REDESCRIPTION OF *EOPELOBATES GRANDIS*, A LATE EOCENE ANURAN FROM THE CHADRON FORMATION OF SOUTH DAKOTA

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ABSTRACT

*Eopelobates grandis*, an anuran from the Upper Eocene Chadron Formation (Ahern Member) of South Dakota, is redescribed and its generic assignment confirmed. The pterygoid, which was originally identified as the suprascapula, and parahyoid bones are described for the first time for this taxon, and the presence of a quadratojugal is verified. *Eopelobates grandis* can be distinguished from other *Eopelobates* species by its highly tuberculated dermal sculpture, broad frontoparietal, and rounded otic ramus of the squamosal. A preliminary analysis of interspecific relationships indicates that *E. grandis* is more closely related to the European *E. anthracinus* and *E. bayeri* than to *E. hinschei* and *E. wagneri*, also from Europe. The Late Cretaceous record of *Eopelobates* from the Lance Formation of Wyoming and the Hell Creek Formation of Montana is placed in doubt. Based on the current fossil record, *Eopelobates* was thus restricted to the Tertiary of North America and Europe. Dispersal of *Eopelobates* probably occurred during the Late Paleocene/Early Eocene when a North Atlantic landbridge connected North America and Europe.

KEY WORDS: Amphibia, Anura, Pelobatidae, *Eopelobates*, Late Eocene, South Dakota

INTRODUCTION

The pelobatid anuran *Eopelobates* was thought to have a Holarctic distribution spanning the Cretaceous to the Miocene, based on descriptions of ten species from North America, Europe, and Asia (Duellman and Trueb, 1986). However, the relatively recent restudy of some of these species has suggested that the diversity, geographic distribution, and geologic time span of this genus may not be as great as was once indicated. Two species from the Upper Cretaceous of Mongolia and Uzbekistan that represented the only described and named Cretaceous and Asian record of *Eopelobates* have been reassigned to a different genus and family (Spinar and Tatarinov, 1986; Roček and Nessov, 1993). In a review of *Anura*, Sanchiz (1998) considered the European record of *Eopelobates*, which is restricted to the Tertiary, to be the only valid one for the genus, because the generic identification of North American *Eopelobates* species had been questioned by Roček (1981). Without giving them new generic names, Sanchiz (1998) tentatively assigned the North American species of *Eopelobates* to Megophryinae following Zweifel (1956) and Estes (1970), who noticed similarities between North American *Eopelobates* and megophryids. The most recent overview of the genus is provided by Roček and Rage (2000) in a review of Tertiary anurans. This paper presents the second part of a study that I have undertaken in an attempt to clarify the taxonomic status of North American *Eopelobates*.

Two species of *Eopelobates* have been described from North America: *E. grandis* and *E. guthriei*. Roček (1981) cast doubt on their placement in *Eopelobates*, because their frontoparietals were figured and/or described as being paired by Estes (1970:fig. 13, 14) in contrast to *Eopelobates* and *Pelobates*, which have a

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frontoparietal derived from three ossifications. Roček further suggested that *E. grandis* and *E. guthrii* are more closely related to the North American pelobatid *Scaphiopus* which, like most anurans, has paired frontoparietals. Presumed lack of a quadratojugal was given as evidence supporting their relationship with *Scaphiopus* (Roček, 1981).

A recent reexamination (Henrici, 2000) of the oldest described North American *Eopelobates*, *E. guthrii* from the Lower Eocene Wind River Formation of Wyoming, reidentified it as cf. *Scaphiopus guthrii*. The generic reallocation was based on the following derived characters: 1) presence of an elongate postchoanal ramus of the vomer that articulates with the pars palatina of the maxilla; 2) lack of hypossification of cranial bones; and 3) presence of a long, low, arcuate ventral flange of the pterygoid. Definite placement of this species in *Scaphiopus* was not made because the postcranial skeleton remains largely unknown, and thus it could not be determined if cf. *S. guthrii* possesses documented derived postcranial features (Henrici, 1994; Maglia, 1998) shared by *Scaphiopus* and the closely related *Spea*.

The taxonomic status of the other described North American *Eopelobates* species, *E. grandis*, is the focus of this study. Zweifel (1956) named this species on the basis of a single, articulated, and well-preserved specimen (YPM-PU 16441) from the Ahern Member of the Chadron Formation of South Dakota. At the time of Zweifel’s (1956) description, the Chadron Formation was regarded as Early Oligocene, but now it is placed in the Late Eocene based on recalibration of the geologic time scale (Berggren et al., 1995). A brief redescription of this specimen was provided by Estes (1970).

Two other occurrences of *Eopelobates* in North America have been reported. Some isolated bones recovered from the Lance Formation of Wyoming were questionably referred to Pelobatidae by Estes (1964). Part of this material, as well as some new specimens (isolated bones) from the Hell Creek Formation, Montana, was questionably identified as either *Eopelobates* or a related pelobatid (Estes et al., 1969; Estes, 1970). Estes and Sanchiz (1982) later identified these specimens as *Eopelobates sp*. Because Sanchiz (1998) did not consider the North American record of *Eopelobates* to be valid, he questioned the assignment of these specimens to this genus. Roček (2000), however, did not dispute the generic assignment of the Lance and Hell Creek anurans in his review of Mesozoic anurans.

