnum, and both condyli occipitales. There is a slight depression on the dorsal

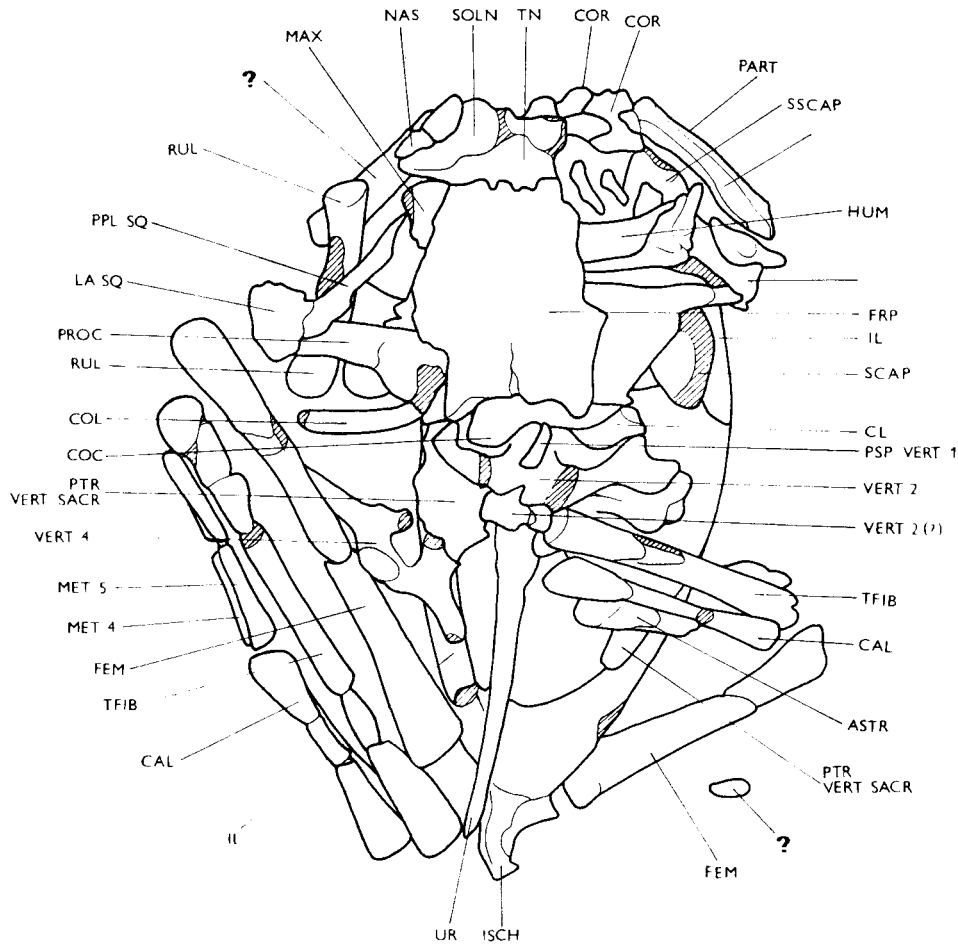


Fig. 1. *Macropelobates osbornii*, dorsal aspect, drawn after holotype. Hatched parts indicate broken bone surfaces. Abbreviations: ASTR - astragalus; CAL - calcaneus; CL - clavicle; COC - condylus occipitalis; COL - columella; COR - coracoid; FEM - femur; FRP - frontoparietal; HUM - humerus; IL - ilium; ISCH - ischium; LA SQ - lamella alaris squamosi; MAX - maxilla; MET - metatarsal; NAS - nasal; PART - praearticulare; PHAL - prae-hallux; PPL SQ - processus posterolateralis squamosi; PROC - prooticocipital; PSP VERT - processus spinosus; PTAR - praetarsal; PTR VERT SACR - processus transversus vertebrae sacralis; PUB - pubis; RUL - radioulna; SCAP - scapula; SPH - sphenethmoid; SQ - squamosum; SSCAP - suprascapula; SOLN - solum nasi; TFIB - tibiofibula; UR - urostyle; VERT - vertebra.

surface of the otic capsule. Obviously rather sharp outgrowth instead of moderate elevation was on the site of the prominentia canalis semicircularis posterioris, which is suggested by the projecting margin of the bone on the left side. Similarly prominent is the crista parotica running from this prominentia anterolaterally. The occipital condyles are widely separated, suggesting that there was quite a wide hypo-

chordal plate consisting of cartilage. However, both condyles are broken off from the prooticooccipitals, and rather displaced.

b) Visceral endocranium

Columella. The pars interna plectri and pars externa plectri are well ossified. The total length of both parts is 9.3 mm.

