

REASSESSMENT OF THE NORTH AMERICAN PELOBATID ANURAN
EOPELOBATES GUTHRIEI

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ABSTRACT

Eopelobates guthriei Estes, 1970, is based on a partial skull and associated right scapula from the Early Eocene Wind River Formation (Lysitean), Fremont County, Wyoming. Reexamination of the holotype and only known specimen reveals that it should no longer be regarded as *Eopelobates* because it lacks characters considered to be diagnostic of that genus. Comparison to other pelobatids indicates it is most similar to *Scaphiopus* and *Spea* in possession of an elongate postchoanal ramus of the vomer. It compares more closely with *Scaphiopus* in its lack of hypossification of cranial bones and possession of a long, low, arcuate ventral flange of the pterygoid. There is no evidence to suggest that it represents a new genus, but because it is not known if the postcranial skeleton was specialized for burrowing, as in *Scaphiopus* and some other pelobatids, it is only tentatively referred to *Scaphiopus* as cf. *S. guthriei* (Estes, 1970). Two derived characters distinguish cf. *Scaphiopus guthriei* from other *Scaphiopus*: 1) frontoparietal narrowest just posterior of the supraorbital flange and 2) otic ramus of squamosal long and thin. Assuming assignment to *Scaphiopus* is correct, then the temporal range for *Scaphiopus* can be extended back from the Middle Oligocene to the Lower Eocene.

KEY WORDS: Anura, Pelobatidae, *Eopelobates*, *Scaphiopus*, Lower Eocene

INTRODUCTION

In 1929 Parker named and described *Eopelobates anthracinus* as the generic holotype for *Eopelobates* on the basis of a single specimen that was collected from strata now considered to be uppermost Oligocene in age (von Koenigswald et al., 1992) from Rott, near Bonn, Germany. Since Parker's (1929) description of *E. anthracinus*, seven other species from North America, Europe, and Asia have been included in this genus. However, the generic assignment of most of these taxa has been either changed or questioned. *Eopelobates bayeri*, from the Oligo-Miocene of the Czech Republic, is regarded as either very closely related to *E. anthracinus*, differing only in its larger size (Špinar and Roček, 1984; Roček, 1995), or synonymous with *E. anthracinus* (Sanchíz, 1998). *Eopelobates leptocolaptus* and *E. sosedkoi* from the Upper Cretaceous of Mongolia and Uzbekistan, respectively, have been reassigned to the gobiid *Gobiatos* (Špinar and Tatarinov, 1986; Roček and Nesson, 1993). Roček (1981), in a monographic study of *Pelobates fuscus*, observed that both *Pelobates* and *Eopelobates* have a frontoparietal derived from three ossifications, the typical paired elements with the addition of a median element situated posterior to them. The three ossifications are easily identified in tadpoles, but in adults the only indication of the presence of the posteromedial element is that it prevents the median suture from reaching the posterior end of the frontoparietal complex. On the basis of this character, Roček (1981) suggested that only two species, *E. anthracinus* and *E. bayeri*, should be retained in the genus *Eopelobates*. Published information about the frontoparietal of *E. hinschei* from the Middle Eocene of Geiseltal, Germany (Kuhn, 1941; Estes,

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1970), led Roček (1981) to suspect that the posteromedial element is absent in this taxon, and thus it should not be regarded as *Eopelobates*. In addition, Sanchíz (1998) maintained that although the species is valid, it lacks a diagnosis and is in need of restudy. More recently, Wuttke (1988) has reidentified *Propelodytes wagneri*, from the Middle Eocene of Messel, Germany, as *Eopelobates wagneri*.

Two species of *Eopelobates* have been described from North America: *E. guthriei* from the Lower Eocene Wind River Formation of Wyoming (Estes, 1970) and *E. grandis* from the Lower Oligocene Chadron Formation of North Dakota (Zweifel, 1956). Roček (1981) concluded that both species are not *Eopelobates* but rather may be more closely related to the North American spadefoots *Scaphiopus* and *Spea*. This conclusion was based on his determination from published descriptions and illustrations that the frontoparietals of *E. guthriei* and *E. grandis* also lack the posteromedial element, the quadratojugal is absent in *E. guthriei* and possibly misidentified in *E. grandis*, and the columella is present in *E. guthriei*. These are characters which all occur in *Scaphiopus* and *Spea* but not *Eopelobates* (Roček, 1981).

The purpose of this study is to provide a revision of *E. guthriei* that considers the more recent published information about this genus and pelobatids in general. Minor preparation of the holotype and only known specimen has also revealed a feature important to its taxonomic assignment. A redescription and reassessment of *E. grandis* is being prepared separately.

The correct identification of North American *Eopelobates* is important for understanding pelobatid evolutionary history and paleobiogeography. *Eopelobates* has been thought to be a primitive pelobatid that is ancestral to the spadefoots (Parker, 1929; Estes, 1970; Špinar, 1972; Savage, 1973), and Estes (1970) speculated that *E. guthriei* was close to the origin of spadefoots. The timing and place of divergence of spadefoots has changed in accordance with new additions to the fossil record, but, in general, the Eocene-earliest Oligocene was considered to be an important time for spadefoot evolution and dispersal (Savage, 1973; Estes, in Sage et al., 1982). More recently, Sage et al. (1982) have suggested that the modern spadefoots (*Pelobates*, *Scaphiopus*, and *Spea*) diverged during the Cretaceous, and the spadefoot morphotype then subsequently underwent little change. Their divergence time was based on immunological evidence.