In a publication on the Middle Eocene Green River fauna and flora, Grande (1984:fig. III.1a) published a photograph of a nearly complete anuran skeleton that he identified as possibly a new species of *Eopelobates*. An additional specimen of this taxon is housed in the collections of the Staattliches Museum für Naturkunde, Karlsruhe, Germany (Wuttke, personal communication). Roček and Rage (2000) provide a brief description of the specimen figured by Grande (1984), and they suggested that it is close to *Eopelobates* and *Pelobates*. As this specimen lacks the burrowing specializations found in the skeleton of *Pelobates*, its affinities most likely lie with *Eopelobates*, and it will thus be referred to here as the “Green River *Eopelobates*.”

**ABBREVIATIONS**

Institutional Acronyms.—CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GM, Geiseltalmuseum, Halle; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt;
YPM-PU, Yale Peabody Museum, Yale University, New Haven (formerly housed at Princeton University).

**Systematic Paleontology**

Class Amphibia Linnaeus, 1758  
Order Anura Rafinesque, 1815  
Family Pelobatidae Bonaparte, 1850  
Genus Eopelobates Parker, 1929

*Revised diagnosis* (modified from Sanchiz, 1998).—*Eopelobates* differs from other pelobatids by the following unique characters: 1) nasal triangular with relatively straight anterolateral margin and long, slender lateral process; and 2) combined length of tibiofibula and femur subequal to or greater than the snout-vent length. *Eopelobates* further differs from other pelobatids by the following unique combination of characters: 1) dermal sculpture present and generally consists of pits and grooves, although tubercles are present in one species; 2) frontoparietal comprised of three ossifications; 3) sphenethmoid anteriorly wide and blunt; 4) ilial shaft strongly arched and bears crest in midshaft region; 5) tibiofibula length equal to or greater than length of femur; and 6) bony spade absent.

**Eopelobates grandis** Zweifel 1956

*Holotype.*—YPM-PU 16441; mostly complete skeleton.  
*Horizon and Type Locality.*—Late Eocene; Ahern Member of the Chadron Formation. Divide between West Fork and Main Fork of Indian Creek, one half mile south of forks. SE1/4, S34, T3S, R.12E, Pennington County, South Dakota.  
*Revised diagnosis.*—*Eopelobates grandis* differs from other members of the genus by the following unique characters: dermal sculpture highly tuberculated; frontoparietal broad, in which the width is about 84% of the length; and otic process of squamosal rounded.

**Description and Comparisons**

The skeleton of the holotype (Fig. 1–4) and only known specimen (YPM-PU 16441) is fairly complete, but lacks the snout, most of the left maxillary arch, the left forelimb, right manus, and portions of both hind feet. Extensive dorsoventral compression has caused considerable overall flattening of the specimen and many of the individual bones, resulting in disarticulation of some of the bones which, for the most part, have remained closely associated. Additionally, numerous cracks and breaks are present in the bones. The skeleton is a large example of *Eopelobates*, having an estimated snout-vent length (snout-vent length measured here as anterior tip of skull to distal end of ischium) of 82 mm.

Since Zweifel's description of *E. grandis* and sometime before this study the specimen underwent a considerable amount of preparation that resulted in exposure of some new features as well as damage to others. Minor preparation has been undertaken for this study to better expose a few aspects of the skeleton, mainly the left nasal, right quadratojugal, and right vomer.

*Skull.*—The frontoparietals, nasals, maxillae, and squamosals are heavily sculpted (Fig. 3). Although matrix obscures the pattern of sculpturing somewhat, it can be discerned that the sculpture is extremely reticulated and tubercular. It most closely resembles that occurring in a large *Scaphiopus holbrooki* specimen.
Fig. 1—Skeleton of *Eopelobates grandis* (holotype, YPM-PU 16441) in dorsal aspect. Scale bar = 1 cm.

(CM 18719, snout-vent length = 73mm). In smaller *S. holbrooki* (CM 374400, snout-vent length = 57mm; CM 118968, snout-vent length = 52mm) the tubercles are more widely spaced and the recticulations are not as well defined. The dermal sculpture differs somewhat dramatically from that of other *Eopelobates*, which have pits that in places form a reticulated pattern, and grooves but no tubercles.

The frontoparietal is broadest at roughly two-thirds the length from the anterior end; its breadth being roughly 84% of the length of the bone. The fontanelle is not exposed. An important character of the frontoparietal is whether it is paired, as in most anurans, or comprised of three ossifications, as in *Eopelobates* and *Pelobates* (Roček, 1981; Henrici, 1994). Although Zweifel (1956) did not state that the frontoparietal of *E. grandis* is paired, Estes (1970: fig. 13A) illustrated it as paired. A median suture is visible (Fig. 3) in a broad, deep groove that extends
two-thirds of the length from the anterior end. The groove appears to be the result of preparation to make the median suture more visible. Posteriorly, the groove narrows and then disappears near the widest point of the frontoparietal. The highly sculpted surface and matrix, which cannot be removed without damaging the specimen, make it impossible to trace the suture farther posteriorly. The posterior margin of the frontoparietal forms a very small, posteriorly-projecting median apex (Fig. 4) that lacks sculpturing and, more importantly, does not bear a median suture. This is in contrast to Scaphiopus, where in some specimens the median suture is obscured by dermal sculpture except for the smooth bone of the median apex where the suture is highly visible. The lack of a median suture on the smooth bone of the median apex in YPM-PU 16441 provides evidence that a postero-median ossification is present because it prevents the median suture from reaching
Fig. 3—*Eopelobates grandis* (holotype, YPM-PU 16441). Photograph of skull. A. Dorsal aspect. B. Ventral aspect. Scale bar = 1 cm.
Fig. 4—Eopelobates grandis (holotype, YPM-PU 16441). Line drawing of skull. A. Dorsal aspect. B. Ventral aspect. Scale bar = 1 cm. Abbreviations: ar, anterior ramus of pterygoid; as, angulosplenial; c, cultriform process of parasphenoid; frag, unidentified bone fragment; fp, frontoparietal; ma, median apex of frontoparietal; la, lateral process of vomer; mr, medial ramus of pterygoid; mx, maxilla; na, nasal; op, otic plate of squamosal; pap, palatine process of maxilla; po, posterior process of pterygoid; pt, pterygoid; qj, quadratojugal; sp, sphenethmoid; sq, squamosal; v, vomer. Finely dotted lines indicate cracks in the bone, whereas coarsely dotted lines indicate incomplete bone margins.
the posterior end of the frontoparietal. Thus the frontoparietal of this specimen is assumed to be derived from three ossifications instead of being paired.