The quadratum is either not preserved or, if present, its identification remains obscure. The same holds for the ossa thyroidea.

c) Neural exocranium

Nasal (ROČEK 1981: 122). What was interpreted by ESTES (1970: 325) as a faint impression of the nasal on the dorsal surface of the sphenethmoid is in fact the broken bone edge, and is quite asymmetrical in relation to the septum nasi. Moreover, if the situation would be comparable to that in *Pelobates cultripes*, *P. fuscus* and small *P. syriacus* as ESTES (l. cit.) believed, then the exposed part of the sphenethmoid surface had to be sculptured similarly to the frontoparietal and nasal (see ROČEK 1981, fig. 12). However, the smooth and flat dorsal surface of the sphenethmoid indicates that it was completely covered. Therefore ESTES' restoration (1970, fig. 27) of the shape of nasals is inaccurate in this respect.

Frontoparietal (ESTES 1970, fig. 27; ROČEK 1981, fig. 48). Besides what was said elsewhere (ROČEK op. cit.: 122) it is possible to add that the original position of the element is preserved only in relation to the prooticooccipital but not to the sphenethmoid (see above). It is rather difficult to understand what NOBLE (1924: 5) meant under the term »sheathed . . . with a secondary deposit of bone«. The sculpture of the dermal bones develops as folds of the ossifying primordium, and is an integral part of the bone during the whole course of ontogeny.

Maxilla (NOBLE 1924, fig. 4A). There was a fragment of the right maxilla (see also NOBLE op. cit.: 5, fig. 1) but it was obviously lost before the specimen came to the hands of the present author. The left maxilla was displaced below the sphenethmoid. Its outer surface is sculptured similarly to the frontoparietal. The posterior part of the bone is broken away, which is indicated also by the fact that the lamina horizontalis maxillae reaches almost the posterior end of the fragment. The bone is very thin in this area, so that it seems that no distinct processus posterior was present (cf. ESTES 1970: 325). However, one can judge from the thickness of the dorsal part of the bone at the level of the crack that there had to be quite a strong processus zygomaticomaxillaris.

Squamosal (fig. 4b; cf. ESTES 1970, fig. 18e). The dorsal margin of the lamella alaris displays no sign of the processus dorsalis. The distal part of the processus posterolateralis is broken off close to its base, so that its long axis is not in the original position. This process passes into the base of the ramus paroticus by a wide mound which is clearly visible in posterior view.

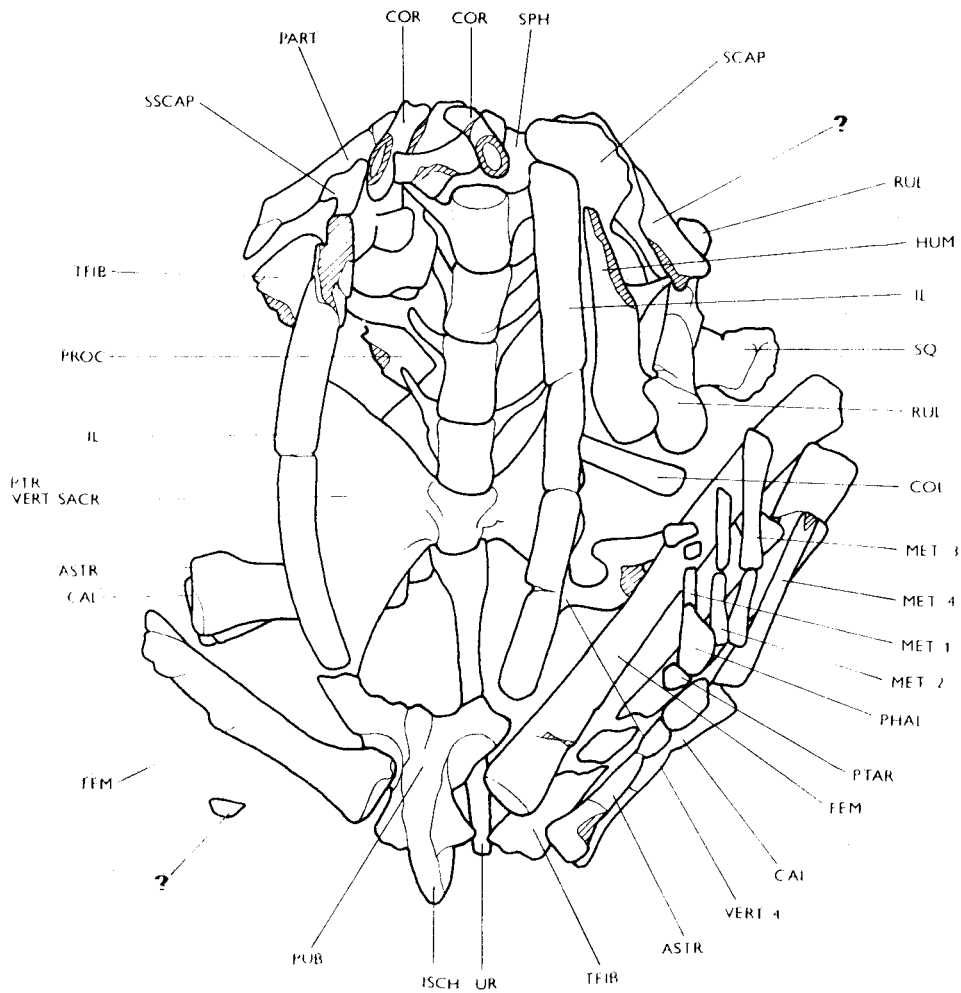


Fig. 2. *Macropelobates osborni*, ventral aspect, drawn after holotype. Hatched parts indicate broken bone surfaces. For abbreviations see fig. 1.