ABBREVIATIONS

Anatomical.—a, angular; c, choana; co, columella; cp, crista parotica; fo, fenestra ovalis; fp, frontoparietal; ipfm, impression of pars facialis of maxilla; jf, jugular foramen; m, maxilla; md, mandible; n, nasal; op, otic plate of squamosal; pa, parasphenoid; pcv, postchoanal ramus of vomer; pf, prootic foramen; pfm, pars facialis of maxilla; pm, premaxilla; ppm, palatine process of maxilla; pt, pterygoid; q, quadrate; s, sphenethmoid; sc, scapula; sq, squamosal; v, vomer; vf, ventral flange of pterygoid.

Institutional.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DESCRIPTION AND COMPARISON OF “*EPELOBATES*” *GUTHRIEI*

The holotype and only known specimen of “*Eopelobates*” *guthriei* (MCZ 3493) consists of a moderate-sized, incomplete skull and associated incomplete

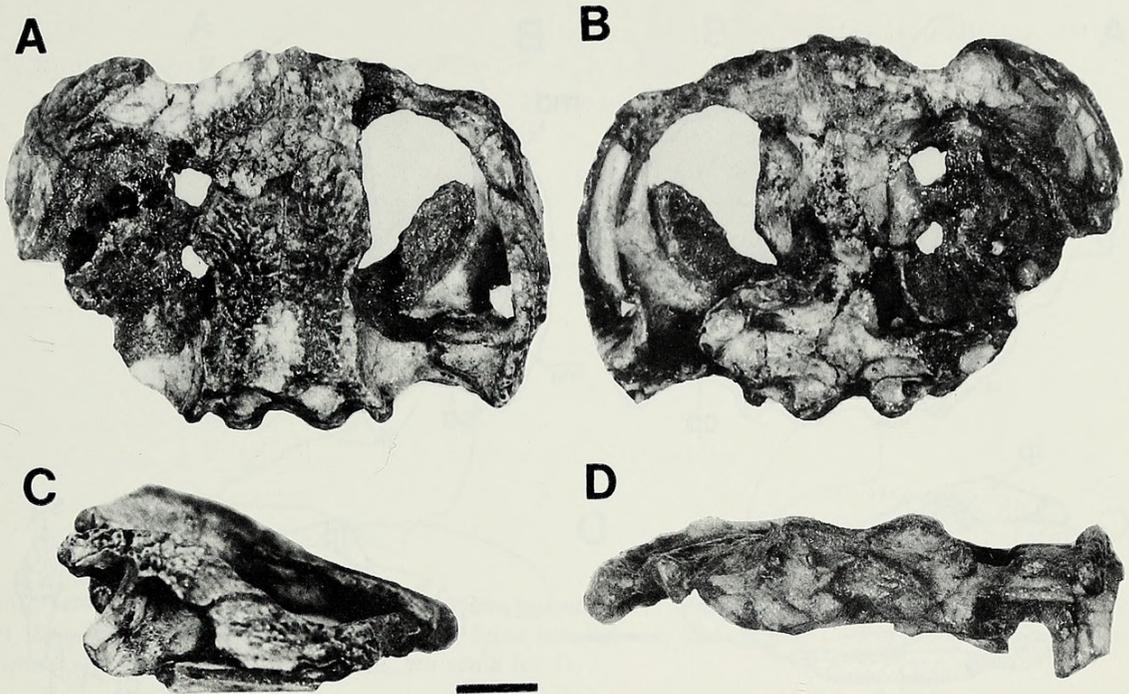


Fig. 1.—Photographs of holotype of cf. *Scaphiopus guthriei*, MCZ 3493. A, dorsal view; B, ventral view; C, right lateral view; and D, occipital view. Scale bar = 5 mm.

right scapula (Fig. 1, 2) collected from the Lower Eocene Lysite Member of the Wind River Formation in the Wind River Basin, Fremont County, Wyoming. The skull is missing bones of the snout, left temporal region, and most of the lower jaws; the preserved bones are in articulation or are very closely associated. Distortion of the right temporal region has resulted in anterior rotation of the otic plate of the squamosal away from the dorsal surface of the right exoccipital-prootic complex. The ventral ramus of the squamosal is missing its base and is pushed inward. Also, the medial ramus of the right pterygoid is not preserved in articulation with the exoccipital-prootic complex.

Estes (1970) argued that the flattened, medially concave dorsal skull roof was not an artifact of preservation but was natural and similar to the skull of other *Eopelobates*. Evidence that the skull was dorsoventrally compressed does exist, however. The left maxilla is not preserved in near vertical orientation but, rather, slopes outward. In conjunction with this, the lateral process of the nasal, which bears evidence of crushing by the numerous cracks running through it, is flattened and oriented horizontally instead of a more vertical orientation. The anterior portion of the left frontoparietal is more depressed than the right, and the dorsal edge of the right squamosal is preserved at the same level as the right frontoparietal rather than at a more ventral level. Additionally, the long axis of the occipital condyles is oriented horizontally instead of having the typical, for pelobatids, transverse orientation.

The undistorted skull roof of MCZ 3493 probably resembled that of *Scaphiopus skinneri* from the Middle Oligocene of North Dakota (Estes, 1970) in being flat and sloping slightly downward anteriorly. It should be noted that currently known specimens of *Eopelobates* are all preserved as flattened skeletons, so the outline of their dorsal skull roof cannot be accurately determined.

