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## CRANIAL ANATOMY AND PHYLOGENETIC AFFINITIES OF THE PERMIAN PARAREPTILE *MACROLETER POEZICUS*

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**ABSTRACT**—The Parareptilia, the sister group to the Eureptilia, is poorly known, with many taxa in need of adequate description. One such taxon, *Macroleter poezicus* is found in Middle Permian strata of the Mezen River Basin in the Arkhangel'sk Province of Russia. The cranial anatomy of *Macroleter* is described from four new well-preserved specimens, and 89 cranial characters are incorporated into a phylogenetic analysis of parareptiles. A single most parsimonious topology is found, consisting of 205 steps, with the novel result that *Macroleter* is the taxon most closely related to pareiasaurs. This result has important implications for the phylogeny of the Parareptilia as well as for the identity of a disputed element (the tabular) in the skull of pareiasaurs.

### INTRODUCTION

Continued disagreement concerning turtle origins has resulted in an increased focus on the Parareptilia, a previously enigmatic fossil group. Not only have there been arguments identifying turtles as diapsid (deBraga and Rieppel, 1997; Rieppel and Reisz, 1999; Rieppel, 2000) or parareptilian (Reisz and Laurin, 1991; Lee, 1993, 1995, 1997a, b; Laurin and Reisz, 1995) reptiles, but even those who conclude that turtles are parareptiles argue over their exact position within the clade. Attempts to sort out the origin of turtles have been frustrated by the fact that many of the taxa within Parareptilia are insufficiently known, inhibiting the ability to discern evolutionary trends within the group, however recent studies have described some of the lesser-known Permian parareptilian taxa, incorporating them into a phylogeny of early amniotes (deBraga and Reisz, 1996; Lee, 1997a; Berman et al., 2000; Modesto, 2000; Reisz and Scott, 2002). The majority of the well-known parareptiles come from the Late Permian of the Karoo Basin, South Africa, but fossils from this clade are also known from sites on practically every continent, including North and South America, Antarctica, Asia, and Europe, with the greatest numbers coming from the expanse of the Russian Platform. Temporally, the range of the non-testudinine parareptiles extends from the Early Permian to the Late Triassic. Minimum divergence times based on the latest phylogenies imply that the proganosaurs (mesosaurs + parareptiles, sensu Anderson and Modesto, 2005) diverged from the Eureptilia at the latest in the Late Carboniferous (Modesto, 2000), indicating the presence of extensive ghost lineages for many clades within Parareptilia.

The distinctive assemblage of parareptiles from Russia plays a key role in our understanding of the diversity of Permian amniotes. Most of these taxa, however, have been only briefly described, and have been only sporadically included in phylogenetic analyses of the clade. One particularly interesting amniote-bearing site, the Mezen River Basin in the Arkhangel'sk Province of Russia, is dated to the Late Kazanian to Early Tatarian in the Middle Permian, and is believed to be contemporaneous with the *Tapinocephalus* Zone of the Beaufort Series in South Africa (Rubidge, 1995). This area is host to an important faunal assemblage that is dominated by parareptilian taxa (Ivakhnenko et al., 1997). Discovered in 1935 by N. I. Novozhi-

lov in localities along the Mezen, Pyoza, and Kimzha rivers of the Mezen River watershed (Tverdokhlebova and Ivakhnenko, 1984), this fauna was first described by Efremov (1938, 1940). The assemblage is notable for the apparent preferential preservation of small terrestrial amniotes, and contains an intriguing mix of synapsids, a single small diapsid, and a number of parareptiles. Oddly, no anamniotes, very common to other contemporaneous faunas, have been found in any of the many localities scattered throughout the basin. The synapsids of the Mezen assemblage represent both basal synapsid 'pelycosaurs', the varanopids *Mesenosaurus* and *Pyozia* and the caseid *Ennatosaurus*, along with the more derived therapsids *Biarmosuchus* and *Niaftasuchus*. Also present in the assemblage is a small diapsid *Lanthanolia ivakhnenkoi* (Modesto and Reisz, 2003) and the parareptiles *Lanthaniscus efremovi*, *Bashkyroleter mesensis*, *Nyctiphruetus acudens*, *Nycteroleter ineptus*, and *Macroleter poezicus* (Ivakhnenko et al., 1997). Most of the taxa are very low in abundance, with the small *Nyctiphruetus* dominating the assemblage. *Nyctiphruetus* comprises over 67% of the specimens found in the basin, with *Macroleter* comprising over 8% of the known specimens.

Initially these two common taxa, belonging to the Nyctiphruetidae (Efremov, 1938) and the Nycteroleteridae (Romer, 1956) respectively, were difficult to classify. The nycteroleterids in particular superficially resemble anamniotes, possessing a definite temporal emargination and conspicuous dermal sculpturing, and they have indeed been allied with diadectids and other anamniote taxa (Olson, 1947; Heaton, 1980). Subsequent analyses, however, have shown that nycteroleterids are clearly amniotes, and have placed these animals well within the Parareptilia, usually as or within the sister taxon to the group including the pareiasaurs and procolophonids (Lee, 1995, 1997a; deBraga and Reisz, 1996; deBraga and Rieppel, 1997; Hill, 2005;). There remains, however, some debate about their exact position within Parareptilia, and even their monophyly as a clade, due in large part to a lack of detailed knowledge about the anatomy of the group.

The largest of the nycteroleterids from the Mezen River basin, *Macroleter poezicus* was named in 1984 (Tverdokhlebova and Ivakhnenko, 1984). At last count, *Macroleter* had been found in 13 different sites throughout the basin, the third most common taxon in the assemblage after *Nyctiphruetus* and the varanopid *Mesenosaurus*. Until a misidentified specimen from the Chickasha Formation in Oklahoma was recognized as a species of *Macroleter* (Reisz and Laurin, 2001), the genus was monospecific, and

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was restricted to the localities within the Mezen Basin. *Macroleter poezicus* can now be studied in more detail due to collecting expeditions to this latter area in the 1990s, which have produced additional specimens. These new specimens consist of well preserved and relatively undistorted cranial, and for the first time, post-cranial material of the genus. This paper details a redescription of the cranial anatomy of *Macroleter poezicus* from the new specimens, and incorporates this morphological information into a phylogenetic analysis of the Parareptilia with the aim of resolving *Macroleter's* relationship to pareiasaurs and procolophonids.

**Institutional Abbreviations**—PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; UTM, University of Toronto at Mississauga, Mississauga, Canada.

**Anatomical Abbreviations**—**a. max. for.**, anterior maxillary foramen; **a**, angular; **ar**, articular; **art. sp.**, articulation area of the splenial; **atc**, atlas centrum; **ati**, atlas intercentrum; **atr**, atlas rib; **axc**, axis centrum; **axi**, axis intercentrum; **bo**, basioccipital; **br**, basisphenoid rostrum; **cbl**, ceratobranthial; **cl**, clavicle; **clin**, clinoid process; **co**, coronoid; **d**, dentary; **dors. sel.**, dorsum sellae; **ect**, ectopterygoid; **eo**, exoccipital; **ept**, epipterygoid; **f**, frontal; **for. orb.**, foramen orbitonasale; **h1**, hyoid; **hyp**, insertion of hypaxial musculature; **j**, jugal; **la**, lacrimal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **pro**, prootic; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **s**, stapes; **scl**, scleral ossicle; **sel**, sella turcica; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **sub. for.**, suborbital foramen; **st**, supratemporal; **t. f.**, temporal fenestra; **t**, tabular; **v**, vomer; **vic**, vidian canal; **I-XII**, foramen for cranial nerves I-XII.

## SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768  
 PARAREPTILIA Olson, 1947  
 ANKYRAMORPHA deBraga and Reisz, 1996  
 MACROLETER POEZICUS Tverdokhlebova and  
 Ivakhnenko, 1984

### Revised Diagnosis

*Macroleter poezicus* is a medium-sized parareptile distinguished by the following cranial autapomorphies: maxilla vomer anterior contact, basicranial articulation and basiptyergoid process facing anteriorly, pterygoids meet anterior to basicranial articulation; sculptureless round indentation just anterior to fronto-parietal suture; posterior portion of suture between parietals highly depressed, skull roof v-shaped in occipital view.

**Holotype**—PIN 3586/1, consisting of an entire skeleton

**Locality and Horizon**—Mezen River Basin, Arkhangel'sk Province, Russia. Uppermost Kazanian or lowermost Tatarian, Middle Permian (Ivakhnenko et al., 1997).

**Referred Specimens**—PIN 4543/3, mostly complete skull and postcranial material; PIN uncatologed immature specimen, complete skull and postcranial material; UTM/Mezen/2001/1, large skull, some postcranial material; UTM/Mezen/2001/2, skull and postcranial material anterior to pelvic girdle.

## OSTEOLOGICAL DESCRIPTION

### Reconstruction

The skull of *Macroleter* was reconstructed in dorsal, ventral, lateral, and occipital views (Fig. 1), based primarily on two specimens, PIN 4543/3 and PIN (uncatologed), which are virtually complete and show little crushing or warping. For the ventral view PIN 4543/3 was the basis for the reconstruction. The dorsal reconstruction was composed based on a combination of PIN

4543/3 and PIN (uncatologed). The lateral reconstruction was based primarily on PIN (uncatologed), and secondarily on UTM/Mezen/2001/2. The occipital view was largely reconstructed from the information available from the two best preserved skulls, but there also exists a slide of a skull now missing (R. Reisz, pers. comm., 2005), in occipital view, which was also used as a reference.

### Skull

*Macroleter poezicus* is a medium-sized parareptile, with skull length of the studied specimens ranging from 7.0 to 10.0 cm. The taxon possesses distinctive sculpturing consisting of small, circular pits interspersed within flat areas and raised bumpy tubercles. The skull is roughly triangular in shape, temporal emargination is present but only slightly incised, and is defined by the squamosal and the quadratojugal. The skull is slightly dorso-laterally compressed (flattened), with a definite median embayment on the posterior edge of the skull roof. The taxon possesses a large parietal foramen and large, posteriorly expanded orbits. Distinctive tubercles are present on the prefrontal, the frontal, and the postfrontal, and there is extensive sculpturing on the jugal under the orbit, with slight ventral flaring of and ornamentation on the quadratojugal consisting of a series of tubercles. A small lower temporal fenestra is present, and is bordered by the jugal, the squamosal, and the quadratojugal. The snout is slightly expanded, forming a 'muzzle' just posterior to the premaxilla-maxilla suture. The interpterygoid vacuity is very short, and is defined both anteriorly and posteriorly by the pterygoid.