Parasphenoid. Only the lateral margin of the pars medialis is visible. As its tip reaches rather far anterior to the postnasal wall (it is attached to the solum nasi of the right nasal capsule) it is possible to suppose that this bone is beyond its original position.

Pterygoid. A fragment of the central part of the pterygoid is preserved, but provides no important information.

The praemaxilla is lacking or its identification is impossible. The quadratojugal either originally was lacking or it was not preserved.

d) Visceral exocranium

Praearticular. There is nothing to be added to what was said earlier (ROČEK 1981: 123)

Vertebral column

Only six praesacral vertebrae are sufficiently preserved, four posterior of them still in articulation. The first vertebra is probably forced below the skull base. The second vertebra is clearly visible in dorsal view, however, its neural arch including prae- and postzygapophyses are broken away. That this is the second vertebra is indicated by the inclination of the processus transversi anteriorly. Whether the dorsal part of the neural arch lying immediately behind this vertebra belongs to it is diffi-

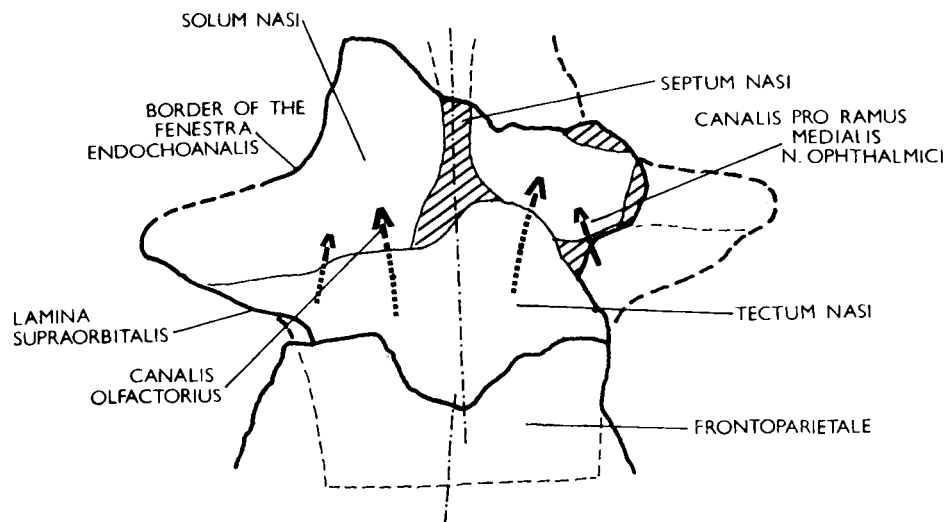


Fig. 3. Sphenethmoid and anterior part of the frontoparietal in dorsal aspect. Hatched parts indicate broken bone surfaces, dashed line indicates restoration, dotted and dashed lines indicate longitudinal axes of both elements.

cult to decide. The distal parts of the processus transversi are rather robust in comparison with their slender proximal parts. The third vertebra probably is missing. The position of the fourth vertebra is well apparent from the figs 1 and 2. That this is the fourth vertebra is suggested by the two processus transversi, which are slender in comparison with those in the second vertebra. The fifth to eighth vertebrae (NOBLE 1924, fig. 2B) bear distinctly anterolaterally directed and pointed processus transversi. The centra at least of anterior vertebrae are compressed dorsoventrally, their dorsal surfaces being flat and not protruding into the neural canal. The centrum of the sacral vertebra is shorter than those of the praesacrals. The proportions of its diapophyses are apparent from the figure given by Noble. Thin laminae covering

dorsally the space where posterior margin of diapophyses reach the centrum are only poorly developed. The urostyle is not ankylosed to the sacral vertebra, and is slightly longer than is the anteroposterior diameter of the sacral diapophyses.

Pectoral girdle

Coracoid. Both coracoids are preserved as fragments. Their shape is apparent from the figs 3B, C given by NOBLE (1924).

Clavicle. The right clavicle is present, but because its medial part is forced below the skull base and only the lateral articular part protrudes, it does not provide much diagnostic information.

Scapula. The right scapula is preserved in a position which prevents restoration of its general shape (fig. 1). The left one is within a conglomerate of bones beneath the sphenethmoid (fig. 2). Its anteriorly expanded proximal part is remarkable. A thin horizontal lamina developed here contrasts with the slender middle part of the bone.

Suprascapula. A fragment of the ossified part of the suprascapula is preserved (see NOBLE 1924, fig. 4B).