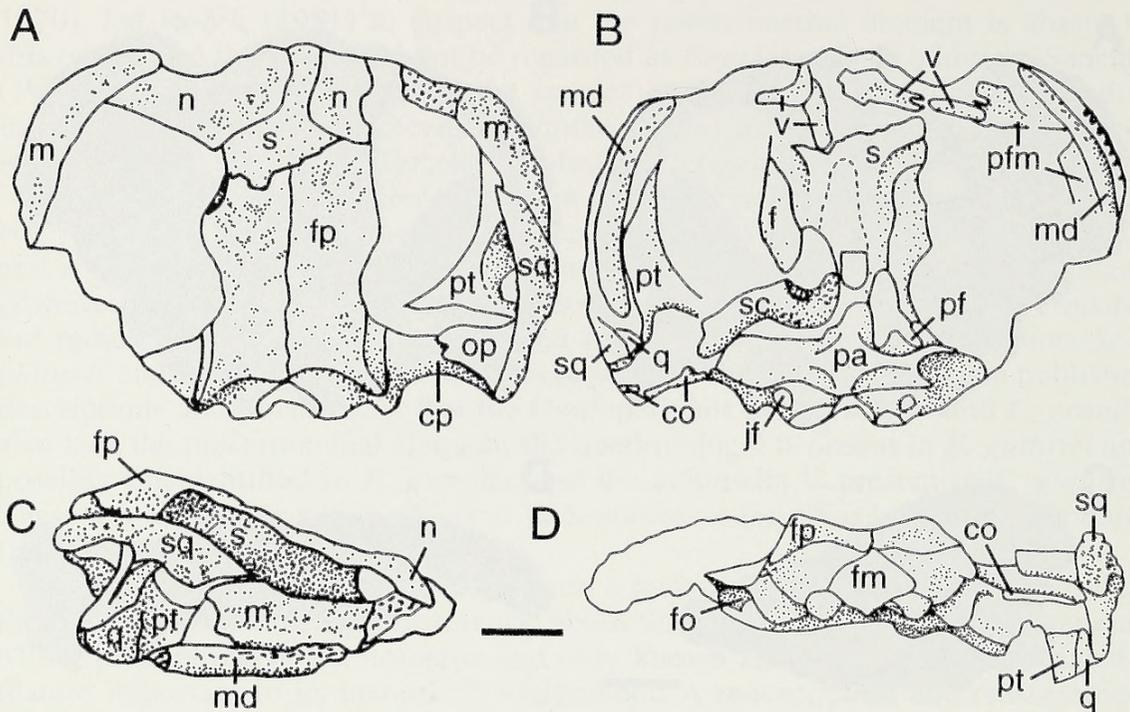


Fig. 2.—Diagrammatic drawings of holotype of cf. *Scaphiopus guthriei*, MCZ 3493. A, dorsal view; B, ventral view; C, right lateral view; and D, occipital view. Scale bar = 5 mm.

Dermal ornamentation occurs on the frontoparietals, nasals, maxillae, and squamosal. Although the dermal ornamentation is somewhat eroded and covered by matrix in places, it can be discerned that it consists of a system of grooves and ridges bearing tubercles, as well as being slightly reticulated in places. This ornamentation pattern most closely resembles that occurring in *Scaphiopus holbrooki*. Špinar and Roček (1984) used as a diagnostic character of *Eopelobates* the presence of a posteromedial element in the frontoparietal, resulting in a frontoparietal complex that is derived from the fusion of three ossifications. A frontoparietal complex derived from three ossifications also occurs in *Pelobates* (Roček, 1981). In contrast, the frontoparietals of MCZ 3493 are paired (Estes, 1970); the median suture clearly extends the entire length between the two halves, indicating that a posteromedial element is absent. The subrectangular frontoparietals bear supraorbital flanges (otic processes in Estes, 1970) that reach their greatest width at approximately one-third their length from the anterior end. The frontoparietal is waisted and narrowest just posterior to the supraorbital flange. At the posterolateral corner of each frontoparietal the posterolaterally oriented posterior tip caps a small boss on the dorsal surface of the exoccipital-prootic complex. This boss was referred to as the paroccipital process by Estes (1970), which is misleading because the paroccipital process is part of the opisthotic, a bone that is absent in anurans. Anteriorly, the right frontoparietal seems to be complete, but the left is not. The posterior edges of the nasals are irregular, which suggests that some bone is missing, although Estes (1970:fig. 13B) illustrates them as being complete. The exposed dorsal surface of the sphenethmoid bears faint impressions of what probably were the posterior and medial edges of the nasals. These impressions suggest that the complete nasals allowed considerably less dorsal exposure of the sphenethmoid than that illustrated by Estes (1970:fig. 13B).