Both nasals are preserved, but the right has been removed, intact, since Zweifel’s (1956) description. The nasal (Fig. 3, 4) has an overall triangular shape in which the anterolateral border is relatively straight, and the posterior border is concave where it forms the anterior orbital rim. The nasals are in contact medially except near their posterior ends where they diverge, allowing for dorsal exposure of the sphenethmoid. Because the anterolateral margin is straight, the nasal does not have distinct rostral, lateral, and parachoanalis processes, and the lateral process is thereby demarcated by its ventral flexure. Even though the relative length of the lateral process cannot be determined because the distal end is missing in both nasals, enough is preserved to indicate that the lateral process is long and slender.

The maxilla (Fig. 3, 4) bears teeth along the length of its pars dentalis, but all of the tooth tips are missing. Medially, a large, well-defined palatine process arises from the pars facialis and projects medially, as in other pelobatids. This process was incorrectly identified by Zweifel (1956) and Estes (1970) as the palatine. Posteriorly, the maxilla bears a well-developed posterior process for articulation with the quadratojugal. Zweifel (1956) was not able to identify a quadratojugal in this specimen, but Estes (1970:308) considered the bone identified by Zweifel (1956) as a columella to be the quadratojugal because it “... is excavated for a posterior projection of the maxilla as in Megophrys.” Roček (1981) speculated that the bone in question is too robust to be a quadratojugal, based on the photograph of *E. grandis* in Zweifel (1956:fig. 1). Comparison of this bone to the quadratojugal of *Pelobates cultripes* (CM 55769) reveals that they are essentially identical in morphology, which thereby confirms Estes’s identification of it. The anterior end of the quadratojugal (Fig. 4A) is robust and bears on its lateral surface, as observed by Estes (1970), a wedge-shaped trough for reception of the posterior process of the maxilla. This trough is not visible in the illustrations of the specimen provided by Zweifel (1956:fig. 1, 2) or those presented here. Posteriorly (Fig. 4B), a broad, ovoid protuberance projects ventrally beyond the level of the shaft of the quadratojugal, and in lateral aspect is separated from the shaft by a channel. This protuberance occurs in *P. cultripes* as well, and in this species the ventral ramus of the squamosal covers the dorsal portion of the protuberance, and the quadratojugal articulates with the inner surface of the protuberance. The quadratojugal of *E. grandis* lacks sculpturing, as is the case in most pelobatids that possess one. Sculpturing does occur on the quadratojugal of *P. decheni* (Böhme et al., 1982), and I also have observed its occurrence in two *P. cultripes* specimens (CM 54755, 55769).

The squamosal (Fig. 3A, 4A) bears a long, deep, rounded otic ramus and a slightly longer, wedge-shaped zygomatic ramus. The unsculpted ventral ramus is subequal in length to the otic ramus. A dorsal process, that in most *Pelobates* articulates with the superior lateral process of the frontoparietal (Roček, 1981), is absent. Zweifel (1956) described a broad contact between the squamosal and frontoparietal, but Estes (1970) later correctly pointed out that this contact was the result of postmortem displacement of the squamosal.

Most of the palate is covered by shoulder girdle and vertebral elements (Fig. 3B, 4B). The right vomer (Fig. 4B) is preserved, and it has rotated about 45° clockwise from its normal orientation. It appears to bear the three typical vomerine processes, two of which bound the choana. The lateral process forms the anterior
border of the choana, and posteriorly the short, triangular postchoanal ramus, or process, forms the medial border of the choana. The palatine process of the maxilla borders the choana posteriorly. A prominent, transverse ridge on the vomer bears seven tooth positions, of which four hold teeth. Three of these teeth are sheared off near their bases and the other at its base. The transverse ridge abuts the medial edge of the vomer and, just lateral of the last vomerine tooth, abruptly thins to become confluent with the lateral process. The distal end of the lateral process appears to be missing. Possibly one of several overlying bone fragments could be the displaced distal end of this process. Anteriorly, the vomer extends as a sheet of bone that also thins laterally, resulting in the medial edge of the vomer being considerably thicker than the lateral edge. A small notch is located on the anterior border of the vomer near the midpoint of its length. The anterior process arises lateral to this notch, but bone fragments cover most of its surface. Only a small portion of the medial end of the left vomer (Fig. 4B) is preserved.