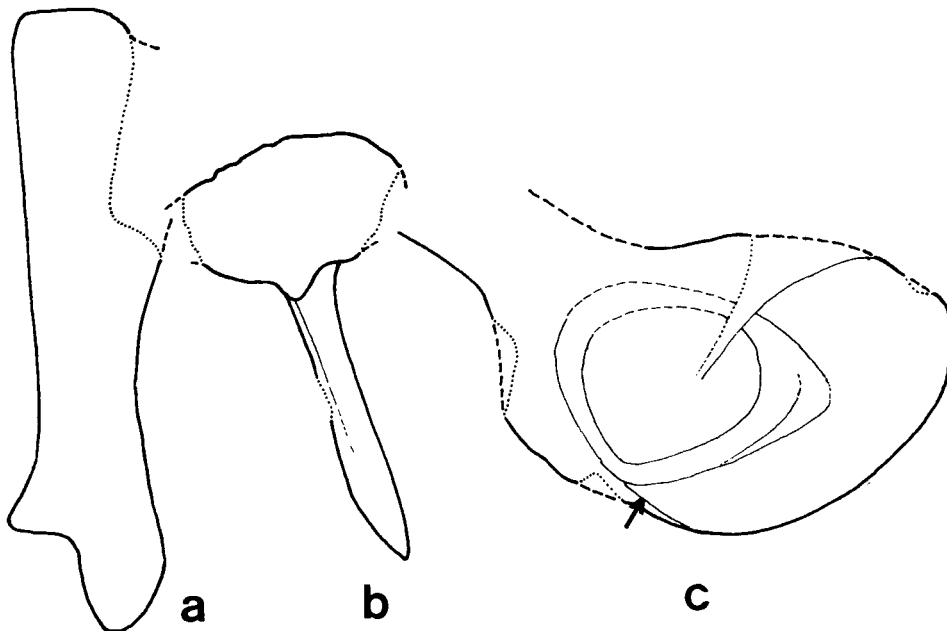


Fig. 4. *Macropelobates osborni*. a - radioulna; b - squamosal; c - posterior part of the pelvis. Dotted line - broken bone surface, dashed line - restoration. Arrow in fig. c indicates peculiar ridge connecting acetabular border with lower margin of the ischium.

Forelimb

Humerus. The left humerus is visible in ventral aspect, the right one is forced into the orbit (fig. 1). Neither fragment provides much diagnostic information.

Radioulna. The left radioulna is present. NOBLE (1924, fig. 3E) apparently figured only its proximal two thirds (cf. fig. 4a), which is why it seemed to him »wider than in *Pelobates* and with a shallower distal articulation« (op. cit.: 6).

The distal section of the forelimbs are not preserved.

Pelvic girdle (fig. 4c; see also NOBLE 1924, fig. 4D; ZWEIFEL 1956, fig. 7C; ESTES 1970, fig. 26D)

Ilium. The anterior ends of both ilii are broken off so that their total length can be only estimated. Dorsally a piece of bone adjacent to the ilio-ischiadical suture is broken off and the suture itself is clearly visible passing the dorsal border of the acetabulum.

Ischium. The acetabular margin is most prominent in its posterior section, and it becomes less prominent anteriorly.

Pubis. As indicated by the presence of bone on the ventral surface of the pelvis in the extent of presumed pubis, this element was ossified (see also NOBLE 1924: 6).

Remarkable on the pelvis is the peculiar crista (indicated by arrow on the fig. 4c) passing from the anteroventral border of the acetabulum onto the ventral margin of the ischium.

Hindlimb

The complete left femur is preserved (the right is only a fragment), as well as the left tibiofibula. Astragalus and calcaneus are in mutual contact (cf. NOBLE 1924: 6) as indicated by ESTES (1970, fig. 28). For the description of the remaining tarsal elements see the latter author. Metatarsals except for their size do not provide much diagnostic information.

PHYLOGENETIC POSITION AND SYSTEMATIC ASSIGNMENT

The survey of diagnostic characters that follows includes those which were used and discussed by earlier authors (references in parentheses), for to give the review of different authors' attitudes. + indicates the same or similar condition as in *Macropelobates*, - the different condition. Further notes are added where necessary.

State of character in <i>Macropelobates</i>	<i>Pelobates</i>	Comparison with <i>Scaphiopus</i>	<i>Megophrys</i>
1. A moderately developed skeletal support of the eminentia olfactoria (= turbinal fold sensu Estes) of the sphenethmoid (ESTES 1970: 325)	+	-	?
2. The surface of the post-nasal wall exposed into the nasal cavity is slanting anteroventrally (ROČEK 1981: 120)	- vertical	?	?
3. The prominentia canalis semicircularis posterioris (= the medial part of the posterior border of the oto-occipital sensu Estes) forms a distinct protuberantia, not a rounded elevation (cf. ESTES 1970: 325)	-	+	-
4. The tip of the prootic part of the prooticooccipital is narrow (ESTES 1970: 325; ROČEK 1981: 122)	+	+	-
5. Skull with roof of dermal encrusting bone (ZWEIFEL 1956: 24)	+	+	-
6. The sculpture of the dorsal surface of dermal bones consists of numerous and regular pits separated by acute ridges (ROČEK 1981: 122)	-	-	-
7. The dorsal surface of the skull is flattened or slightly concave (ESTES 1970: 325; ROČEK 1981: 122)	-	+	+
8. The posterior process on the maxilla poorly developed (cf. ESTES 1970: 325)	-	+	-
9. The processus zygomatico-maxillaris strongly developed (cf. ESTES 1970: 325)	-	+	-