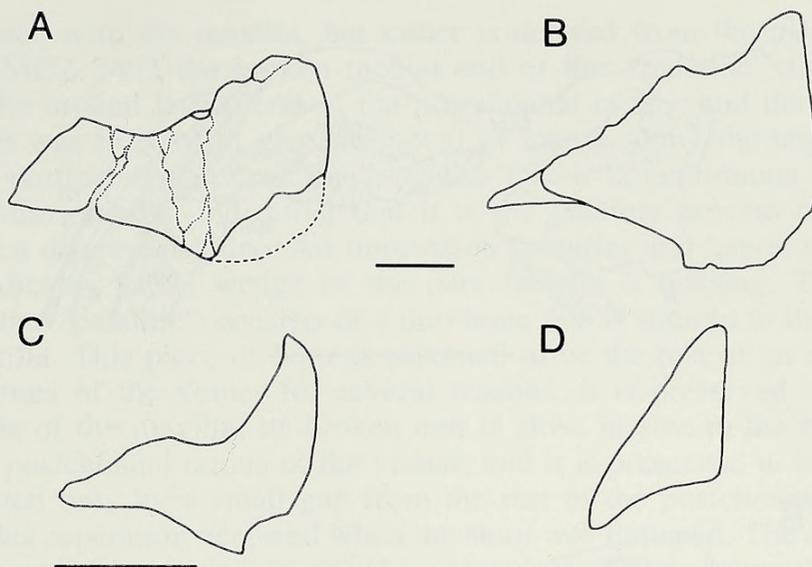


Fig. 3.—Comparison of some pelobatid nasal bones. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 32300; C, *Spea bombifrons*, CM 48932; D, *Eopelobates bayeri* (from Špinar, 1972). Scale bars = 2 mm. No scale for D.

Flattening of the left nasal has distorted its shape somewhat. Its short lateral process is preserved in articulation with the maxilla. Bone making up the somewhat concave anterolateral edge of the nasal is rounded, indicating that the shape of this edge is not the result of breakage. It is apparent that the anterolateral margin of the nasal was not straight but was probably concave as in *Scaphiopus*, *Spea*, and *Pelobates* (Fig. 3). A straight anterolateral margin coupled with a long and slender lateral process is considered a diagnostic character for *Eopelobates* (Špinar and Roček, 1984). All that remains of the right nasal is its posteromedial corner.

Only the posterior end of the right maxilla is preserved, and its posterior process is broken off. The left maxilla is missing its anterior and posterior ends. Small, bicuspid, pedicellate teeth are preserved along the pars dentalis of the left maxilla, and a few tooth bases are preserved on the right. Bicuspid, pedicellate teeth occur in *Eopelobates* (Wuttke, 1988), as well as in other pelobatids.

The right squamosal is nearly complete, missing only the base of its ventral ramus, and the left squamosal is absent. The zygomatic ramus is deep proximally, bearing a concavity along its ventral margin, and tapers distally where it articulates with the zygomatic process of the maxilla. The otic ramus becomes deeper distally, although it is not as deep as and is only slightly shorter than the zygomatic ramus. It bears a longer and deeper concavity on the ventral margin than that occurring on the zygomatic ramus. The otic plate, which has rotated anteriorly from its articulation with the crista parotica, extends slightly beyond the midpoint between the frontoparietal and lateral edge of the skull and does not contact the frontoparietal, as occurs in most megophryines. A dorsal process, which in all *Pelobates* species except *P. fuscus* articulates with the superior lateral process of the frontoparietal (Roček, 1981), is absent. In *P. fuscus* a ligament bridges the squamosal and frontoparietal (Roček, 1981). The quadrate forms a wedge between the pterygoid and ventral ramus of the squamosal. A quadratojugal is not preserved. As noted by Estes (1970), it was either absent or was lost during dis-

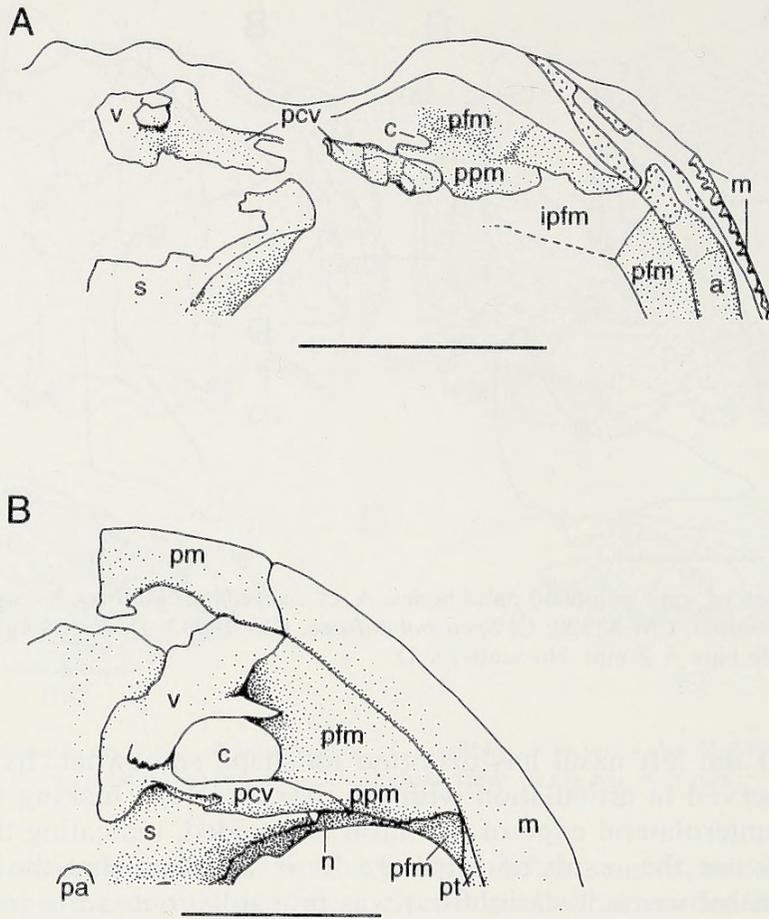


Fig. 4.—Comparison of vomer region of palate. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 18719. Note that dorsoventral compression of skull figured in A has caused lateral displacement of part of the postchoanal ramus of the vomer and jaw elements. Scale bars = 5 mm.

placement of the posteroventral corner of the maxilla and ventral ends of the squamosal and quadrate. Among pelobatids only *Scaphiopus* and *Spea* lack a quadratojugal.