The right anterolateral corner of the sphenethmoid is now dorsally exposed (Fig. 3A, 4A) because the right nasal was removed. Although the tectum nasi is somewhat fragmented, it can be determined that it did at least partially roof the nasal capsules. The tectum nasi is preserved as a step-like series of fragments leading from the midline down to and ending at the ridge of what Estes (1970) termed the "turbinal fold" of the solum nasi. Posteriorly, the tectum nasi extends laterally as a sheet of bone to the distal end of the lateral process of the sphenethmoid. The portion of the solum nasi that is exposed includes the posterolateral slope of the turbinal fold and the valley that lies between it and the postnasal wall. The septum nasi is not visible, although it was figured by Estes (1970:fig. 4b). In ventral aspect the sphenethmoid (Fig. 3B, 4B) has a broad and rounded anterior process. Lateral processes extend only a short distance from the main body of the sphenethmoid and would have been underlain by the palatine process of the maxilla in life. A prominent suture scar on the left lateral process and main body of the sphenethmoid indicates that the palatine process of the maxilla would have extended across the lateral process to reach slightly onto the main body of the sphenethmoid. The right palatine process of the maxilla lies in line with the right lateral process, but it is ventrally displaced and thus does not contact the lateral process. The orbitonasal foramen is located on the posterior surface of the base of each lateral process. Posteriorly, the sphenethmoid seems to end near the midpoint of the length of the orbit, but overlying bone fragments and matrix makes this difficult to determine with certainty. A linear series of bone fragments, which probably are the remains of the cultriform process of the parasphenoid, extend along the exposed portion of the midline of the sphenethmoid. The remainder of the parasphenoid is not visible.

The bone identified by Zweifel (1956:fig. 4) as the suprascapula is here interpreted as the left pterygoid (Fig. 4B) for the following reasons: 1) the suprascapula is cartilaginous in extant pelobatids, and because it has never been reported as ossified in Eopelobates (Spinar, 1972; Špínař and Roček, 1984) it is assumed to be cartilaginous in this taxon as well. 2) The shape of this bone does not resemble a suprascapula, which in pelobatids forms a thin sheet that is bordered anteriorly by the cleithrum. 3) Finally, it exhibits the typical triradiate pattern of an anuran pterygoid. Only the proximal portion of the anterior ramus of the pterygoid is preserved, so it cannot be determined if this process has the typical broad articulation with the maxilla. The medial ramus of the pterygoid is broken off from and displaced slightly ventral and anterior to the rest of the pterygoid,
Fig. 5—Posteromedial processes of parahyoid plate and some similarly-shaped bones of the shoulder girdle, as preserved in the holotype of *Eopelobates grandis* (YPM-PU 16441). Scale bar = 5 mm. Abbreviations: co, coracoid; pp, posteromedial process of hyolaryngeal apparatus; st, sternum.

and its proximal end disappears into some bone fragments and matrix. The posterior process of the pterygoid is nearly complete and short. A short, prominent ventral flange, similar in shape to that of *Pelobates*, is present.

**Hyolaryngeal apparatus.**—Both posteromedial processes of the hyoid plate are preserved (Fig. 5). These were illustrated in the line drawing of the skeleton in Zweifel (1956:fig. 4) but are not identified or described. The right posteromedial process rests along the ventral midline of the specimen at the level of the first and second presacrals, whereas the left is preserved on the ventral surface of the right transverse processes of presacrals II–IV. It is flat and very broadly expanded anteriorly with a slender shaft that expands slightly at its distal end. A parahyoid bone is not preserved and may have been absent, as in other pelobatids.

**Postcranial skeleton.**—Eight presacral vertebrae are present. The unfused presacral vertebrae I and II are dorsally exposed, whereas presacrals II–VIII are visible on the ventral side of the specimen (Fig. 1, 2). Neural arches, on the basis of presacrals I and II, are imbricate, elongate, and bear a strong, longitudinal neural spine. Transverse processes on presacrals II–IV are long, stout, and laterally oriented. Transverse processes on presacral V are not as long as the preceding ones and are oriented slightly anteriorly. Those on presacrals VI and VII are missing their distal ends, but their bases are present and oriented more strongly anteriorly than the transverse processes on presacral V. In presacral VIII only the right transverse process is preserved, and it is oriented strongly anteriorly. The presence of transverse cracks near the bases of transverse processes on presacrals II–IV makes it appear as though free ribs are present. However, a crack does not occur on the left transverse process of presacral IV, and in the other vertebrae the cracks occur in different positions on the transverse processes. This indicates that
they are just cracks and not the line of articulation between rib and transverse process. The vertebrae are procoelous as indicated by presacral VI and VII, in which the posterior condyle is exposed, and by presacral VII and VIII, in which the anterior cotyle is visible. The outline of the anterior cotyle in presacral VIII forms an oval, in which the long axis is laterally oriented. The centrum is not pierced for passage of the notochord. The sacral vertebra has been separated from the specimen and the left diapophysis lost since Zweifel’s (1956) description. The right sacral diapophysis is intact but only partly exposed in ventral aspect, being covered by vertebrae and the right ilium. Zweifel (1956) described the joint between the sacrum and urostyle as unfused and probably monocondylar. Although the sacral vertebra is now isolated from the skeleton, damage to its condylar region and also to the cotylar region of the urostyle makes it impossible to determine with certainty the condition of the joint. Measurements of the sacral diapophyses in Zweifel (1956) indicate that they are slightly wider (20.0 mm) than long (19.1 mm). The urostyle, which is incomplete distally, bears two short diapophyses, as observed by Zweifel (1956).