10. Maxilla and squamosal probably in contact (ZWEIFEL 1956: 24)	+	+	—
11. Maxillary teeth guarded mesially by a ridge (NOBLE 1924: 1)	+	+	+
12. Dorsal and posterior margins of the lamella alaris squamosi giving no distinct processes (ROČEK 1981: 123)	—	<i>holbrooki</i> — <i>couchi</i> + <i>hurteri</i> —	quite different
13. The diameter of the lamella alaris squamosi (measured in prolongation of the longitudinal axis of the processus posterolateralis) is contained in the length of the mentioned process almost two times.	—	+	quite different
14. The base of the processus posterolateralis squamosi passes into the base of the ramus paroticus by a mound clearly apparent in posterior view.	—	+	quite different
15. The posterior margin of the facies dorsalis of the frontoparietal is only slightly convex, giving off no distinct outgrowth (ROČEK 1981: 122)	<i>cultripes</i> + <i>syriacus</i> — <i>varaldii</i> — <i>fuscus</i> —	+	quite different
16. The posterior part of the frontoparietal distinctly paired, with a suture in the midline (ROČEK 1981: 122)	—	+	+
17. The proximal section of the praearticular is nearly straight in dorsal view (ROČEK 1981: 123)	—	—	—
18. The columella is present.	—	+	?
19. Centra of the anterior vertebrae flattened.	—	—	—

20. Processus spinosi (= neural processes sensu Noble) of anterior vertebrae long and pointed (NOBLE 1924: 1, 5)	+	+	-
21. The forward inclination of the transverse processes of the posterior praesacral vertebrae (NOBLE 1924: 5; ZWEIFEL 1956: 25; ESTES 1970: 326)	less	different in all 3 more	more
22. The sacral diapophyses are expanded to about the length of four praesacral vertebrae (NOBLE 1924: 5; Estes 1970: 326)	+	-	variable
23. Transverse diameter of sacral wings contained in the longitudinal diameter approximately two times (NOBLE 1924: 5)	more	different in all 3 less	less
24. The urostyle free from the sacral vertebra (NOBLE 1924: 5; ZWEIFEL 1956: 25)	-	-	-
25. The length of urostyle exceeding the length of the sacral diapophyses (NOBLE 1924: 5; ESTES 1970: 326; cf. ZWEIFEL 1956: 12)	-	+	+
26. The urostyle (incl. the length of the sacral vertebra) equals to the total length of 5 (5 and 1/2 according to Zweifel 1956: 25) praesacral vertebrae.	shorter	different in all 3 longer	longer
27. Coracoid with an expanded mesial end (NOBLE 1924: 5)	+	-	+
28. The medial part of the scapula expanded into a thin lamina anteriorly, which contrasts with the slender middle part of the bone.	-	+	+
29. The ischial projection posteriorly (ESTES 1970: 326)	+	+	-

30. Puboischial plate shorter than three praesacral vertebrae (cf. NOBLE 1924: 5)	+	- longer	+
31. Ilium (measured from the dorsal border of the acetabulum to the anterior tip of the bone) longer than the femur (despite some possibility that the anterior tip of the ilium is broken off) (NOBLE 1924: 5; ESTES 1970: 326)	shorter	+	ilium and femur of the same length
32. Pubis ossified (NOBLE 1924: 5)	--	--	--
33. Peculiar crista running from the anteroventral border of the acetabulum onto the ventral margin of ischium.	--	--	--
34. Tibiofibula shorter than the femur (ESTES 1970: 326)	+	+	--
35. Astragalus and calcaneus shorter than radioulna (cf. ESTES 1970: 325)	--	+	--
36. Praetarsal and praeallux separated (ESTES 1970: 325 - 326; cf. NOBLE 1924: 5)	+	<i>holbrooki</i> <i>couchi</i> <i>hammondi</i>	+ -- ?

Two characters given by ESTES (1970: 326), namely uncovered part of the sphenethmoid between the frontoparietal and nasals, and the general shape and lack of thickened and projecting anterior process of the sphenethmoid cannot be considered a reliable diagnostic characters, as the former is obviously dependent on the degree of ontogeny (see BASOĞLU and ZALOĞLU 1964: 236), and as for the latter the comparison is prevented because of anterior part of the sphenethmoid being broken away. But perhaps also the latter character is modified by ontogeny.