**Dermal Skull Roof**—The premaxilla bears no sculpturing, unlike the majority of the other elements of the skull roof. It is a roughly triradiate structure that sutures with the maxilla posterolaterally, the vomer posteriorly, and sends up a tall, thin dorsal process that overlaps the nasal (Figs. 2, 3). This bone forms the anterior portion of the external naris, which is oblong in shape, and whose long axis is directed on an angle slightly posterodorsally. The dorsal process of the element is narrow in comparison with the condition seen in other basal amniotes, resulting in the nares being directed more dorsally than laterally, a synapomorphy of parareptiles (Laurin and Reisz, 1995). This process extends nearly to the posterior edge of the external naris, and its lateral surface bears a slight groove that acts to receive the nasal (Fig. 3). Thus in lateral view only a sliver of the premaxilla can be seen above the anterior ramus of the nasal. Ventral to the dorsal process, the premaxilla forms a broad, flat shelf comprising the base of the naris, where it forms a curving, anteriorly concave suture with the maxilla that is visible on the dorsal surface (Fig. 3). Posteriorly, the premaxilla takes the form of a small median projection that lies atop the vomer (Fig. 3). The antero-medial part of the premaxilla cannot be seen in ventral view due to the adduction of the lower jaw to the skull, although what can be observed of the suture between the premaxilla and the maxilla appears to mirror that of the dorsal surface.

A foramen is present on the dorsal surface of the premaxilla at the base of the dorsal process (Fig. 3), in all likelihood homologous to the prepalatal foramen of *Procolophon* (Carroll and Lindsay, 1985). The premaxilla carries five teeth, best observed in UTM/Mezen/2001/2, with the front tooth being the largest, and the size of the teeth declining posteriorly.

After suturing anteriorly with the premaxilla, the maxilla continues to form the ventral and posterior border of the external naris in the form of a tall and wide dorsal process (Fig. 3). This morphology characterizes all parareptiles except millerettids and bolosaurids. There are a number of foramina on the lateral surface of the maxilla (Fig. 3), with the largest and most anterior of these occurring just under the posterior border of the external naris. This foramen is the anterior maxillary foramen (Laurin and Reisz, 1995), a distinctive parareptilian synapomorphy. Al-

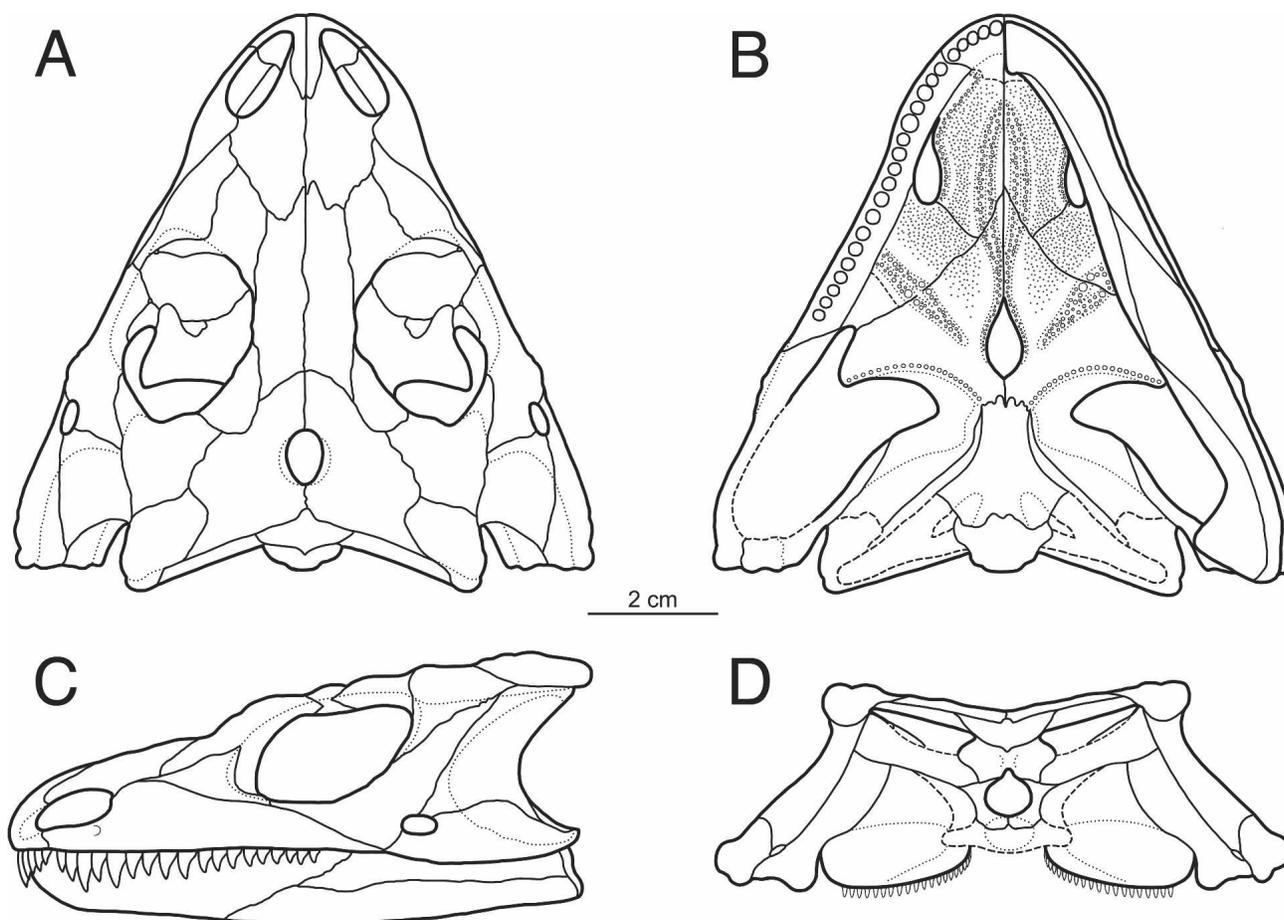


FIGURE 1. Cranial reconstruction of *Macroleter poezicus*. **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, occipital view. Small dotted lines delineate within element, non-sutural features, dashed lines represent inferred sutural contacts or element shape.

though the lateral surface of the maxilla is relatively smooth ventrally, dorsally it begins to show slight sculpturing, becoming extensively so at a level halfway up the external naris (Fig. 3). The maxilla is just excluded from the ventral rim of the orbit by contact between the lacrimal anteriorly, and the jugal posteriorly. The posterior ramus of the maxilla thins to a sliver as it approaches the level of the posterior border of the orbit, where it sutures with the thin anterior ramus of the quadratojugal. This condition contrasts with that of the majority of pareiasaurs and procolophonids, in which the quadratojugal is excluded from contact with the maxilla, though it appears that the two bones do make contact in some pareiasaurs.

Removal of the skull roof in PIN (uncataloged) allows a clear view of the dorsal surface of the maxilla (Fig. 3). Anteriorly, the medial edge of the bone lies in very close proximity to the vomer, and at one point slightly overlaps the lateral flange of this element. As a result, the anterior extent of the choana is largely closed off or reduced to a small channel if it is present at all. There is a large pocket on the dorsal surface of the maxilla, the beginning of the supramaxillary canal (Heaton, 1979), which continues posteriorly over the tooth row. Posteromedially, an anterior process of the vomer forms an anteromedially directed suture with the maxilla, deflecting the posterior end of the choana towards the midline, a character that *Macroleter* and *Nyctiphuretus* share with pareiasaurs. The posterodorsal edge of the maxilla is formed by a suture with the lacrimal as the latter element rises dorsally from the palate.

In the larger individuals, the maxilla bears 18–20 teeth. There

is a caniniform area in which the teeth are larger than the others in the row, but there is no single caniniform tooth. In this area the maxilla swells slightly laterally, indicating that these larger teeth were implanted deeply. Because of this implantation, the snout region of the skull is slightly blunt anteriorly, a morphology that is similar to that of pareiasaurs. The teeth themselves are fairly broad at the base and subcircular in cross section. They are slightly recurved, such that the tip just reaches the level of the posterior side of the tooth in occlusal view. The teeth also show a shovel-shaped morphology, being slightly mediolaterally compressed, with two faint cutting edges more closely placed relative to each other on the lingual side of the tooth (Fig. 4). The base of the majority of the teeth shows fluting consisting of longitudinal grooves of varying depths and heights, most visible on the labial side. These grooves are very similar in morphology to those seen in *Colobomycter* (Modesto, 1999), and millerettids (Gow, 1972). This fluting is also present on some of the larger premaxillary teeth.

The lacrimal, in contrast with the condition seen in most early tetrapods, is a shortened bone in most parareptiles, and is excluded from contact with the naris in most parareptiles save millerettids and pareiasaurs, though only barely so in the case of *Macroleter*. It is quite a long bone nonetheless, extending farther anteriorly than the prefrontal (Fig. 2), in contrast to the condition depicted in other nycteroleterids (Ivakhnenko et al., 1997). About midway down the lateral surface of the lacrimal, the heavy sculpturing that characterizes the dermal skull roof ceases, and the element becomes very smooth, a texture which continues