All of the shoulder girdle bones that are typically ossified in anurans are preserved, except for the cleithrum. Zweifel (1956) identified some bone fragments adjacent to the left scapula as the suprascapula, but, as previously mentioned, they have been interpreted here as the left pterygoid. The right scapula is long and bears a well-developed anterior lamina that makes the anterior border straight, as observed by Estes (1970). A narrow cleft separates the broad pars acromialis from the pars glenoidalis. The left clavicle is preserved in articulation with the scapula. Although the right coracoid covers most of the joint between the clavicle and scapula, it can be seen that the clavicle does not articulate with the anterior edge of the scapula, and thus the clavicle most likely abuts the medial edge of the scapula as in other pelobatids. The distal end of the clavicle is expanded slightly anteriorly. The right clavicle, which was removed intact since Zweifel’s (1956) description, is strongly arched. The sternal end of the left coracoid is covered by the right posteromedial process of the hyoid apparatus, and the glenoid end is overlain by the left humerus. The better exposed right coracoid (Fig. 5), on which the following description is based, is preserved in articulation with the right scapula. The coracoid’s contribution to the glenoid fossa forms a cup. A triangular prominence arises from the glenoid end, extends anteriorly, and probably contacted the clavicle in life. The preserved portion of the sternal end is flat and broadly expanded, more so anteriorly, being approximately three times the width of the narrowest part of the cylindrical shaft.

Zweifel (1956) mentioned the presence of an ossified sternum, although he did not identify it in his figure 4. The dorsoventrally thin sternum (Fig. 5) is preserved perpendicular to the long axis of the skeleton with its posterior end resting between the glenoid end of the right coracoid and the anterior margin of the left posteromedial process of the hyoid. The anterior half describes a fan with relatively straight sides. The shaft is narrowest near the midpoint of the sternum’s length, from which point it gradually widens posteriorly. The posterior end is roughly a quarter of the width of the anterior end.

The forelimb is represented by the humerus, radioulna, and some scattered phalangeal elements (Fig. 1, 2). The left humerus is exposed in dorsomedial aspect, and only the ventral aspect of the proximal end of the right is exposed. The shaft is gently bowed ventrally. A moderately developed crista ventralis extends from the midpoint of the shaft to near the proximal end. Medial of the crista
ventralis is a shorter but well-developed crest. The distal ball, eroded in places, is round and positioned slightly medial to the long axis of the shaft. In both humeri the medial epicondyle is broken off. A medial crest is absent. The lateral epicondyle is broken off as well, although the lateral crest is present. Assuming that Eopelobates, like other pelobatids, had better-developed crests in males than in females, then this specimen represents a female. Determination of the size and shape of the fossa is hindered by crushing. Dorsally, the olecranon scar is situated with its apex lateral to the midline of the humerus, but the scar does not reach the lateral edge of the bone.

The right radioulna has been exposed in anterior aspect since Zweifel’s (1956) description. Only the proximal-most end of the left radioulna is visible. The proximal end is broad, being subequal in width to the distal end. This, coupled with a short olecranon process, results in a broad and shallow cup for articulation with the humeral distal ball. The manus is represented by a few scattered phalanges.

Both ilia are partially exposed, the left being more visible (Fig. 1, 2). The shaft approximately equals the combined length of presacrals II–VII. The strongly arched shaft broadens dorsoventrally in the midshaft region where a thin crest arises from the dorsal surface. The crest is restricted to the midshaft region. Longitudinal ridges and narrow grooves for articulation with the sacral diapophyses are present on the dorsal surface of the proximal end of the shaft. Near the acetabular region the shaft is thin, and in cross-section would form a compressed oval that becomes less compressed towards the distal end of the shaft. Pelobatoids have a characteristic spiral groove that extends from the medial side of the shaft, across the dorsal surface, and opens into the preacetabular region. In the left ilium of E. grandis, the spiral groove appears to be absent, although small chips of bone are missing from the region in which the groove would occur, which could account for its apparent absence. This region in the right ilium is covered by the right femur. In E. wagneri the spiral groove exhibits varying degrees of development, from being barely visible to a deep groove, and this variation may have occurred in E. grandis as well. Dorsal and ventral acetabular expansions are of subequal length. Their junction with the shaft describes a slightly concave line for the dorsal acetabular expansion and a strongly concave line for the ventral acetabular expansion. The edges of the symmetrical and bell-shaped acetabular fossa are eroded. The dorsal protuberance consists of a small, low bump. A shallow depression that opens posteriorly lies just posterior to the dorsal protuberance.

Only the left ischium is exposed. It extends greatly posteriorly, and, as depicted by Zweifel (1956:fig. 7B), would have extended beyond the apex of the dorsal acetabular expansion. Zweifel (1956:6, fig. 7B) stated that “the pubis was probably ossified” and indicates its presence with dashed lines in his illustration of the pelvic girdle. Fragments of bone and bone impression adjacent to the ischium may represent the ossified pubis.

The right hind limb is more nearly complete and better preserved than the left, so the following description is based on the former. The femur has a sigmoid curve and is of subequal length with the slender tibiofibula. The tibia is relatively long, has a slender shaft, and is missing its proximal end. Only the proximal half of the fibulare is preserved. Metatarsals and phalanges are scattered about the specimen, making determination of the phalangeal formula impossible. Distal tarsal bones are not exposed, and spades have not been identified. Zweifel (1956) theorized that spades were absent because the tibia and fibulare are long and slender rather than short and stocky as in spade-bearing, burrowing anurans, a
theory with which I am in agreement. The combined length of the femur and tibiofibula (94.4 mm) is greater than the snout-vent length (82 mm).