Above comparison with *Pelobates* and *Scaphiopus* (*Scaphiopus*) which undoubtedly are morphologically closest to *Macropelobates* reveals that it conforms to *Pelobates* (and differs at the same time from *Scaphiopus*) in following characters: morphology of skeletal support of eminentia olfactoria (1); degree of sacral diapophyses expansion (22); coracoid medial part morphology (27); relative size of the puboischial plate (30); and separated praetarsal and praeallux (however, this character is shared with *S. holbrooki*; see also NOBLE 1924: 5). On the other hand, it conforms

to *Scaphiopus* (and differs at the same time from *Pelobates*) in following characters: prominentia canalis semicircularis posterioris strikingly protruding posteriorly (3); dorsal surface of skull flattened and slightly concave along midline (7); processus zygomaticomaxillaris strongly developed (9); lamella alaris squamosi small in relation to posterolateral process (13); morphology of processus posterolateralis and ramus paroticus bases (14); morphology of posterior margin of facies dorsalis of frontoparietal (only *P. cultripes* shares similar condition) (15); posterior part of frontoparietal paired, with a suture in midline (16); presence of columella (18); urostyle long (25); morphology of scapula - though there is much ontogenetic difference according to ESTES (in litt.) (28); relative length of ilium (31); and relative length of astragalus and calcaneus (35). Only with *S. couchi* it shares the nature of the lamella alaris squamosi dorsal and lateral margins (12). Of the lesser importance in this context are the characters in which *Macropelobates* agrees with both *Pelobates* and *Scaphiopus*: morphology of prooticocooccipital in dorsal aspect (4); sculptured dermal bones (5); maxilla and squamosal probably in contact (10); presence of lamina horizontalis maxillae (11); long and pointed neural processes of anterior vertebrae (20); ischial projection posteriorly (29); and ratio between tibiofibula and femur (34).

Macropelobates displays transitional conditions between *Pelobates* and *Scaphiopus* in following characters: degree of inclination of transverse processes of posterior praesacral vertebrae (21); transverse diameter of sacral diapophyses (23); and length of urostyle in relation to length of vertebrae (26). Finally, *Macropelobates* (if compared with the mentioned genera incl. *Megophrys*) displays unique conditions in the following characters: type of sculpture (6); shape of praearticular (17); flattened centra of anterior vertebrae (19); urostyle free from sacral vertebra (24); ossified pubis (32); and peculiar crista on puboischial plate (33).

This schematical and thus superficial analysis only roughly indicates relations, because it is based only on the morphological similarities. It however reveals that the conditions in *Macropelobates* resemble those in *Pelobates* only in four characters, while there are similarities to *Scaphiopus* in thirteen characters (characters shared with both these genera at the same time are not taken into this account). The morphologically distinct position of *Megophrys* is quite evident. However, for a more profound analysis it is necessary to weigh the importance of characters used. Quite obviously more important are those characters that remain comparatively more stable during evolution (i. e. conservative, archaic or primitive characters) than those which are easily affectable (i. e. derived characters). In frogs apparently the skull structures (esp. the internal ones, e. g. endocranium), the general structure of the pectoral girdle, the composition of carpus and tarsus, and in certain aspects also the vertebral column belong among the former, whereas e. g. the relative size and the proportions of the hind limb belong among the latter, as they are dependent on adaptation to the mode of locomotion appropriate for the prevailing type of environment. Besides, it is necessary to decide if the states of the characters, even

in homologous ones, are the result of parallel or convergent evolution. For this reason it is necessary to know the evolutionary trends in investigated characters.

Taking into consideration what was said above it can be stated that without further knowledge of the functional anatomy and of the structure of the related vertebrates on the apparently lower evolutionary level (in the case of frogs it concerns labyrinthodonts and crossopterygian fishes), it is not possible to ascertain evolutionary trends of characters 1–4, 7, 11, 12, 14, 15, 19–23, 25–31, 33–35. These characters can serve only as diagnostic ones, for the introductory analysis given above. Besides, the extent of sacral diapophyses (22, 23), despite it is most strikingly resembling *Pelobates*, suggests only that the strongly burrowing animal is concerned, perhaps not to such an extent as *Pelobates*. This character, however, does not indicate any phylogenetic relationship.

In contrast to this the presence of sculptured bones (5), if it represents primary state (cf. ESTES 1970: 299), is undoubtedly an archaic feature (ROČEK 1981: 112). However, this character is without any use for determining the relationships neither between *Macropelobates* and *Pelobates*, nor *Macropelobates* and *Scaphiopus*, because all the three genera possess the sculpture. There have been attempts to ascertain evolutionary trends in the type of sculpture (6). According to SHISHKIN (1973: 149–152, fig. 63) the trend leading to the pit-like sculpture (present in *Macropelobates*) is different from that leading to the nipple-like sculpture (present in *Pelobates*). The sculpture in *Scaphiopus* seems to be transitional but closer to *Macropelobates*. However it seems that ascertainment of the trends in this character represents the problem which remains to be studied more in detail. This is indicated by the presence of quite different types of sculpture in *Pelobates* and European forms of *Eopelobates* despite their close relationship.