The sphenethmoid (ethmoid in Estes, 1970) is incompletely preserved, lacking the right lateral process, most of the anterior process, and portions of the ventral and anterior surfaces of the left lateral process. All that remains of the right vomer is the proximal portion of the postchoanal ramus and bone forming the postero-medial border of the internal nares. The somewhat more complete left vomer (Fig. 4A) has a raised area medial to the postchoanal ramus that Estes (1970) suggested was the vomerine tooth plate. The lateral end of the postchoanal ramus ends in a break, and lateral to this is a thin, fragmented rod of bone identified as a probable palatine by Estes (1970). It should be noted that discrete palatines (neopalatine of Trueb, 1993) do not occur in any known pelobatid (Cannatella, 1985). Various authors have argued that in pelobatids each palatine fuses with either the postchoanal ramus of the vomer (Roček, 1981) or the maxilla (Kluge, 1966; Zweifel, 1956). A study on the development of *Spea bombifrons* by Wiens (1989) revealed that the elongate postchoanal ramus of the vomer arises from either the vomer ossification or an independent ossification. Wiens (1989) also observed that the palatine process of the pars facialis of the maxilla does not represent a

palatine fused with the maxilla, but rather is derived from the maxillary ossification. In MCZ 3493 the broken medial end of the “palatine” is preserved in line with the broken lateral end of the postchoanal ramus, and the gap that separates them was filled with glue. Removal of matrix along the anterior edge of the lateral portion of the “palatine” reveals that it is continuous with the pars facialis of the maxilla, indicating that it is the palatine process of the maxilla rather than a discrete palatine. An impression posterior and lateral to the palatine process indicates that a wedge of the pars facialis is missing. The remaining portion of the “palatine” consists of a thin bone that is sutured to the pars facialis of the maxilla. This piece of bone is assumed to be the rest of an elongate postchoanal ramus of the vomer for several reasons: it is preserved sutured to the pars facialis of the maxilla; its broken end is close in size to the broken, lateral end of the postchoanal ramus of the vomer; and it is preserved in alignment with and separated only by a small gap from the rest of the postchoanal ramus. Presumably, this separation occurred when the skull was flattened. The only pelobatid genera possessing an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla are *Scaphiopus* (Fig. 4B) and *Spea* (Cannatella, 1985). The anterior portion of both vomers is missing.

The three rami of the pterygoid are broad proximally and taper distally. As in *Scaphiopus*, a long, low, arcuate ventral flange runs along the lateral edge of the pterygoid, extending from the base of the anterior ramus to near the tip of the posterior ramus (Fig. 5). The anterior ramus of the pterygoid articulates with the medial edges of the zygomatic ramus of the squamosal and maxilla. The dorsal margin of the distal end of the medial ramus is broken off. Matrix and the overlying right lateral ala of the parasphenoid obscure the ventral portion of the distal end of the medial ramus.

The prootic foramen is widely emarginate as in other pelobatids, except *Spea*, where it is completely surrounded by bone. The occipital condyles appear to be widely separated, but this is probably the result of dorsoventral compression and bone loss. The right occipital condyle is kidney shaped, whereas the left has a more circular outline due to bone loss along the medial margin of the condyle. The shape and position of the right occipital condyle indicates that the condyles were probably narrowly separated, which is typical for pelobatids (Lynch, 1971). A columella is present, as noted by Estes (1970).

A crushed, incomplete right scapula, mistakenly identified as a left by Estes (1970), is exposed in medial aspect and rests against the anterior edge of the right lateral ala of the parasphenoid. Most of the anterior half of the scapula is preserved, but missing are all of the pars glenoidalis except for its base, the distal-most edge of the scapular blade, and the posterodistal corner of the scapula. Enough of the scapula is preserved to determine that it is long. As in other pelobatids, the scapula bears a large and bulbous pars acromialis, which indicates that the clavicle articulated with its ventral edge rather than its anterior edge. When the clavicle articulates with the anterior edge of the scapula, the pars acromialis narrows considerably distally. Although only the base of the pars glenoidalis is preserved, it was obviously a distinct process that was separated from the pars acromialis by a cleft. The anterior edge of the scapula is strongly concave and lacks an anterior lamina (Estes, 1970), as in *Scaphiopus* and *Spea*. Presence of an anterior lamina was demonstrated by Henrici (1994) to be a synapomorphy of *Eopelobates*, *Macropelobates*, and *Pelobates*.