**Generic Assignment of *Eopelobates grandis***

At the time that Zweifel (1956) described *E. grandis* the genus was poorly understood, being known by only a few, incomplete specimens. The genotype, *E. anthracinus*, then consisted of the dorsal impression of a skeleton housed in the Natural History Museum, London (Parker, 1929), and it was not until much later that the counterpart to this specimen was discovered by Dr. Špinar in the collections of the Geological Paleontological Institute of the Rheinische Friedrich-Wilhelms-Universität, Bonn (Špinar and Roček, 1984). The only other described species was *E. bayeri*, which was then represented by incomplete specimens (Špinar, 1952). Zweifel (1956) based his identification of YPM-PU 16441 as *Eopelobates* on its overall similarities to *E. anthracinus*, in particular the shape of the squamosal and sacral diapophyses, lack of a bony prehallux, limb proportions, and presence of a complete temporal arch. Concerning the latter most feature, Estes (1970) correctly determined that the apparently complete temporal arch was the result of postmortem deformation that caused the right squamosal to be preserved resting against the frontoparietal.

More recently, Roček (1981) questioned the generic assignment of *E. grandis* and suggested that it may be more closely related to the North American *Scaphiopus* and *Spea*, based on the number of bones comprising the frontoparietal. His justification was founded mostly on a drawing of the frontoparietal of *E. grandis* in Estes (1970:fig.13A) that depicted a median suture extending between the anterior and posterior margins of the element. This is in contrast to *Eopelobates* and *Pelobates*, which have three ossifications, rather than two, forming the frontoparietal. Roček (1981), in a detailed study of the ontogeny of *Pelobates fuscus*, documented the presence of a median ossification situated posteriorly adjacent to the paired frontoparietal ossifications. During the course of ontogeny the median ossification fuses with the paired frontoparietal ossifications, leaving no trace of sutures where it adjoins the paired frontoparietal ossifications. Furthermore, the presence of this median ossification prevents the median suture from reaching the posterior end of the frontoparietal complex, which is the only way that the presence of the median ossification can be inferred in adults. Roček (1981) demonstrated that this pattern occurs in *Eopelobates* as well, using a series of *E. bayeri* fossils representing several stages of premetamorphic tadpoles and adults. Roček (1981) further strengthened his theory of relationship of *E. grandis* by arguing that as in *Scaphiopus* and *Spea*, but unlike *Eopelobates*, the quadrate jugal is absent. Estes (1970) had suggested that the bone identified by Zweifel (1956) as the stapes was actually the quadrate jugal, but Roček (1981) argued that this bone is merely an unidentified fragment. He did caution that the holotype should be examined to verify the identity of this bone.