The morphology of the posterior part of the maxilla (8, 9), contrary to the statement of ESTES (1970: 325), suggests probable absence or at least reduction of the quadratojugal. This is undoubtedly very advanced specialization (ROČEK 1981: 109, 113) which indicates the relationship with *Scaphiopus*. In this respect *Pelobates decheni* from the Oligocene-Miocene boundary of central Europe (BÖHME, ROČEK and ŠPINAR, 1982) is more archaic (= more primitive), as it still retains a large and sculptured quadratojugal. Also the proportions of the squamosal (13) suggest that the tip of the processus posterolateralis reached more ventrally than the level of the crista dentalis maxillae, which is quite in agreement with the conditions in *Scaphiopus*. The problem of the nature of the frontoparietal (16) has been discussed elsewhere (ROČEK 1981: 143–144, 149–150, 151, 153). Briefly summarized, *Scaphiopus* belongs among these frogs whose frontoparietal complex develops embryonically without participation of the median unpaired element adjoining the tectum synoticum, whereas in *Pelobates* and *Eopelobates* (*E. anthracinus*, *E. bayeri*) this element is incorporated into the mentioned complex. Considering the evolutionary trend of this character it appears that frogs possessing these different conditions belong to the independent evolutionary lines. The course of the proximal

section of the praearticular (17) indicates only that *Macropelobates* retained also some archaic character states (see ROČEK 1981: 112, 113). The presence of the columella (18) is a similar situation. It is retained in *Scaphiopus* (though not so large), but only a sign of it appears in *Pelobates* during ontogeny (KOTHE 1910: 59–60; PLASOTA 1974: 119; ROČEK 1981: 44). Undoubtedly archaic, too, is that the urostyle is free from the sacral vertebra (24). This condition is found in earlier ontogenetic stages both in *Pelobates* and *Scaphiopus*. The ossified pubis (32) and separated praetarsal and praehallux (36) also represent archaic character states, but the latter may be the result of convergence and thus may not provide much information on phylogenetic relationships.

From the above discussion on the relations of *Macropelobates* from the point of view of its anatomy it follows that certain archaic characters are retained in which it is unique in comparison with *Pelobates* and *Scaphiopus* but which tell us nothing about the mutual relations among these genera. On the other hand it displays certain characters which represent advanced specializations shared with *Scaphiopus* and not with *Pelobates* and *Eopelobates* (excl. non-European forms described under this generic name); these are manifested in the structure and morphology of the posterolateral region of the skull. The nature of the frontoparietal complex seems to be rather archaic, and the presence of the columella is another archaic character shared with *Scaphiopus*. If we take into account that the conformities with *Scaphiopus* strikingly exceed those with *Pelobates*, it becomes apparent that *Macropelobates* belongs close to the stock of *Scaphiopodidae* (see ROČEK 1981: 151–156).

That *Macropelobates* could not have any close phylogenetic relationship to European pelobatids is clear also when one considers palaeogeographical conditions in the region of contemporary Europe and Asia, which were separated by the Turgai Strait (Ural Sea of some authors), which frogs were not able to cross. This epicontinental strip of sea existed from the Jurassic until the Eocene (and entirely ceased to exist only during the Oligocene). It is supposed now that possibly at southern variable extent of Turgai Strait there were some Eocene exchanges between Europe and Asia, e. g. *Placosaurus* during Middle Eocene (ESTES in litt.). However, in these times pelobatids already existed in Europe (for the survey of records see BÖHME, ROČEK and ŠPINAR, 1982). This situation thus precludes the possibility that *Macropelobates* can be taken for the ancestor of European pelobatids.

Briefly summarized, *Macropelobates* appears to belong to the lineage of *Scaphiopodidae*. Its anatomy and palaeogeographical conditions contradict the view held by some earlier authors that it represents the form ancestral to European Pelobatidae. It rather seems that it is a form that had already attained typical scaphiopodid features.

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MACROPELOBATES OSBORNI NOBLE, 1924 - PŘEHODNOCENÍ FYLOGENETICKÉ POZICE NA PODKLADĚ REVIDOVANÉHO POPISU

ZBYNĚK ROČEK

Detailní anatomický rozbor, který umožnila dodatečná preparace doposud jediného známého exempláře *Macropelobates osborni* naznačuje, že se jedná o formu s bližšími vztahy k rodu *Scaphiopus* než k rodu *Pelobates* a evropským zástupcům rodu *Eopelobates*. Avšak nejen z anatomických, ale i z paleogeografických příčin nutno odmítnout názor starších autorů, že *Macropelobates* je předkem evropských pelobatidů, neboť mezi Asií a Evropou existovala až do oligocénu výrazná zoogeografická bariéra ve formě Turgajské úžiny. Zdá se tedy, že *Macropelobates* je spíše formou patřící do okruhu vývojové linie Scaphiropodidae.