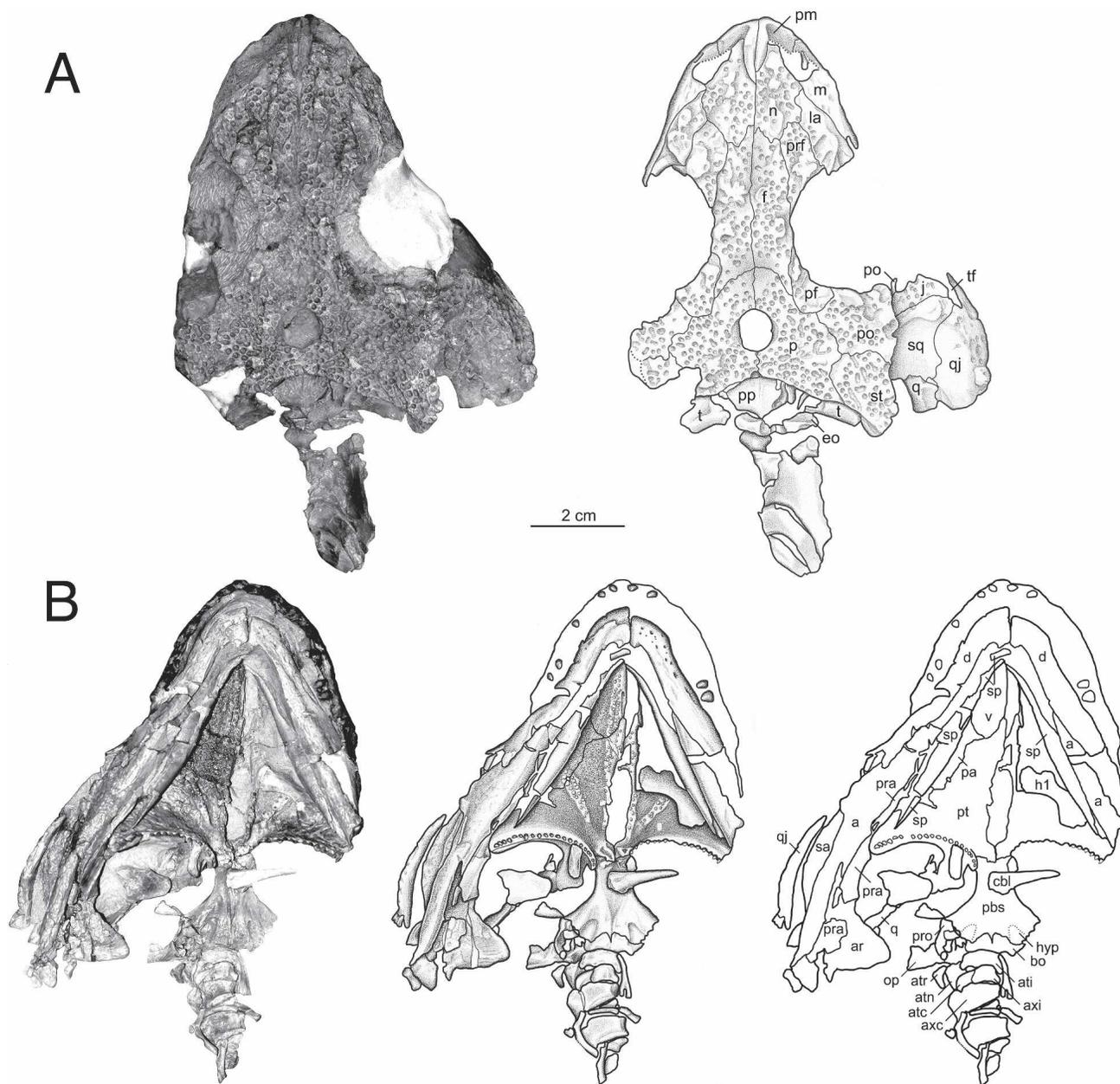


FIGURE 2. Skull of *Macroleter poezicus* (PIN 4543/3). **A**, dorsal view; **B**, ventral view.

on the lateral surface as it forms a short suture with the jugal along the ventral margin of the orbit (Fig. 3). This suture extends down into the orbit to meet the palate. No lacrimal foramen can be seen on the exposed posterior surface of the ventral process of the lacrimal, though this feature may lie further laterally and has been obscured from view in these specimens. The foramen orbitonasale is represented by a gap in the area around the confluence of the lacrimal, the prefrontal medially, and the underlying palatine (Fig. 3).

As a pair, the nasals are roughly wing-shaped, their anterior processes excluded from contact with each other for the first third by the dorsal process of the premaxilla (Fig. 2). From their slightly pointed origin at the anterior end, the nasals widen laterally to form the medial and dorsal border of the naris. Posterior to this structure, the nasal forms a short suture with the dorsal process of the maxilla. Continuing posteriorly, the antero-

lateral edge of the nasal is formed primarily by a short undulating suture with the lacrimal, and the lateral border is oriented slightly posteromedially as a suture with the prefrontal. The posterior border of the nasal is formed by contact with the frontal via a horizontally directed undulating suture, with the two nasals meeting in a relatively straight median suture. The dorsal surface of the bone shows the distinctive sculpturing pattern, with a notable tubercle just posterior to the naris, whereas the ventral surface is smooth (Fig. 5).

The prefrontal is a stout bone that forms the majority of the anteromedial border of the orbit (Figs. 2, 3, 5). It has a broad, robust ventral extension, which is sutured firmly to the palatine, very clearly demonstrated by PIN (uncatalogued) (Fig. 3). This thickened state is common for parareptiles, including the bolosaurids and procolophonids (Laurin and Reisz, 1995), and a firm suture is also found in pareiasaurs (Lee, 1995). As the bone

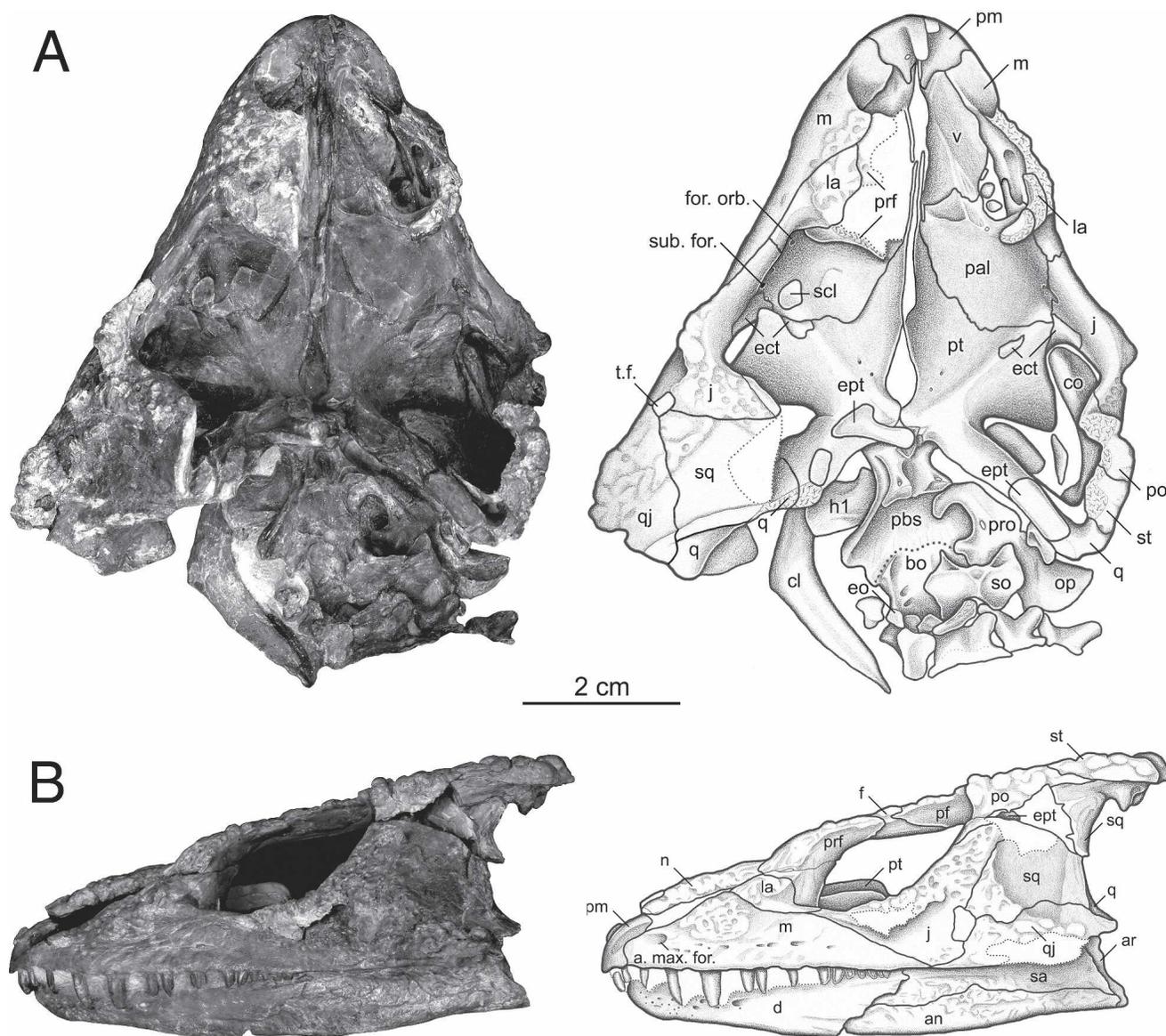


FIGURE 3. Skull of *Macroleter poezicus* (PIN (uncataloged)). **A**, dorsal view; **B**, left lateral view.

extends anteriorly along the skull roof, it is incised by the lacrimal laterally, and appears slimmer on the dorsal surface. Anteriorly, the prefrontal extends only two-thirds of the extent of the lacrimal onto the snout region. On each of the specimens examined, there is a prominent tubercle on the prefrontal a short distance away from the orbital rim. In lateral view, the frontal displays a noticeable hump comprising the majority of the level change between the relatively flat snout area of the skull and the skull table (Fig. 3).

More than twice as long as it is wide, the frontal is subrectangular in shape, and noticeably longer than the nasal (Figs. 2, 5). Posterior to the nasal suture, the frontal widens very slightly until it forms a small portion of the dorsal border of the orbit, although it is nearly excluded from this structure by the posterior and anterior process of the prefrontal and the postfrontal, respectively. On its posterior half, the frontal meets the postfrontal in a primarily anteroposteriorly directed suture that extends slightly medially, tapering the bone posteriorly. The suture with the parietal initially extends laterally from the midline, but shortly curves posterolaterally, meeting the postfrontal-frontal

suture at an acute angle, the posterolateral edges of the frontals thus wrapping back around the anterior extension of the parietals (Figs. 2, 5). There is a raised tubercle close to the lateral edge where it contributes to the orbit. A distinctive sub-circular dent is also present, centered just anterior to the fronto-parietal suture, in each of the observed specimens of *Macroleter*, including those specimens that show little distortion (Figs. 2, 5). This depression is bereft of sculpturing.