The most recent diagnosis for *Eopelobates* is given by Sanchiz (1998), who combined characters from Estes (1970) and Špinar and Roček (1984). It should be mentioned that Sanchiz (1998) did not include the North American species of *Eopelobates*, including *E. grandis*, in his diagnosis because their generic identification was then uncertain. The revised diagnosis given in the Systematic Paleontology section (above) was based on this diagnosis, in which several characters were omitted and a new one was added. Each of the diagnostic characters of
Sanchiz (1998) and its distribution among pelobatids as well as justification for omission of some of his characters from the revised diagnosis is discussed below. 1) Skull roof is concave to flat. This character was omitted from the diagnosis as it cannot be accurately assessed in Eopelobates because all of the known specimens are dorsoventrally flattened, some considerably so (Henrici, 2000). 2) Dermal sculpture is well developed, consisting of pits and grooves, but lacking tubercles. This is the one diagnostic character in which E. grandis differs from other Eopelobates. Although the sculpturing of E. grandis is well developed, having pits and grooves, it is also highly tuberculated. However, because the style of dermal sculpture can vary between species as well as within a species and ontogenetically, assignment of E. grandis to a new genus on the basis of this character is not justified. Dermal sculpture with tubercles also occurs in Pelobates and Scaphiopus; megophryines lack dermal sculpture. The dermal sculpture of Macropelobates is reticulated but is too damaged to determine if tubercles were present. 3) The frontoparietal is embryonically derived from three ossification centers. This character cannot be directly evaluated in E. grandis as the only specimen is a fully ossified adult. However, because the median suture is absent in the unsculpted median apex of the frontoparietal, a postero medial element is assumed to be present in that it prevents the median suture from reaching the posterior end of the frontoparietal complex. A similar developmental pattern for the frontoparietal occurs in Pelobates as well. The other pelobatids have paired frontoparietals. 4) The frontoparietal complex is not in contact with the squamosal. As mentioned previously, Estes (1970) correctly pointed out that the frontoparietal and squamosal are not in contact. Some megophryines have contact between the frontoparietal and squamosal (Estes, 1970), via the inferior lateral process of the frontoparietal and the otic plate of the squamosal, and Pelobates, except for P. fuscus, has contact between the superior lateral process of the frontoparietal and the dorsal process of the squamosal (Roček, 1981). Other pelobatids lack contact between the squamosal and frontoparietal. Because most pelobatids lack contact between the squamosal and frontoparietal this character was removed from the diagnosis. 5) The sphenethmoid is anteriorly wide and blunt and dorsally roofs the nasal capsules. Eopelobates grandis complies with the former part of this character, but determination of the latter is problematic because of preservation. When Estes (1970) described this character he stated that it was only in E. grandis that the condition of the roof of the nasal capsule could be determined. Wuttke (1988) has since confirmed that in at least E. wagneri the sphenethmoid does roof the nasal capsule. In this region of the skull of E. grandis the bone is preserved as a series of descending step-like fragments, making it difficult to determine how much of the nasal capsule was actually roofed by the sphenethmoid. For this reason, only the shape of the anterior end of the sphenethmoid will be considered here. Megophryines are the only other pelobatid that have a wide, blunt anterior margin of the sphenethmoid. 6) The nasal is triangular with a relatively straight anterolateral margin and long and slender lateral process (Fig. 6). The nasal of E. grandis has an overall triangular shape and a straight anterolateral margin. Although the lateral process is not completely preserved in either nasal, enough is present to indicate that it was long and slender. Eopelobates is unique among pelobatids in having a triangular nasal. Megophryines also have a relatively straight anterolateral border of the nasal as well as a long, slender lateral process, but their nasal is reduced. The nasal of Pelobates, Scaphiopus, and Spea has a concave anterolateral border and the lateral process is short and blunt. The nasal
of the Oligocene Macropelobates is not known. 7) The sternum is ossified. Eopelobates grandis possesses a well-ossified sternum as do the megophryines and Pelobates. A sternum has not been identified in Macropelobates and is absent in Scaphiopus and Spea. As an ossified sternum is present in all but two pelobatids, its presence is not considered to be diagnostic of Eopelobates and was not included in the revised diagnosis. 8) Length of the tibiofibula is equal to or greater than that of the femur. In E. grandis the tibiofibula length (47.2 mm) equals that of the femur (47.2 mm). These bones are of subequal length in megophryines, and the femur is longer than the tibiofibula in other pelobatids. 9) The combined length of the femur and tibiofibula is subequal to or exceeds the snout-vent length. In E. grandis the combined length of the femur and tibiofibula (94.4 mm) is greater than the snout-vent length (82 mm). This is the second character in which Eopelobates is unique from other pelobatids. Using the same measure for comparison, megophryines, Macropelobates, Pelobates, and Scaphiopus have hind limbs that are considerably shorter than the snout-vent length. 10) A prehallux is not modified as a bony spade. A bony spade is not preserved in E. grandis and is assumed to be absent (see description section above for justification). Megophryines also lack a spade, whereas a spade is present in Macropelobates, Pelobates, Scaphiopus, and Spea. The following is a new character included in the revised diagnosis presented in this paper. The ilial shaft is strongly arched and bears a crest along the midregion of the shaft. The only other pelobatids that have a strongly arched shaft of the ilium are the megophryines examined for this study: Megophrys, Leptobrachium, and Scutiger. A crest occurs in varying degrees of development in Megophrys and Leptobrachium.

**Specific Assignment of Eopelobates grandis**

Two characters were identified by Zweifel (1956) to distinguish E. grandis from the other species of Eopelobates known at that time: large size and broad frontoparietal. Large size can no longer be regarded as a specific character for E. grandis because at least one specimen of E. wagneri (SMF 2576b) is of equivalent size. As for the breadth of the frontoparietal, in E. grandis it is roughly 84 percent of the length of the frontoparietal, whereas the range for the other species is 58 percent to 68 percent. Estes (1970) added to these characters the distinctive shape of the sphenethmoid and the rounded tympanic process (otic ramus in this paper) of the squamosal. Concerning the sphenethmoid shape, this character is problematic as Estes (1970) did not elaborate as to how the sphenethmoid of E. grandis
differs from other species. Because the sphenethmoid of *E. grandis* is not well exposed and the portion that can be seen is somewhat fragmentary, it will not be considered here. Sanchiz (1998) presents a lengthy specific diagnosis that is more descriptive in nature than diagnostic. His diagnosis includes characters discussed here as well as those that describe a condition that occurs either in other *Eopelobates* or other pelobatids. The remaining characters in his diagnosis are currently not useful as they are not preserved in some or all of the other species of *Eopelobates*. Characters that can be used to distinguish *E. grandis* from other *Eopelobates* include: highly tuberculated dermal sculpture; broad frontoparietal; and rounded otic ramus of the squamosal (Fig. 3, 4).