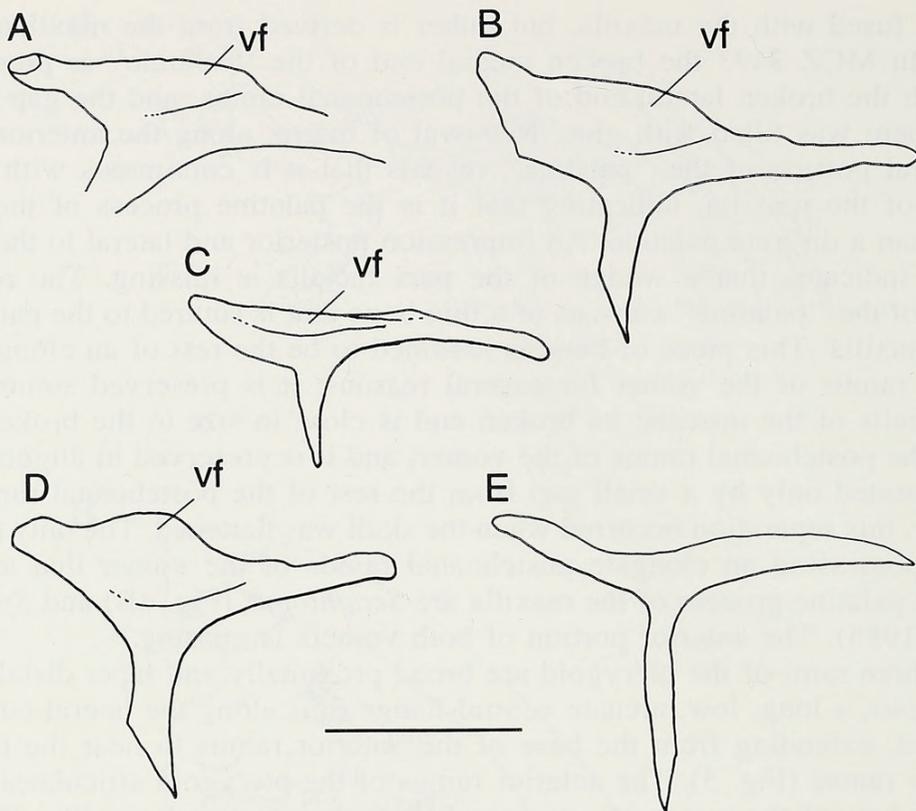


Fig. 5.—Comparison of some pelobatid pterygoid bones. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 18719; C, *Spea bombifrons*, CM 48932; D, *Pelobates cultripes*, CM 55769; E, *Leptobrachium hasselti*, FMNH 131998. Anterior is to the right and medial to the bottom of the page. Scale bar = 5 mm.

DISCUSSION

Estes (1970:313) assigned MCZ 3493 to *Eopelobates* based on its possession of “. . . a concave skull roof, approximately subequal orbital and temporal openings, as well as the distinctive shape of the squamosal and ethmoid.” As noted in the description, dorsoventral compression of the skull of MCZ 3493 most likely caused the skull roof to appear concave. Also, as previously mentioned, all known specimens of *Eopelobates* are preserved as flattened skeletons, and the configuration of their dorsal skull roof cannot be accurately determined. The other characters used by Estes (1970) are either not preserved or are not diagnostic at the generic level. The sphenethmoid of MCZ 3493 is incomplete anteriorly, making comparison to other pelobatid sphenethmoids impossible. Estes (1970) observed that the orbital and temporal openings are of subequal size in *Megophrys* and *Eopelobates*, whereas in pelobatines the orbit is enlarged and the temporal area reduced. However, this character is difficult to interpret and varies intergenerically. The shape of the squamosal is diagnostic at the species level for at least *Pelobates* and *Scaphiopus* and thus is not a useful character for differentiating pelobatid genera.

Four of the characters currently considered as diagnostic for *Eopelobates* (Špi- nar and Roček, 1984; Sanchíz, 1998) can be analyzed in MCZ 3493. Polarity of these characters is based on the phylogenetic analysis of pelobatoids in Henrici (1994) or outgroup comparison (using methodology of Wiley et al., 1991) in

which pelodytid and pipoid anurans comprise the outgroup. The characters are as follows: 1) frontoparietal is derived from three ossifications (derived state); 2) frontoparietal does not contact squamosal (primitive state); 3) nasal has a straight anterolateral margin and a long, slender lateral process (derived state); and 4) dermal sculpturing is pitted and lacks tubercles (state indeterminate). The first character also occurs in *Pelobates*, the second occurs in *Macropelobates*, *Scaphiopus*, and *Spea*, and the latter two characters appear to be unique. The first of these characters, incorporation of a posteromedial element into the frontoparietal complex, warrants further discussion, because it has had some bearing on theories of anuran phylogeny. Roček (1981) homologized the posteromedial element with the median extrascapular of *Eusthenopteron*, considered it to be a primitive character, and used it to form the basis of a phylogeny that placed *Eopelobates* and *Pelobates* outside of Salientia (sensu Sanchíz, 1998). Milner (1988) pointed out that the occurrence of an extra ossification wedged between the parietals and postparietals, which he identified as the interparietal, is not unprecedented and observed its occurrence in several temnospondyls. He (Milner, 1988:63) suggested that the interparietal “. . . is a recurrently occurring derived condition” and further stated that the posteromedial element in *Eopelobates* and *Pelobates* is either a neomorph or a character reversal and, thus, is derived and most likely defines a subclade within Pelobatidae. The phylogeny of Pelobatoidea proposed by Henrici (1994) supports Milner's theory that the occurrence of the posteromedial element in the frontoparietal complex of *Eopelobates* and *Pelobates* is derived and represents a synapomorphy of a subclade within Pelobatidae.