In dorsal view, the paired parietal is a roughly triangular element, forming an undulating, posterolaterally-oriented suture anteriorly with the frontal (Figs. 2, 5). Ventrally, the parietal underlaps the postorbital and the supratemporal so that it appears larger on the ventral surface than it does dorsally, thereby helping to reinforce the skull roof. A large pineal foramen lies on the suture between the two parietals, displaced slightly anteriorly in relation to the full size of the bone, though it appears to be posteriorly placed due to the median embayment of the skull table. The foramen itself is laterally constricted by a small flange on the ventral surface of the bone, directed slightly anterolaterally from the posterior edge of the foramen, giving it the appear-

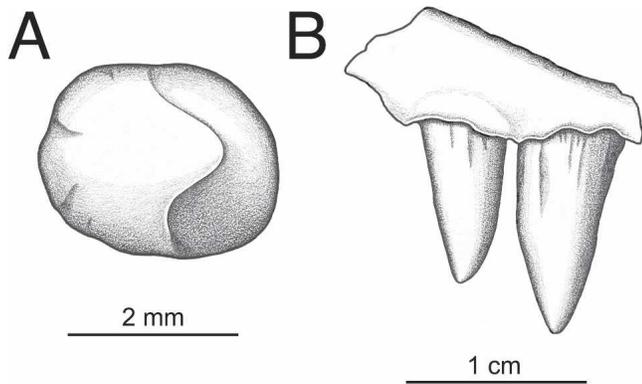


FIGURE 4. Maxillary teeth of *Macroleter poezicus* (PIN 4543/3). **A**, occlusal view (anterior to the top); **B**, lateral view (anterior to the right).

ance of being teardrop in shape (Figs. 4, 5). The posterior edge of the skull table is significantly incised, with the rounded apex of the emargination centred at the suture between the two parietals. Notably, the two parietals also dip towards each other along their median suture, a morphology that is most easily observed in occipital view (Fig. 1). Posteriorly the parietal ceases to be sculptured, and drops down to a lower level where it sutures with the postparietal a short distance from the skull table.

The postparietal is a small element that is clearly exposed in dorsal view, although unlike the rest of the skull roof elements it lacks the characteristic sculpturing on the dorsal surface (Fig. 2). In the original description of *Macroleter* the postparietal is integrated into the skull roof, contacting the posterior border of the pineal foramen (Tverdokhlebova and Ivakhnenko, 1984; Ivakhnenko, 1987), but in all specimens examined in this study, the foramen is formed solely by the parietals. The postparietal is in fact an occipital element that is subtriangular in shape, with the apex pointing posteriorly. It is oriented downwards at about 45°, and ventrally attaches to the supraoccipital of the braincase. In the available specimens the postparietal is present as a single, median element in PIN 4543/3 and UTM/Mezen/2001/2, whereas it is a paired element in PIN (uncataloged) and UTM/Mezen/2001/1. This condition is apparently not dependent on the maturity of the specimen. Fusion of the postparietals is a synapomorphy of pareiasaurs, whereas other parareptiles show a clear suture between the two sides. Although the bone itself is not sculptured on the dorsal surface, it bears slight ridges extending parallel to the long axis of the skull (Fig. 2).

The tabular in *Macroleter* is a small, thin, occipital element that lies lateral to the postparietal, posterior to the parietal, and medial to the supratemporal. It is exposed dorsally for a short time before curling ventrally (Fig. 2), ending in a small anteriorly projecting lip. As a result, the tabular appears convex when observed in occipital view. The bone underlies the parietal for a distance anteriorly, sutures to the supratemporal laterally, and appears to be just excluded from contact with the squamosal (Fig. 5). The full extent of the tabular is only preserved in PIN (uncataloged), whereas in the other specimens the element is lost or fragmented beyond recognition. This ability to be easily lost may signify a loose sutural attachment to the underside of the parietal.

The supratemporal of *Macroleter* has fused with the intertemporal as is the case for all other amniotes. It is a large subtriangular element that forms the posterolateral corner of the skull table (Figs. 2, 5). On the dorsal surface, the bone has a definite tubercle on its posterolateral corner. Anteriorly it forms a nearly horizontal suture with the postorbital, about halfway between the posterior rim of the orbit and the back of the skull

table. There is a nub of the posterolateral corner of the supratemporal that extends ventrally onto the occiput, where it forms a loose attachment medially with the tabular (Fig. 2). This structure may serve as reinforcement of the posterolateral corner of the skull table where it makes contact with the paroccipital process of the opisthotic.

The postfrontal is a small element, possessing two tubercles on the dorsal surface, one on the anterior portion, along the suture with the frontal, and another along the orbit close to the suture with the postorbital (Figs. 2, 5). Posteromedially the postfrontal forms a curving suture in its short contact with the parietal. Posterolaterally it attaches to the postorbital, the suture curving around to head anterolaterally. On the ventral surface the postfrontal extends further medially under the postorbital than is apparent on the dorsal surface, with its silhouette becoming more long and vermiform around the posteromedial rim of the orbit, reaching to the middle of the posterior edge of this structure (Fig. 5).

The postorbital is a large bone that extends posteriorly approximately halfway along the skull roof, where it forms a transversely directed suture with the supratemporal (Figs. 2, 5). Anteromedially, the postorbital sutures with the postfrontal, and it forms a short suture posteromedially with the parietal. The dorsal surface bears a tubercle along the posterior border of the orbit. There is a significant ventral ramus of the postorbital that extends onto the lateral surface of the skull, excluding the jugal

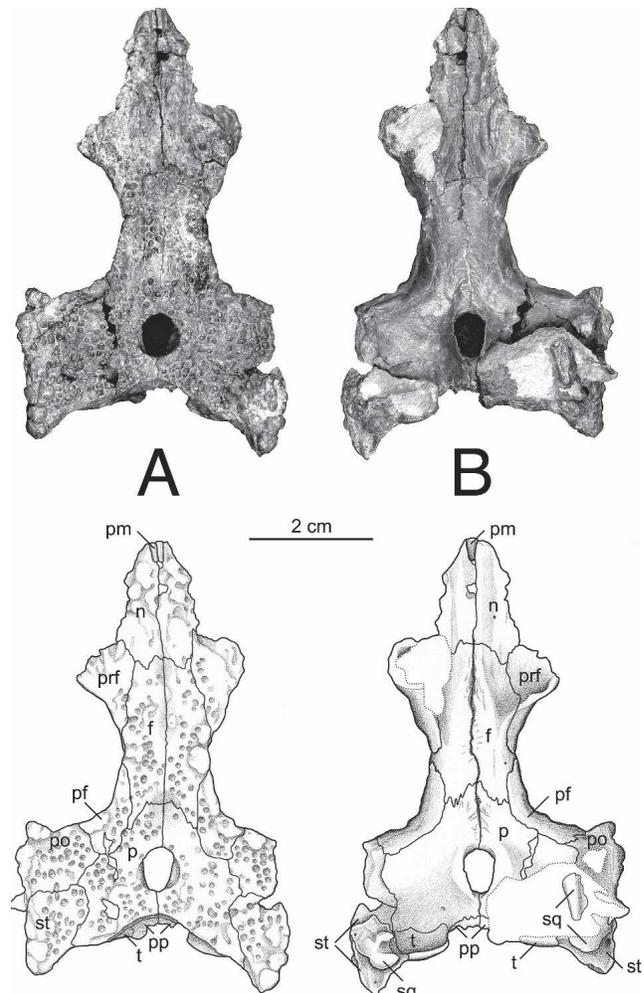


FIGURE 5. Dorsal skull roof of *Macroleter poezicus* (PIN (uncataloged)). **A**, dorsal view; **B**, ventral view.

from forming most of the posterior margin of the orbit (Fig. 3). This ventral process is enforced by a thickening of the bone that can be seen extending into the orbit on its internal surface (Fig. 3). The orbits are expanded similarly to procolophonids, more so on the posterodorsal edge, though not to the extent seen in *Nyctiphruetus*.

The jugal forms most of the ventral rim of the orbit. It begins long and thin anteriorly in a short suture with the lacrimal, and then flares posteriorly, where it forms the anterior border of the small temporal fenestra of *Macroleter* (Figs. 2, 3). The bone increases in height posteriorly, forming a gently wavering, posterodorsally directed suture with the squamosal. The tall dorsal expansion of the jugal forms the ventral part of the posterior edge of the orbit, but the bone does not reach the skull table, as the anteroventrally directed suture with the postorbital terminates its dorsal extent. Posteriorly, the jugal is just excluded from the temporal emargination. On the internal (medial) surface, the jugal sutures anteriorly and medially with the palatine, and further posteriorly with the small ectopterygoid (Fig. 3).

A prominent bumpy ridge of sculpturing projects laterally a considerable distance at the posteroventral border of the orbit, and consists of a series of tubercles and pits. Although the jugal is sculptured on its entire lateral surface, this sculpturing does not extend very far ventrally, and only very sparsely under the aforementioned ornamentation (Fig. 3). This morphology may be homologous to the ornamentation in the form of bosses seen in pareiasaurs.

The squamosal is a broad plate of bone that forms a large section of the temporal emargination, and has a restricted dorsal contribution to the temporal fenestra (Figs. 2, 3). It is firmly sutured to the underside of the skull roof, and the detached skull table of PIN (uncataloged) allows for the examination of this area of the squamosal in ventral view. The articulation of the dermal skull roof and palate with the paroccipital process of the braincase is very complicated, with the confluence of the pterygoid, the quadrate, the squamosal, the tabular, and the supratemporal within a small area. The squamosal is broadly sutured to the ventral surface of the supratemporal, a short distance from the posterolateral corner. There is a structure that has double condyle-like processes, a larger posterior one and a smaller anterior one, separated by a groove into which the paroccipital process of the opisthotic fits. The notch itself is directed at an angle, twisted slightly from the short axis of the skull (Fig. 5).

Laterally, the squamosal defines the majority of the temporal emargination, and sutures posteriorly with the quadrate, which it overlaps to a large extent as the latter bone extends anteriorly to suture with the pterygoid. The ventral suture with the quadratojugal gently undulates, and is directed slightly posterodorsally. A large portion of the squamosal in the area of the temporal emargination is unsculptured. There is a thick ridge bordering the posterior part of the temporal emargination, possibly homologous to the tympanic ridge. A posterolaterally directed flange of the squamosal wraps on to the occiput, but this area cannot be observed directly because none of the specimens are exposed in occipital view. The quadrate foramen has been exposed in PIN (uncataloged), however, and is contained between the occipital flange of the squamosal, the quadrate, and the quadratojugal (Fig. 1).

The quadratojugal is thin anteriorly where it sutures to the posterior process of the jugal, but it expands posteriorly to a height that is about half of the total length of the bone, a morphology that is typical of parareptiles (Laurin and Reisz, 1995) (Figs. 2, 3). Its anterior edge forms the posterior border of the small temporal fenestra, with a process extending ventral and anterior to this structure to contact the maxilla. The quadratojugal forms the ventral portion of the temporal emargination, with its posterior edge overlapping the quadrate. The free posteroventral edge of the quadratojugal extends slightly below the

ventral edge of the maxilla, and on this portion of the bone the sculpturing becomes more ornate, with prominent tubercles visible on the ventrolateral flange, especially towards the posterior edge (Figs. 2, 3).