**Discussion**

*Eopelobates* at one time was thought to have as many as ten species, ranging in age from the Cretaceous to the Miocene, and a Holarctic distribution. Its diversity has been greatly reduced with only three to five species currently recognized (Roček and Rage, 2000). The North American record now contains only one valid, described species, *E. grandis*. The number of European species is controversial, ranging from two to four, depending on whether the suggested synonyms of *E. bayeri* with *E. anthracinus* and *E. hinschei* with *E. wagneri* are accepted. Spinar and Roček (1984) proposed that *E. anthracinus*, from the Late Oligocene of Germany, and *E. bayeri*, from the Oligo-Miocene of central Europe, may be conspecific. Their reasoning was that the only difference between the two species was size, and as the then only known specimen of the smaller *E. anthracinus* represented an immature individual, it seemed likely that a fully grown *E. anthracinus* would be close in size to an adult *E. bayeri*. This theory was countered, however, when Roček (1995) described an adult specimen of *E. anthracinus* that was still considerably smaller in size than *E. bayeri*. Despite this evidence, Sanchiz (1998) continued to treat the two species as one. There are differences in the proportion of the squamosal, however, that support the theory they are distinct species: in *E. anthracinus* the zygomatic ramus is longer and narrower than the otic ramus, whereas in *E. bayeri* the otic and zygomatic rami are of similar size and shape. Roček and Rage (2000) suggested that *Eopelobates hinschei*, which occurs in the Middle Eocene of Germany (Estes, 1970) and possibly the Late Eocene of England (Milner et al., 1982; Milner, 1986), might be conspecific with the slightly younger Middle Eocene, German species, *E. wagneri* (Wuttke, 1988). Wuttke (1988), however, noted some differences between their frontoparietal, nasal, squamosal, and scapula. The brief description of *E. hinschei* provided by Sanchiz (1998) indicates that the differences noted by Wuttke (1988) in the frontoparietal and nasal are no longer valid. *Eopelobates hinschei* and *E. wagneri* do share some striking similarities. These include: a uniquely-shaped frontoparietal in which the posterior third is greatly constricted; nasals that are widely separated along the midline, which allows for considerable dorsal exposure of the well-ossified sphenethmoid; and slender zygomatic and otic rami of the squamosal. As pointed out by Sanchiz, (1998) *E. hinschei* lacks an adequate diagnosis and is in need of preparation using modern techniques before it can be fully evaluated.

With the reassignment of the Late Cretaceous, Asian species of *Eopelobates* (Spinar and Tatarinov, 1986; Roček and Nessov, 1993), *Eopelobates* now is definitely known only from the Tertiary of North America and Europe. The oldest,
definitive record of *Eopelobates* in North America is the Late Eocene *E. grandis*. If the identification of the Green River anuran as *Eopelobates* is correct (Grande, 1984), then the record extends back to the Middle Eocene, which roughly coincides with the oldest European record. Estes (1970; et al., 1969) had described some isolated bones from the Late Cretaceous Lance Formation of Wyoming and Hell Creek Formation of Montana as questionably *Eopelobates* and later (Estes and Sanchiz, 1982) confirmed this identification, observing that the squamosal most closely resembles that of *E. guthriei*. As *E. guthriei* has now been referred by Henrici (2000) to *Scaphiopus*, the identity of the Lance and Hell Creek anurans as *Eopelobates* is once more uncertain.

Preliminary study of *Eopelobates* suggests that two clades are present with one, possibly both, clades including species from Europe and North America. One clade consists of *E. anthracinus*, *E. bayeri*, and *E. grandis*, which share the characters of a well-ossified skull with deep otic and zygomatic rami of the squamosal. Using Pipioidea as an outgroup for determining character polarity indicates that a deep otic and zygomatic ramus is a derived character. *Eopelobates hinschei* and *E. wagneri* comprise the other clade. They have a less well-ossified skull in that the nasals do not meet along the midline, which allows for considerable dorsal exposure of the sphenethmoid, and the otic and zygomatic rami of the squamosal are slender. The “Green River *Eopelobates*” also possesses these features. Employing the same outgroup indicates that the former character is derived and the latter is primitive.

Estes (1970) had earlier observed that two lineages of *Eopelobates* were present, based on the length of the skull table, although his grouping of the species differs from that presented here. Using nasal-frontoparietal proportions he suggested that *E. hinschei* and *E. bayeri* comprised the long-skulled lineage, and that the more primitive short-skulled lineage consisted of *E. guthriei*, (now referred to *Scaphiopus* by Henrici, 2000), *E. grandis*, and *E. anthracinus*. A detailed phylogenetic analysis of interspecific relationships of *Eopelobates* cannot be undertaken at this time for the following reasons: 1) *E. wagneri* should be formally described and diagnosed as it currently appears only in dissertation form (Wuttke, 1988); 2) *E. hinschei* needs to be thoroughly redescribed and diagnosed, assuming that it is not synonomized with *E. wagneri*; and 3) An identification and thorough description of the “Green River *Eopelobates*” needs to be made.

Estes (1970) theorized that *Eopelobates* achieved a Holarctic distribution no later than the Late Paleocene or Early Eocene, observing that it was yet another example of similarity between North American and European faunas. The range of *Eopelobates* is now thought to be only North American and European, rather than Holarctic, but the timing of distribution suggested by Estes (1970) is reasonable. Recent studies (McKenna, 1983; Marincovich et al., 1990; Knox, 1998) indicate that a North Atlantic land-bridge passing through southern Greenland connected North America and Europe from the Late Paleocene into the Early Eocene (roughly the lower two-thirds of the reversed interval of Chron 24 of the magnetic polarity time scale). This bridge allowed for a broad interchange of terrestrial vertebrates between these continents (Marincovich et al., 1990). The high latitudes of the land-bridge would not have been inhospitable to frogs as the climate was considerably warmer in the North Atlantic realm than at present (Marincovich et al., 1990). As an example, the lower vertebrate fauna of the Lower Eocene, Eureka Sound Formation of Ellesmere Island includes a salamander, anguid and varanid lizards, a boid snake, several types of turtles including a
tortoise, and an alligator; of these taxa the varanid, tortoise, and alligator indicate an equable climate with winters that rarely experienced freezing temperatures (Estes and Hutchison, 1980). Thus it seems likely that Eopelobates could have taken part in the broad interchange of terrestrial vertebrates between North America and Europe.

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