Of the four diagnostic characters, MCZ 3493 is similar to *Eopelobates* and other pelobatines except *Pelobates* only in the primitive character of lack of contact between frontoparietal and squamosal. It differs from *Eopelobates* in three of these characters: 1) frontoparietal is paired (primitive state); 2) anterolateral margin of nasal is not straight but probably was concave, and the lateral process is short (Fig. 3; primitive state); and 3) dermal sculpturing consists of ridges and grooves, which are arranged in a slightly reticulated pattern in places, and tubercles (state indeterminate). Another distinction from *Eopelobates*, as well as *Macropelobates* and *Pelobates*, is the absence of an anterior lamina of the scapula. Presence of an anterior lamina was determined by Henrici (1994) to be a synapomorphy of *Eopelobates*, *Macropelobates*, and *Pelobates*. Based on these differences, it is apparent MCZ 3493 should not be regarded as *Eopelobates*.

Comparison of MCZ 3493 to other pelobatids reveals that it most closely resembles *Scaphiopus* and *Spea* in possession of an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla (Fig. 4). Among pelobatids this character is unique for *Scaphiopus* and *Spea* and has been regarded as one of several synapomorphies uniting them (Cannatella, 1985; Henrici, 1994; Maglia, 1998). It should be mentioned that besides pelobatids, the postchoanal ramus of the vomer is known to articulate with the palatine process of the maxilla in at least some species of *Discoglossus*: *D. sardus* (Púgener and Maglia, 1997) and *D. pictus* (pers. obs.). However, in these species of *Discoglossus* the postchoanal ramus is not elongate, in contrast to that of *Scaphiopus*, *Spea*, and MCZ 3493.

The skull of MCZ 3493 compares more closely with *Scaphiopus* than with *Spea*. *Spea* exhibits cranial hyposossification that is evidenced by the loss of dermal ornamentation, reduced ossification of the frontoparietals and nasals which allows dorsal exposure of the frontoparietal fontanelle and sphenethmoid, and reduction

of the otic plate and the zygomatic and otic rami of the squamosal with consequent loss of contact between the squamosal and maxilla (Kluge, 1966; Wiens, 1989; Maglia, 1998). This hyossification of the skull does not occur in MCZ 3493 or other pelobatids and is thought to be pedomorphic in *Spea* (Wiens, 1989). *Scaphiopus* and MCZ 3493 possess a similarly shaped ventral flange of the pterygoid that is long, low, and arcuate, and differs from the low, straight ventral flange in *Spea*, and the prominent, short ventral flange in *Pelobates* and *Eopelobates* (Fig. 5). *Leptobrachium* and presumably other megophryines lack a ventral flange. Maglia (1998), in a cladistic analysis of extant pelobatoids, considered the presence of a ventral flange to be derived and its absence to be primitive. It stands to reason, then, that the different shapes of the ventral flange in pelobatids represent independently derived states.

Because there is no evidence suggesting that MCZ 3493 represents a new genus, it is tentatively referred to *Scaphiopus* on the basis of the following characters: 1) presence of an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla, 2) lack of hyossification of cranial bones, and 3) presence of a long, low, arcuate ventral flange of the pterygoid. It is acknowledged, however, that the first character is based on somewhat fragmentary evidence. This, together with the lack of a postcranial skeleton for MCZ 3493, which in *Scaphiopus* and some other pelobatids is specialized for burrowing, is the reason for only tentatively referring MCZ 3493 to *Scaphiopus*. Confident generic assignment of MCZ 3493 must await discovery of more complete specimens to determine if it has a postcranial skeleton similar to *Scaphiopus*. Assuming assignment to *Scaphiopus* is correct, then two unique characters distinguish it from other species of this genus. These represent two of the three characters used by Estes (1970) in his diagnosis of MCZ 3493 as a new species of *Eopelobates*, but are described here using different terminology: 1) frontoparietal is waisted and narrowest just posterior of the supraorbital flanges and 2) otic ramus of squamosal is relatively thin and almost as long as the zygomatic ramus. These characters are unique among pelobatids and, based on comparison to pelodytids and pipoids, are judged to represent the derived state in cf. *S. guthriei*.

Several assumptions can be made about pelobatid evolution and paleobiogeography if assignment of MCZ 3493 to *Scaphiopus* is correct. The temporal range of *Scaphiopus* can now be extended back from the Middle Oligocene to the Early Eocene. The currently known first occurrences of extant and extinct spadefoots indicates that their dispersal across Laurasia must have occurred very early in the Paleogene, if not earlier. In addition to the Early Eocene record of *Scaphiopus*, the oldest-known record of *Pelobates* is *P. decheni* from the Late Eocene of Belgium (Böhme et al., 1982). Additionally, the oldest known record for the extinct spadefoot, *Macropelobates*, is *M. osborni* from the Early Oligocene of Mongolia (Noble, 1924). Unfortunately, the fossil record of spadefoots is too sparse to allow speculation on their center of origin or dispersal routes. Finally, the presence of extant spadefoots in both North America and Europe by the Late Eocene adds support to the theory of Sage et al. (1982) that they are an ancient and morphologically stable group that most likely diverged during the Cretaceous.

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Figure 1. A. R. Milner and Z. Roček provided helpful discussion about pelobatids. The following institutions loaned specimens used in this study: Field Museum of Natural History, Harvard Museum of Comparative Zoology, and the United States National Museum, Washington D. C. This project was supported in part by funds from the M. Graham Netting Research Fund.