**Palate**—The vomer, the most anterior element of the palate, carries a shagreen of denticles on the ventral surface, although the anterior portion is obscured in PIN 4543/3 by the firm adduction of the mandible to the skull (Fig. 2). The vomer sutures anteriorly to the premaxilla and forms the anterolateral edge of the choana. Posterior to its suture with the premaxilla the vomer expands laterally, a structure termed the alar flange by Damiani and Modesto (2001). This flange results in the appearance of an inwardly curving, medially incised choana, a morphology that is a distinctive feature of pareiasaurs and some testudines. The vomer is very wide in *Macroleter* such that the alar flange closes off most of the anterior extent of the choana (Fig. 3). The ventral surface of the palate displays a prominent ridge of denticles on each side extending posteriorly along the suture between the pair of vomers. This ridge divides into two parallel ridges about halfway along the bone, and continues onto the pterygoid. The dorsal surface of the bone is smooth but bears, along with the palatine, part of the curving orbitonasal ridge for the articulation of the orbitonasal membrane, forming a depression for the parasagittal cartilage of the nasal capsule, a morphology very similar to that seen in captorhinids (Heaton, 1979). The vomer also displays a median dorsal flange that contributes to the nasal septum (Fig. 3). This distinctive feature was recently proposed as an autapomorphy of the pareiasaurian vomer (Damiani and Modesto, 2001), and its presence in *Macroleter*, along with the extensive alar flange also thought to be a pareiasaurian autapomorphy, serves to strengthen the plausibility of a close relationship between these taxa.

The palatine is a partially denticulate element articulating anteromedially with the vomer (Figs. 2, 3). Posteromedially the palatine forms a suture with the pterygoid, and its posterolateral border is formed on the dorsal surface by a suture with the ectopterygoid. However, the exact position of this latter suture cannot be seen in ventral view because the ectopterygoid is missing from PIN 4543/3. The ventral surface of the palatine bears denticles, most notably on the continuation of the anterolaterally directed ridges from the pterygoid in addition to a field of small denticles scattered over the surface (Fig. 2). Dorsally the palatine bears the posterior portion of the orbitonasal ridge that continues from the vomer. An anterior process of the palatine extends along the lateral edge of the choana to suture with the maxilla, approximately halfway to the front of the dorsal exposure of the choana. This morphology results in the palatine forming the entire posterior, and part of the lateral border of the choana, a feature also found in pareiasaurs and some testudines (Gaffney, 1979; Lee 1995, 1997a). Because of the wedge-shaped anterior extent of this process the internal naris does not run parallel to the maxilla for its entire extent, but rather is inflected medially along its posterior edge.

The pterygoid is the dominant element of the palate in *Macroleter*, and is broadly triangular in shape, contacting the vomer anteriorly, the palatine anterolaterally, the quadrate posterolaterally, and articulating posteriorly with the parabasisphenoid (Figs. 2, 3). On the ventral surface there is a high ridge bearing denticles that extends on a diagonal anterolaterally from close to the midline, dividing into two parallel ridges a short distance from its origin, which continue onto the palatine. The ventral surface of the pterygoid also bears a denticulated double ridge that lines the edge of the interpterygoid vacuity, continuing anteriorly along the median edge of each pterygoid and rostrally onto the vomer. There are denticles scattered over the anterior ramus of the pterygoid, but the remainder of the element is largely devoid of denticles. The suture between the pterygoid and the palatine on the ventral surface of the palate is angled

anteromedially, with the anterior process of the pterygoid extending just past the posterior end of the choana. On the dorsal surface seen in PIN (uncataloged), the pterygoid presents a tall thin flange of bone dorsally, which continues anteriorly past the main portion of the bone, medial to the vomer. This flange interdigitates with a smaller, but similar, flange of the vomer that projects posteriorly (Fig. 3). The combination of these two flanges serves to divide the interorbital region posteriorly, and anteriorly forms the ventral osseous portion of the internarial septum.

The two pterygoids meet anterior and posterior to the very short interpterygoid vacuity (Fig. 3), which is just less than 15% of the total length of the skull in PIN (uncataloged). A short interpterygoid vacuity is a character that defines the group including the bolosaurids, procolophonids and pareiasaurs. The dorsal surface of the pterygoid is smooth, and shows an odd suture pattern with the ectopterygoid. The pterygoid, in concert with the palatine, appears to incise the dorsal exposure of the ectopterygoid, dividing the latter bone into two sections.

The transverse flange of the pterygoid is recurved, and bears large and well-formed teeth. The largest of these teeth are gently fluted at the base, bearing a resemblance to those in the maxillary tooth row. These teeth also possess slight cutting edges, and appear to be implanted in a subthecodont fashion, with definite sockets visible where teeth have been lost (Fig. 2). Unlike most procolophonids, the transverse flange is extensively recurved, such that it is pointing almost directly laterally, and is rather large. This character has often been used to place the nycteroleterids in a more basal position within parareptiles, the more derived of which show an anteriorly or anterolaterally directed transverse flange (Laurin and Reisz, 1995; Lee, 1995).

The quadrate flange of the pterygoid is arcuate, presenting a thin, vertical flange in ventral view. As it projects dorsally the bone curves in a broad arc so that it is medially concave. It receives the long anterior flange of the quadrate on its lateral surface, but this area is obscured in each of the specimens, so the nature of the contact cannot be described in detail. Posteriorly, the pterygoid divides into a dorsolaterally directed quadrate flange, and a dorsomedially directed process for articulation with the parabasisphenoid that actually meets its mate at the midline (Figs. 2, 3), a morphology that is an apparent autapomorphy of the taxon. In the larger specimen (PIN 4543/3), this posterior process of the pterygoid appears to suture to the braincase (see PIN 4543/3), immobilizing the area. This condition is considered to be an autapomorphy of pareiasaurs that seems to have convergently evolved in the group consisting of *Acleistorhinus* and the lanthanosuchids (deBraga and Reisz, 1996). In dorsal view, the process by which the pterygoid articulates with the parabasisphenoid displays a dorsally directed flange that appears to preclude an anterior projection of a cultriform process (Fig. 6).

The ectopterygoid exhibits an interesting morphology on the dorsal surface, appearing as two separate sections (Fig. 3). It is not possible to observe the ventral surface of the ectopterygoid in any of the specimens, because in PIN 4543/3 it is lost on one side and obscured by the lower jaw on the other. Therefore it is impossible to determine if this element demonstrates the parareptilian synapomorphy of being edentulous. It is, however, significantly smaller than is indicated in the initial reconstruction (Tverdokhlebova and Ivakhnenko, 1984), and does not continue onto the transverse flange of the pterygoid (Figs. 2, 3). Anteriorly the ectopterygoid sutures with the palatine, and close to the convergence of these two bones with the jugal a small suborbital foramen is present, a reptilian synapomorphy (Reisz and Laurin 1995), though it appears in slightly different positions on either side of the specimen. In dorsal view, the main portion of the ectopterygoid consists of a small, subtriangular piece bordered by the palatine anteriorly and the jugal laterally, forming the anterolateral border of the subtemporal fenestra. The other por-

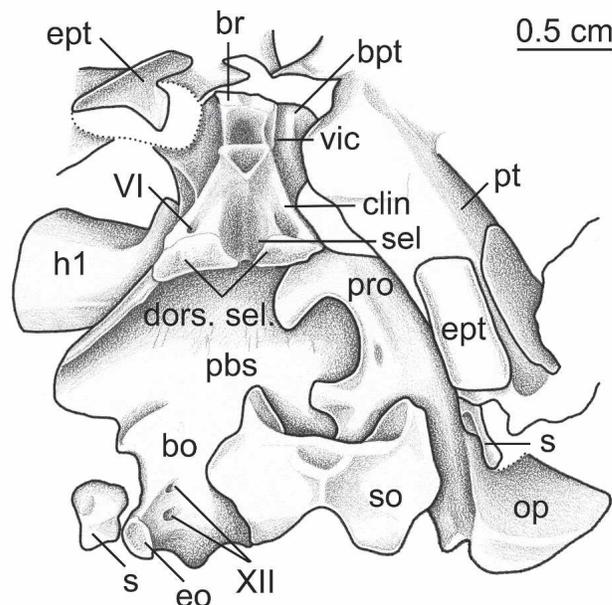
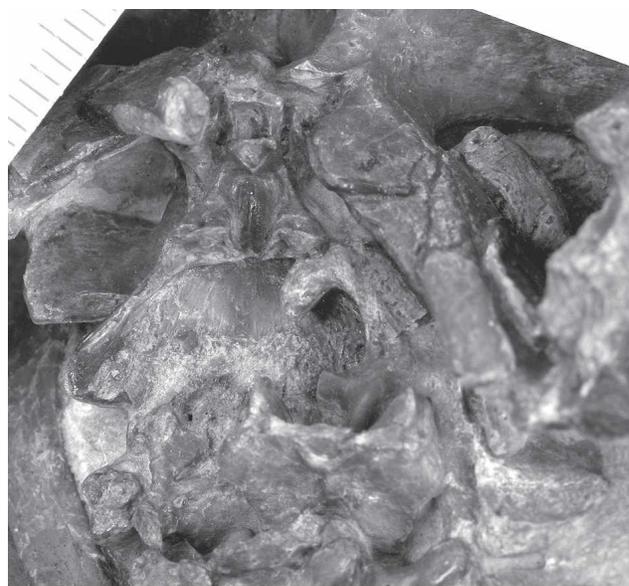


FIGURE 6. Braincase of *Macroleter poezicus* (PIN (uncataloged)) in dorsal view.

tion of the ectopterygoid exposed on the dorsal surface of the palate is slightly smaller than the other, and its anterior border lies along the pterygoid-palatine suture (Fig. 3). The two separate portions of the ectopterygoid present on the dorsal surface indicate that the ventral exposure of the bone is likely more extensive than the dorsal. A similar view of the dorsal surface of the palate has been exposed in *Procolophon*, and though the ectopterygoid has not been divided into two parts, it shows a similarly restricted dorsal exposure, along with a more conventional ventral morphology (Carroll and Lindsay, 1985).

The left epipterygoid is well preserved in PIN (uncataloged), and appears to have remained in place (Fig. 3). The base is sub-triangular and lamellar in form, where it is closely applied to the pterygoid. Dorsally, it narrows and rounds out to become cylindrical in shape, angling slightly medially, the typical morphology for tetrapods (Romer, 1956). This is the process by

which the palate would have braced against the skull roof, with the unfinished dorsal tip in *Macroleter* indicative that this contact was most likely via a cartilaginous connection in this animal. In lateral view the epipterygoid can be seen just poking out above the broken portion of the skull (Fig. 3), and falls short of making contact with the skull roof. There is also no indication on the underside of the skull roof where this attachment would have occurred, supporting the inference that the articulation was cartilaginous. In *Macroleter*, the epipterygoid does not take part in the basiptyergoid articulation.