MACROPELOBATES OSBORNI NOBLE, 1924 —
ПРЕОЦЕНКА ФИЛЕТИЧЕСКОЙ ПОЗИЦИИ

ЗБЫНЕК РОЧЕК

Детальный анатомический анализ, который стал возможным после дополнительной препарации до сих пор единственного экземпляра *Macropelobates osborni* указывает, что эта форма имеет более близкие отношения к роду *Scaphiopus* чем к роду *Pelobates* и европейским представителям рода *Eopelobates*. Однако, не только на основе анатомического анализа, но тоже из палеогеографических соображений необходимо отказаться от мнения старших авторов, что *Macropelobates* предок европейских чесночниц, потому что между Азией и Европой существовал до олигоцена выразительный зоогеографический барьер — Тургайский пролив. И так кажется что *Macropelobates* — форма принадлежащая к филогенетической линии Scaphiropodidae.

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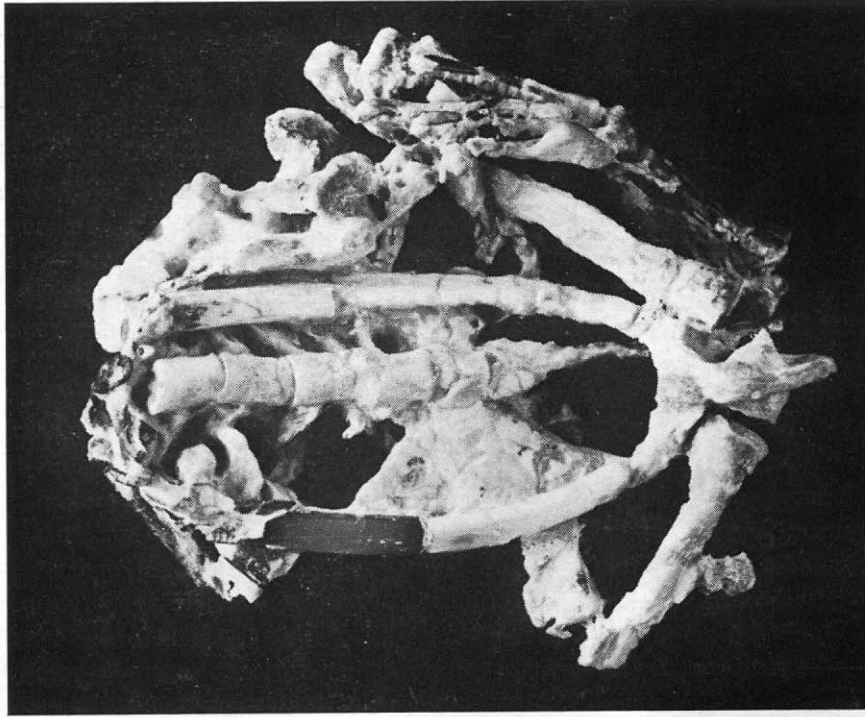


Fig. 2. *Macropelobates osborni* NOBLE, 1924, holotype (AMNH 6252).
Photo by V. Šilhan.

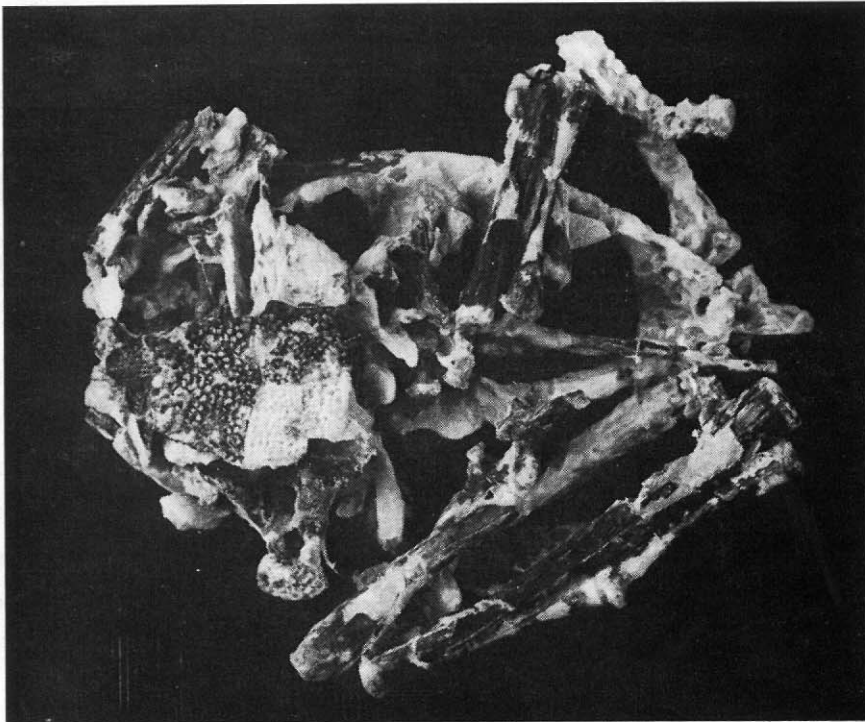


Fig. 1. *Macropelobates osborni* NOBLE, 1924, holotype (AMNH 6252).
Photo by V. Šilhan.