LITERATURE CITED

- BÖHME, W., Z. ROČEK, AND Z. ŠPINAR. 1982. On *Pelobates decheni*, 1861, and *Zaphrissa eurypelis* Cope, 1866 (Amphibia: Salientia: Pelobatidae) from the Early Miocene of Rott near Bonn, West Germany. *Journal of Vertebrate Paleontology*, 2:1-7.
- CANNATELLA, D. C. 1985. A phylogeny of primitive anurans (archaeobatrachians). Unpublished Ph.D. Dissert., University of Kansas, Lawrence, Kansas.
- ESTES, R. 1970. New fossil pelobatid frogs and a review of the genus *Eopelobates*. *Bulletin Museum Comparative Zoology*, 139:293-339.
- HENRICI, A. C. 1994. *Tephrodytes brassicarvalis*, a new genus and species (Anura: Pelobatidae), from the Arikareean Cabbage Patch Beds of Montana, USA, and pelodytid-pelobatid relationships. *Annals of Carnegie Museum*, 63:155-183.
- KLUGE, A. J. 1966. A new pelobatine frog from the Lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. *Contributions in Science*, Los Angeles County Museum, 113:1-26.
- KOENIGSWALD, W. VON, T. MARTIN, T. MÖRS, AND H. U. PFRETZSCHNER. 1992. Die oberoligozäne Wirbeltierfauna von Rott bei Hennef am Siebengebirge. *Synonymien und Literatur 1828-1991. Decheniana*, 145:312-340.
- KUHN, O. 1941. Die Eozanen Anura aus dem Geiseltale nebst einer übersicht über die fossilen Gattungen. *Nova Acta Leopoldina*, 10:345-376.
- LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Miscellaneous Publications*, University of Kansas Museum of Natural History, 53:1-238.
- MAGLIA, A. M. 1998. Phylogenetic relationships of extant pelobatoid frogs (Anura: Pelobatoidea): evidence from adult morphology. *Scientific Papers*, University of Kansas Museum of Natural History, 10:1-19.
- MILNER, A. R. 1988. The relationships and origins of living amphibians. Pp. 132-182, in *Evolutionary Biology and Classification of the Tetrapods*, Volume 1, (M. J. Benton ed.). *Systematics Association Special Volume 35A*, Clarendon Press, Oxford, United Kingdom.
- NOBLE, G. K. 1924. A new spadefoot toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidae. *American Museum Novitates*, 132:1-23.
- PARKER, H. W. 1929. Two fossil frogs from the Lower Miocene of Europe. *Annals and Magazine of Natural History*, 4:270-281.
- PÚGENER, L., AND MAGLIA, A. M. 1997. Osteology and skeletal development of *Discoglossus sardus* (Anura: Discoglossidae). *Journal of Morphology*, 233:267-286.
- ROČEK, Z. 1981. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Universitatis Carolinae-Biologica*, 1980(1-2):1-164.
- . 1995. A new specimen of *Eopelobates* (Anura: Pelobatidae) from the Tertiary near Bonn (Germany) and the problem of *E. anthracinus*–*E. bayeri* relations. *Paläontologische Zeitschrift*, 69:283-287.
- ROČEK, Z., AND L. A. NESSOV. 1993. Cretaceous anurans from central Asia. *Paleontographica Abteilung A*, 226:1-54.
- SAGE, R. D., E. M. PRAGER, AND D. B. WAKE. 1982. A Cretaceous divergence time between pelobatid frogs (*Pelobates* and *Scaphiopus*): Immunological studies of serum albumin. *Journal of Zoology*, London, 198:481-494.
- SANCHÍZ, B. 1998. *Encyclopedia of Paleoherpétology*, Part 4, Salientia, Verlag Dr. Friedrich Pfeil, München, Germany.
- SAVAGE, J. M. 1973. The geographic distribution of frogs: patterns and predictions. Pp. 351-445, in *Evolutionary Biology of the Anurans* (J. L. Vial ed.). University of Missouri Press, Missouri.
- ŠPINAR, Z. V. 1972. *Tertiary Frogs from Central Europe*. W. Junk, The Hague, Netherlands.
- ŠPINAR, Z. V., AND Z. ROČEK. 1984. The discovery of the impression of the ventral side of *Eopelobates anthracinus* Parker, 1929 holotype. *Amphibia-Reptilia*, 5:87-95.
- ŠPINAR, Z. V., AND L. P. TATARINOV. 1986. A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi Desert. 1986. *Journal of Vertebrate Paleontology*, 6:113-122.
- TRUEB, L. 1993. Patterns of cranial diversity among Lissamphibia. Pp. 255-343, in *The Skull*. Volume 2. *Patterns of Structural and Systematic Diversity* (J. Hanken and B. K. Hall eds.). The University of Chicago Press, Chicago, Illinois.

- WIENS, J. J. 1989. Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae). *Journal of Morphology*, 202:29-51.
- WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, AND V. A. FUNK. 1991. The compleat cladist. The University of Kansas Museum of Natural History Special Publication, 19:1-158.
- WUTTKE, M. 1988. Untersuchungen zur Morphologie, Paläobiologie und Biostratonomie der mitteleozänen Anuran von Messel. Mit einem Beitrag zur Aktuopaläontologie von Anuren und zur Weichteildiagenese der Wirbeltiere von Messel. Unpub. Ph.D. Dissert., Johannes-Gutenberg-Universität, Mainz, 350 pp, Germany.
- ZWEIFEL, R. G. 1956. Two pelobatine frogs from the Tertiary of North America and their relationships to fossil and Recent forms. *American Museum Novitates*, 1762:1-45.



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