The quadrate is largely obscured from ventral view in the specimens available for examination at this time due to the attachment of the mandible to the skull. A sliver of the quadrate can be seen in lateral view (Fig. 3), but the posterior flanges of the quadratojugal and the squamosal cover the majority of the lateral surface. The occipital flange of the squamosal obscures the quadrate as it extends dorsally, with the quadrate interposed between the squamosal medially and the pterygoid laterally as it approaches the skull roof. The anterior ramus of the quadrate by which it contacts the pterygoid is long, extending approximately two-thirds of the length of the pterygoid, and it broadly overlaps this bone medially.

**Braincase**—There is a rare opportunity to examine the braincase of *Macroleter* whereby the skull roof can be removed (and replaced) in PIN (uncataloged). The braincase can thus be observed in dorsal view, and this feature, combined with the well-preserved ventral surface of PIN 4543/3, allows for a thorough description. Detailed descriptions of parareptilian braincases are rare (Ivakhnenko, 1973; Kemp, 1974; Spencer, 2000), but most of the general features and much of the anatomy is comparable to modern reptiles (Carroll and Lindsay, 1985). Despite the fact that PIN (uncataloged) is immature and lacks some fully ossified bones, many of the elements of the braincase have fused, suggesting that those of a full-sized individual would have been quite massive and fully fused.

The parasphenoid consists of the sheath of dermal bone underlying most of the braincase and forming the cultriform process when this structure is present. This bone is partially sutured to the basisphenoid, and in many parts of the braincase these two elements are indistinguishable. Unless specifically referring to one or the other of the fused elements, the structure will henceforth be referred to as the parabasisphenoid.

The single, median parabasisphenoid is a complicated structure. Anteriorly, the basiptyergoid processes of *Macroleter* show a different morphology from those of known procolophonids (Ivakhnenko, 1973; Carroll and Lindsay, 1985; Spencer, 2000), as those of the latter project anterolaterally from their origin on the anteromedial surface of the parabasisphenoid, and are separated medially by the basisphenoid rostrum (sensu Spencer, 2000), which normally bears the cultriform process. The basiptyergoid processes of *Macroleter*, on the other hand, are small and project directly anteriorly, with only a small space between them. Ventrally, the suture between the parabasisphenoid and the pterygoids is tightly convoluted, and the processes themselves are very short (Fig. 2). A great deal of infolding can be seen on the ventral surface in PIN 4543/3, with the basiptyergoid processes sutured firmly to the pterygoid, and there is no doubt that very little kinesis was possible in this area. This area does not appear to be so closely attached in the dorsal view of PIN (uncataloged), although the basiptyergoid processes are still short and anteriorly directed with little separation between them (Fig. 6). This difference in joint morphology may be because the latter specimen is immature, and the area has yet to fully ossify. A fused basiptyergoid joint is a synapomorphy of pareiasaurs, and also occurs convergently in *Lanthanosuchus*. Its presence in *Macroleter* is recognized here for the first time.

At the anteromedial end of the parabasisphenoid is the dorsal body, or basisphenoid rostrum (Fig. 6). It is from this structure

that the cultriform process of the parasphenoid extends when present, but similar to the morphology of *Leptopleuron* (Spencer, 2000), there is no discernable trace of this structure in *Macroleter*. Rather, the dorsal body extends anterodorsally in high relief, and does not continue anteriorly. The cultriform process is a shortened structure in procolophonids and pareiasaurs, but rarely to the extent seen here. Caudal to the dorsal body lies a significant depression, the sella turcica (termed the retractor pit by Heaton, 1979), in which would have lain the pituitary body (Fig. 6). Rising posterodorsally on either side of this depression are the clinoid processes, which are smooth and rounded on the medial and lateral sides, and flare both dorsally and mediolaterally from their origin at the base of the dorsal body. There is a foramen piercing the posterodorsal end of the clinoid processes for the passage of cranial nerve VI, almost identical to the morphology seen in millerettids (Gow, 1972). The nerve would have passed from the floor of the braincase posteriorly through the foramina to the pituitary fossa then extended laterally into the orbit (Romer, 1956). The two clinoid processes are generally connected transversely by a vertical sheath of bone; the dorsum sellae. In PIN (uncataloged), however, the clinoid processes end in unfinished bone, and no transverse sheet is present. It is possible that the dorsum sellae was lost or broken, or it is also likely that it had yet to fully ossify in this specimen.

The parasphenoid sheath of this bone complex is visible in ventral view, and consists of a constricted waist that flares posteriorly (Figs. 2, 6). A notable feature of the ventral surface of this element is the presence of paired excavations for the insertion of the hypaxial cervical musculature, almost identical to those found in mesosaurs (Modesto, 2006). Most other parareptiles lack this feature, with the ventral surface of the parasphenoid being smooth, or bearing a paired or a single median tubercle. Posteriorly the parasphenoid sutures with the basioccipital.

The supraoccipital is a single, median element that is dorsoventrally flattened. It is present in PIN (uncataloged), but is not in place because it has fallen anteriorly, leaving only the dorsal surface readily available for observation (Figs. 3, 6). The element is slightly ventrally concave, and contains a low median sagittal ridge that is typical for parareptiles, as is the notable reduction in the lateral extent of the bone. There is an anterior semi-circular crest whose apex is centred on the median sagittal ridge (Fig. 6), which serves as the surface for articulation dorsally with the postparietal. The supraoccipital, when in place, would have angled posteroventrally, with the posterior edge forming the dorsal border of the foramen magnum. A central notch in the posterior edge of the bone results in a foramen magnum that has been reconstructed as keyhole shaped (Fig. 1).

The left exoccipital is exposed in dorsal view in PIN (uncataloged) (Fig. 6), and in PIN 4543/3 careful preparation has revealed much of the dorsal and part of the lateral surface. No suture can be discerned between the exoccipital and the basioccipital on the lateral surface, and perhaps PIN (uncataloged) is a juvenile, most of the dorsal process for articulation with the supraoccipital has been broken, or was not fully ossified and subsequently drifted away. In PIN 4543/3, however, nearly the entirety of the exoccipitals can be seen, revealing the dorsal, and a good deal of the lateral surface of the bones. At the base of the exoccipital where it meets the basioccipital, two foramina are present for the passage of cranial nerve XII. Two of these foramina can be seen on the medial surface in PIN (uncataloged), and presumably the same two can be seen continuing through to the lateral surface in PIN 4543/3.

The two exoccipitals meet below the foramen magnum, excluding the basioccipital from the posterior part of this structure (Fig. 2). From their ventral origin in chunky, boot shaped bases, the exoccipitals rise as small columns that form the lateral margins of the foramen magnum. The dorsal processes of the

exoccipitals have both a medial and a lateral projection, of which the medial is more extensive. It has been noted in some pareiasaurs that the medial process of the exoccipital is larger than the lateral, a feature clearly visible in the rare occurrence of an isolated pareiasaurian exoccipital (Jalil and Janvier, 2005). In fact, a case has been noted in the pareiasaurs *Bradysaurus baini* where the exoccipitals meet dorsally, excluding the supraoccipital from the foramen magnum (Haughton, 1929), but since isolated or unfused elements are rarely found, it is difficult to determine how prevalent this feature is. In *Macroleter* it is evident that the exoccipitals would not have met at the midline. The smaller lateral process of the exoccipital is also prominent, and would have extended a significant distance under the paroccipital process of the opisthotic (Fig. 2). This morphology is considered to be a pareiasaurian synapomorphy, although it is often difficult to discern in pareiasaurs because of the fusion of many of the braincase elements (Lee, 1997a).

In ventral view, the basioccipital sutures with the basisphenoid anteriorly via an undulating suture with a median apex oriented anteriorly (Fig. 2). The basioccipital is excluded from the posterior portion of the foramen magnum by the convergence of the two exoccipitals, but it forms the ventral part of the tripartite occipital condyle. It is difficult to discern the exact structure of the dorsal surface of the basioccipital, as in PIN (uncataloged) it appears to be fused with the dorsally projecting exoccipitals, and the suture with the anterior parasphenoid appears to be cartilaginous (Fig. 3). This condition may be due to the immaturity of the individual specimen, but it has been noted in other parareptiles that this area is often incompletely ossified resulting in a basicranial fissure (Laurin and Reisz, 1995; Lee, 1995, 1997a). Posterior to the suture with the parasphenoid the basioccipital is quite rugose.

The right prootic is visible in PIN 4543/3, but has fallen onto the floor of the braincase and has collapsed outwards, leaving only the medial surface visible (Figs. 3, 6). The anterior extent of the bone has a ventrally projecting process that would have approached the clinoid process of the parabasisphenoid. This anterior process is rounded anteriorly, but no obvious articulation surface can be identified. Dorsally the prootic typically supports the supraoccipital, but again no surface for articulation can be discerned, in part because the dorsal edge of the bone cannot be seen. A small foramen midway along the bone would have served for the passage of cranial nerve VII. Posteriorly the prootic contacts the opisthotic, and usually contributes a small part to the paroccipital process, but the two bones have indistinguishably fused in PIN (uncataloged). The anterior part of the foramen ovalis is bordered by the prootic, and receives the footplate of the stapes (Romer, 1956).

There is an anteroventrally directed process of the opisthotic that interrupts the fenestra ovalis, and the stapes would have sat between this process and the anterior border of the fenestra formed by the prootic. This morphology bears a striking resemblance to that of *Proganochelys* (Gaffney, 1990). Posteriorly the opisthotic forms the majority of the paroccipital process, which serves to brace the braincase against the skull table. The paroccipital process itself is a flattened flange of bone that flares slightly towards the distal end. In PIN 4543/3, the opisthotic, undoubtedly forming the majority of the paroccipital process, is in place and can be traced up to the contact with the skull roof, where it fits into a process within the squamosal, and also appears to make contact with the overlying supratemporal (Fig. 2). Though the skull is not visible in occipital view, it is clear that the direction of the paroccipital process is dorsolateral rather than strictly lateral as it is in most diapsid reptiles and primitive colophonoids (sensu Lee, 1995).

**Lower Jaw**—The lower jaw in each of the specimens available for study is attached to the skull, and therefore some elements are difficult to describe, particularly the dorsal aspects. Overall it

appears to be fairly conservative in morphology, not differing in any great respect from other more basal parareptilian taxa. It is, however, fairly robust and relatively tall in lateral aspect.

The dentary is the tooth-bearing bone of the lower jaw, forming the majority of the anterolateral surface of this structure, as well as being the only element involved in the symphysis. It has only mild sculpturing on the lateral surface of the bone, and this surface bears a number of foramina and small pores (Figs. 2, 3). On the anteromedial surface, a short distance away from the symphysis, there are small excavations on each side to receive the splenials (Fig. 7), along with a ridge demarcating the location medial to which the splenials would have articulated. Posteriorly the medial surface of the dentary bears the anterior portion of the Meckelian canal, which begins at the adductor (or mandibular) fossa and proceeds as a deep excavation anteriorly. Laterally the dentary overlaps the anterior tip of the angular and the surangular (Fig. 2). It is impossible to determine the number of teeth or their morphology due to the occlusion of the lower jaw to the skull.

Anteriorly, the splenial forms the medial edge of the lower jaw, running along much of the length of the dentary (Figs. 2, 7). It cannot be seen in lateral view in PIN (uncataloged), though in ventral view it appears that a very small portion would wrap onto the lateral surface (Fig. 2). This bone is excluded from the symphysis by a slight posterior projection of the dentary. Additionally, the splenial demonstrates the forked-shaped morphology common to parareptiles (Lee, 1995), with both a dorsal and a ventral 'tine' (Fig. 7), the dorsal tine being slightly shorter than the ventral. A small foramen can be seen on the medial surface, which is the anterior segment of the foramen intermandibularis

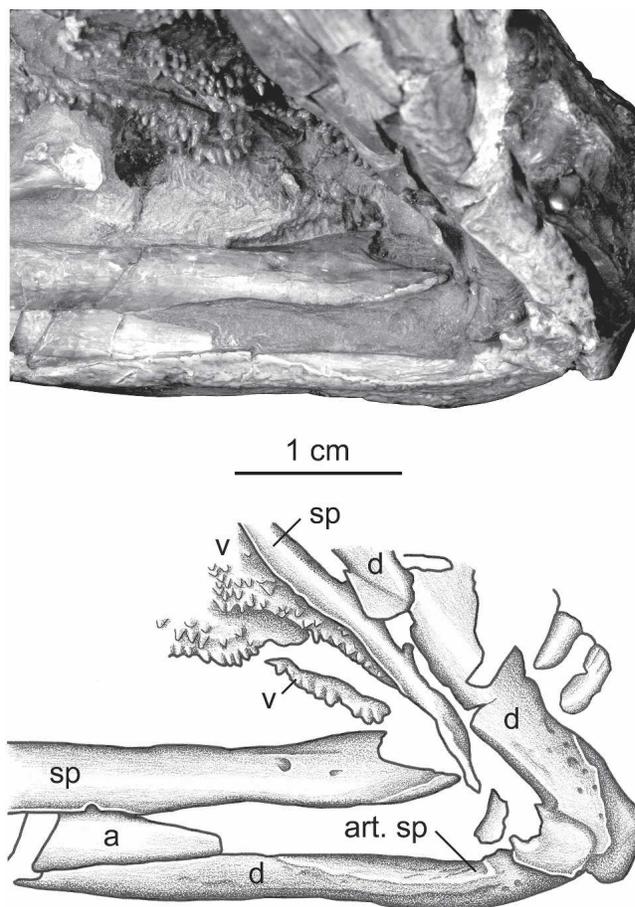


FIGURE 7. Lower jaw and ventral surface of palate of *Macroleter poezicus* (PIN (uncataloged)) in ventromedial view.

(the foramen intermandibularis oralis of Heaton, 1979). The posterior part of the intermandibular foramen (foramen intermandibularis caudalis of Heaton, 1979) can be seen enclosed between the splenial, prearticular, and angular. Posteriorly the splenial overlaps the anterior end of the prearticular.

Very little of the coronoid is visible in the available specimens of *Macroleter*, although the top of the coronoid process can be seen in the dorsal view of PIN (uncataloged) (Fig. 3). This process appears to be well defined, and composed primarily of the single coronoid.

The anterior part of the prearticular lies between the splenial medially and the angular laterally. The posterior end of the prearticular of PIN 4543/3 has been fragmented, but can be seen to have covered the medial surface of the articular. The posterior end closely approaches but does not extend beyond the base of the retroarticular process.

The surangular forms the dorsal part of the lateral surface of the mandible, and is slightly sculptured on its lateral surface (Figs. 2, 3). It sutures ventrally with the angular, and its posterior border overlies the lateral exposure of the articular. Also on the lateral surface, the dorsal portion of the surangular is deflected outwards, forming a shelf. The size of this feature, however, may have been exaggerated in PIN 4543/3 and PIN (uncataloged) due to the crushing associated with the skull being forced down onto the lower jaw.

The large angular forms the ventral extent of the lateral surface of the lower jaw, constituting about half its total length (Figs. 2, 3). Its lateral surface is characterized by faint sculpturing consisting of a series of shallow intricate ridges. Dorsally, the angular forms a roughly horizontal, though slightly wavering suture with the surangular. The angular sutures anteriorly with the dentary and underlies it as the dentary wraps around the ventral surface of the jaw. Ventrally, the angular can be seen extending medial to the dentary, its anterior extent covered by an overlapping portion of the splenial (Fig. 2).

A small sliver of the articular is visible on the lateral surface of the lower jaw, and is just visible projecting posterior to the angular (Fig. 3). The retroarticular process can be partially reconstructed, because both the lateral and a portion of the medial surfaces can be seen in two of the specimens. It appears to retain the procolophonian morphology of being transversely expanded and dorsally concave (Laurin and Reisz, 1995). In PIN 4543/3, a dorsal projection of the articular has been crushed inwards, with the mesial side of this process becoming visible in ventral view (Fig. 2). It is clear from what can be seen in this view that the retroarticular process is concave dorsally from the area of articulation, ending in a tall pointed process. This process is overlain medially by a thin sheath of the prearticular, but it is quite large and robust considering the size of the animal.

**Hyoid Apparatus**—*Macroleter* possesses a large ossified hyoid apparatus, a feature shared with a number of other parareptiles, including *Procolophon*, *Owenetta*, and various pareiasaurs (Lee, 1995; Reisz and Scott, 2002). The larger, median element, which is referred to by some as the copula or the corpus hyoideum (Reisz and Scott, 2002), is approximately 16 mm in width, and is shaped like a bow tie, with a central constriction, and two flaring ends (Fig. 2). The ossification of this element may be a common feature of the Parareptilia, as first noted by Gow (1977), but as it is not sutured to any other element, it is easily lost. This structure exists in modern reptiles but is primarily cartilaginous. A potential ossified basibranchial has recently been found in the early eureptile *Protorothyris* (J. Müller, pers. comm., November 2005), suggesting its ossification may in fact be primitive for early amniotes. The other element of the hyoid apparatus is the ceratohyal, which is roughly an elongated cone shape (Fig. 2). This paired element would have attached to either end of the copula.

## PHYLOGENETIC ANALYSIS

A phylogenetic analysis of 16 taxa was completed to determine the position of *Macroleter poezicus* within the parareptiles. Thirteen Paleozoic and Early Mesozoic ingroup taxa were considered in the present analysis: *Eunotosaurus*, Millerettidae, *Acleistorhinus*, *Lanthanosuchus*, *Eudibamus*, *Belebey*, *Procolophon*, *Owenetta*, *Barasaurus*, *Nyctiphruetus*, *Macroleter poezicus*, *Bradysaurus*, and *Scutosaurus*. Three outgroup taxa, Synapsida, Captorhinidae, and Mesosauridae, were included in the analysis. Synapsida is a large, diverse group that was scored following the methodology of Laurin and Reisz (1995), whereby coding was based on a composite of four basal synapsid groups to try to determine the ancestral state for the node.

The analysis consisted of 89 characters (see Appendix 1 for character list, Appendix 2 for character matrix). The majority of the characters were taken from Reisz and colleagues (in press), which was in turn based on Laurin and Reisz (1995), with two new characters added (40, 45). Since this investigation involved the study of the cranial anatomy of *Macroleter*, the focus was on the addition and redefinition of cranial characters. Characters for taxa other than *Macroleter* were scored either based on information from previous analyses or descriptions of specific taxa in the literature (including Laurin and Reisz, 1995; Lee, 1995, 1997a, b; Meckert, 1995; deBraga and Reisz, 1996; deBraga and Rieppel, 1997; Modesto, 1999a, 2006; Reisz et al., in press). The data set was analysed using the branch-and-bound parsimony algorithm in PAUP\* 4.0b10 (Swofford, 2002). Character states were optimized using the DELTRAN algorithm, were all weighted equally, and left unordered. To assess the robustness of the topology, a bootstrap analysis was run using a heuristic search with random step-wise addition, with 100 repetitions for 1000 replicates. A decay analysis was also performed.

## Results

A single most parsimonious tree was found, with a length of 205 steps (Fig. 8). The consistency index (CI) was 0.5561, and 0.5473 when uninformative characters were excluded. The homoplasy index (HI) was 0.4439. The retention index (RI) was 0.6750, and the rescaled consistency index (RC) was 0.3754. The results of the bootstrap analysis, along with the decay indices are displayed in Figure 8. Nodes were assigned letters for discussion.

## DISCUSSION

### Phylogenetic Implications

The phylogeny produced by this analysis differs substantially from that of other recent studies (Lee, 1997a; Jalil and Janvier, 2005), which suggested that a strongly supported, monophyletic Nyctiphruetia (including the nyctiphruetids and the nycteroloterids) formed the sister group to Clade H (Lee, 1997a). The present study does not replicate these results, although this may be in part because 'nyctiphruetians' are poorly known in the literature. The results of this analysis preclude a monophyletic Nyctiphruetia; forcing *Macroleter* and *Nyctiphruetus* to be monophyletic resulted in a tree three steps longer than the 205 of the most parsimonious reconstruction. However, 19.1% of the characters could not be scored for *Nyctiphruetus*, including all lower jaw characters, because no description or illustration of these elements exists in the literature. This missing data may be the cause of the low bootstrap support (45%) for Node K. Although it has been argued that the presence of missing data has little influence on the topology of a tree, assuming the characters have been scored correctly (Kearney, 2002; Kearney and Clark, 2003; Müller, 2004), the inclusion of more data would likely either improve support for the current grouping, or support a monophyletic Nyctiphruetia. Indeed, if *Nyctiphruetus* is re-

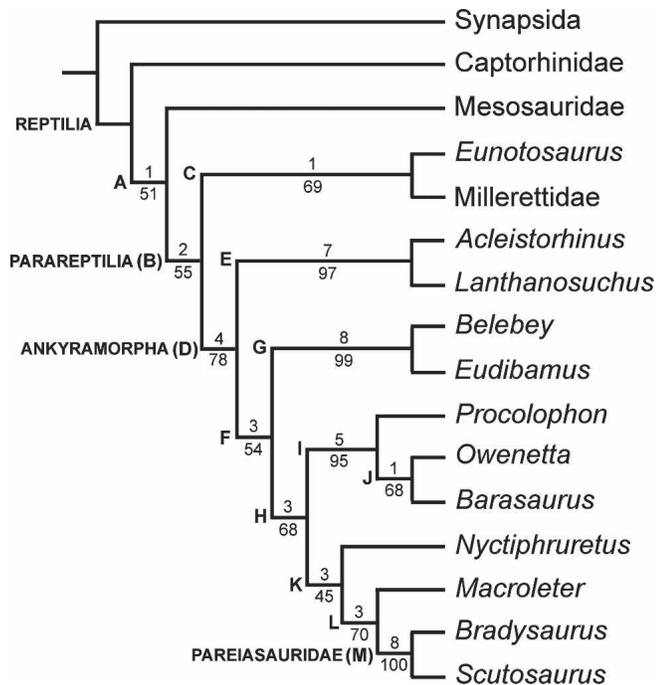


FIGURE 8. Single most parsimonious pattern of parareptilian interrelationships obtained in the phylogenetic analysis. Support values for clades are listed on the branch leading to the node, with decay index above and bootstrap support (percentage) below the branch.

moved from the analysis, the CI of the resulting phylogeny is higher (0.5787), and the bootstrap support for some of the other clades in the analysis increases. The bootstrap support for Node L increases to 74%, and support for Node H increases to 71%, and the decay indices for nodes J and L increase by one step. These differences suggest that *Nyctiphruetus* is a problematic taxon, with conflicting data suggesting multiple possible topologies, and certainly requires further study. It has been suggested that nyctiphruetids are more closely related to procolophonids, whereas nycteroleterids are more closely related to pareiasaurs (Tverdokhlebova and Ivakhnenko, 1984; Ivakhnenko, 1987, 1991). Thus, there exists the possibility that the two taxa do not form a monophyletic group. It is interesting to note that after examining *Nyctiphruetus* material, the reconstruction produced by Lee (1997a) differed substantially from those previously published (Efremov, 1940; Ivakhnenko, 1979). An in depth study of the *Nyctiphruetus* may result in the further alteration of the phylogenetic position of the taxon. *Macroleter*'s relationship to the other nycteroleterids is also not quite certain. Very little is known about the other members of the group, or if it is indeed monophyletic. At this point it is only assumed that the clade is monophyletic and only examination of the other taxa, such as *Bashkyroleter* and *Nycteroleter*, and their inclusion in a phylogenetic analysis can definitively resolve the issue.

One of the most interesting results of this study is the position of *Macroleter* as the sister taxon of Pareiasauridae. As a group, pareiasaurs are extremely autapomorphic and well differentiated from all other parareptiles; it takes eight additional steps to decay the node, which is supported by a 100% bootstrap value. Whereas some researchers believe *Lanthanosuchus* and *Sclerosaurus* to be the closest relatives of pareiasaurs (Lee, 1995, 1997a; Jalil and Janvier, 2005), in other analyses, including this one, the lanthanosuchoids fall outside the group that includes procolophonids and pareiasaurs. In addition, re-examination of *Sclerosaurus* has caused many scholars to consider this taxon a derived

procolophonid (Cisneros et al., 2005; R. Reisz, pers. comm., February 2005), although this identification is not universally accepted (Spencer and Storrs, 2002); an extensive revision of this taxon is clearly necessary. In recent analyses where it was included, *Macroleter* fell out as the sister taxon to the group that included pareiasaurs and procolophonids (deBraga and Reisz, 1996; deBraga and Rieppel, 1997; Hill, 2005). Thus, to find that it is in fact more closely related to pareiasaurs contributes significantly to our understanding of the evolution of this highly derived clade. Russian researchers have already suggested the possibility of a close relationship between the nycteroleterids and pareiasaurs (Ivakhnenko et al., 1997), and the present study is the first phylogenetic analysis supporting these predictions. *Rhipaeosaurus tricuspidentis*, a Russian taxon initially thought to be a pareiasaur (Ivakhnenko, 1987), is now considered to be a large nycteroleterid (Lee, 1995), and the present study actually reconciles these two classifications. It has been suggested that the large *Rhipaeosaurus* may in fact be referable to the genus *Macroleter* (R. Reisz, pers. comm., February 2005).

### **Macroleter and Temporal Fenestration in Parareptiles**

The nomen Anapsida has been frequently applied to taxa both within and including the parareptiles, but as increasing numbers of parareptiles are found to possess lower temporal fenestrae, it becomes clear that presence of fenestrae may in fact be a synapomorphy of the group (Cisneros et al., 2004). Initial descriptions of *Macroleter* made no mention of the presence of a lateral temporal fenestra, perhaps because poor preservation obscured this feature. All specimens of this taxon that were examined over the course of this study, however, possess a small lower temporal fenestra bordered anteriorly by the jugal, dorsally by the squamosal, and posteriorly by the quadratojugal. The presence of a lower temporal fenestra appears to be a plastic character in parareptiles, appearing in many parareptilian lineages throughout the Permian and Triassic. In millerettids the presence of a temporal fenestra appears to vary even between individuals of differing ontogenetic stages (Gow, 1972). Whereas the formation of lateral temporal fenestrae has been attributed to an increase in the area for jaw musculature or a reduction of the weight of the skull (Frazetta, 1968; Tarsitano et al., 2001), the very small size of this feature in *Macroleter* raises doubts about a strictly functional purpose in this taxon. The term Anapsida continues to be used occasionally to define groups inclusive of Parareptilia (Modesto, 1999a; Reisz and Scott, 2002) but there is a general desire to abandon the use of this name (Modesto and Anderson, 2004) because it is based on a feature not possessed by a number of its members (Cisneros et al., 2004).

### **Temporal Emarginations in Parareptiles**

A temporal emargination is a feature that is present in the majority of parareptilian, but few other amniote taxa. Believed to support a tympanum, the otic notch appears at the base of Parareptilia. The morphology of the emargination, however, is different from that of the anamniotes. While mesosaurs lack a temporal emargination, basal parareptiles possess an emargination bordered by the quadratojugal and the squamosal, a morphology also shared by the procolophonoids, *Nyctiphruetus* and *Macroleter*. *Acleistorhinus*, *Lanthanosuchus* and pareiasaurs, on the other hand, have a temporal emargination that faces posteriorly and is exposed on the occiput, and is bordered by the squamosal, the quadratojugal, and the quadrate. This morphology appears to be convergent among these taxa, however, given the phylogeny, but the evolutionary pattern certainly raises interesting issues with regards to the function and evolution of this feature.

### The ‘Supernumerary Bone’ in Pareiasaurs

The identity of the ‘extra ossification’ on the posterior surface of the skull roof in pareiasaurs has been the subject of frequent speculation over the years. Wild (1985) identified the ossification as the tabular, whereas other researchers contend that it is a cervical osteoderm that has been incorporated into the skull (Brink, 1955; Walker, 1973 in Lee et al., 1997). The most recent argument asserts that this element is in fact a neomorphic ossification (Lee, 1997a; Lee et al., 1997; Spencer and Lee, 2000; Jalil and Janvier, 2005). However, the presence of the tabular bone in *Macroleter* and this taxon’s close phylogenetic affinity to pareiasaurs suggest that this ossification in pareiasaurs is in fact the tabular. This ‘supernumerary bone’ appears to be, in all respects, merely the tabular that has moved, along with the post-parietal, to the dermal skull roof. Lee et al. (1997) argue that the closest outgroups to pareiasaurs do not have a tabular, but the phylogeny presented in this paper suggests that possession of the tabular is primitive for parareptiles, and that successive pareiasaurian outgroups (*Macroleter* and *Nyctiphruetus*) possess a tabular. Two of the most basal pareiasaurs, *Bradysaurus* and *Embrithosaurus*, are not known to have a bone in this position, but, as in all pareiasaurs, the cranial sutures are very difficult to discern. In the reconstructions of these pareiasaurs many sutures, especially those in the postparietal region, are uncertain. The presence of a supernumerary element has been ‘discovered’ in other pareiasaurian taxa upon closer inspection (Jalil and Janvier, 2005), and because the element appears to be smaller in the more basal pareiasaurs, the possibility exists that it is difficult to distinguish in the basal taxa. Even so, in non-pareiasaurian parareptiles, it appears that the tabular bone was reduced or lost only in the procolophonoids (*Procolophon* + *Owenetta* + *Barasaurus*) and *Lanthanosuchus*. To examine the evolution of the tabular, the presence of the element was mapped onto the phylogeny produced in this analysis. To avoid circularity, all characters involving the presence of a tabular (16, 17) were removed from the analysis, and it was run again without these characters (arguments for and against this practice; Kluge and Wolf, 1993; de Queiroz, 1996 vs. Grandcolas et al., 2001). The topology of the tree remained the same, and when the character was mapped onto the cladogram, each outgroup to pareiasaurs, excluding procolophonoids and *Lanthanosuchus*, was found to possess a tabular (Fig. 9). Even if the monophyly of *Macroleter* and pareiasaurs should not stand up to further scrutiny, the most parsimonious optimization of that character dictates that the possession of the tabular is primitive for parareptiles and was lost convergently three times in *Lanthanosuchus*, procolophonoids, and possibly the basal pareiasaurs.

The identification of this element as a tabular has also been called into question because of its position on the skull. Lee and colleagues (Lee et al., 1997) argue that the position of this element in pareiasaurs is not the same as the position of the tabular in other early amniotes, correctly stating that the tabular is primarily an occipital bone in all other parareptiles that possess it. It is important to note, however, that the postparietal, a bone that is integrated into the skull table in pareiasaurs, is also primarily an occipital element in all other amniotes. It follows logically that both elements moved together onto the skull table in pareiasaurs as the occipital region of the skull was elongated. Positional homology supports the identity of the bone as a tabular. Lee et al. (1997) dismiss the possibility that the element can be identified as the tabular because it lies medial to the supratemporal. It is true that when it is present, the tabular in some Paleozoic taxa runs posterior to the supratemporal to contact the squamosal (Laurin and Reisz, 1995), but the derived condition within Tetrapoda appears to consist of an occipital tabular that is bordered laterally by a large supratemporal (Berman, 2000). In the parareptiles in which it is known, except notably in *Acleisto-*

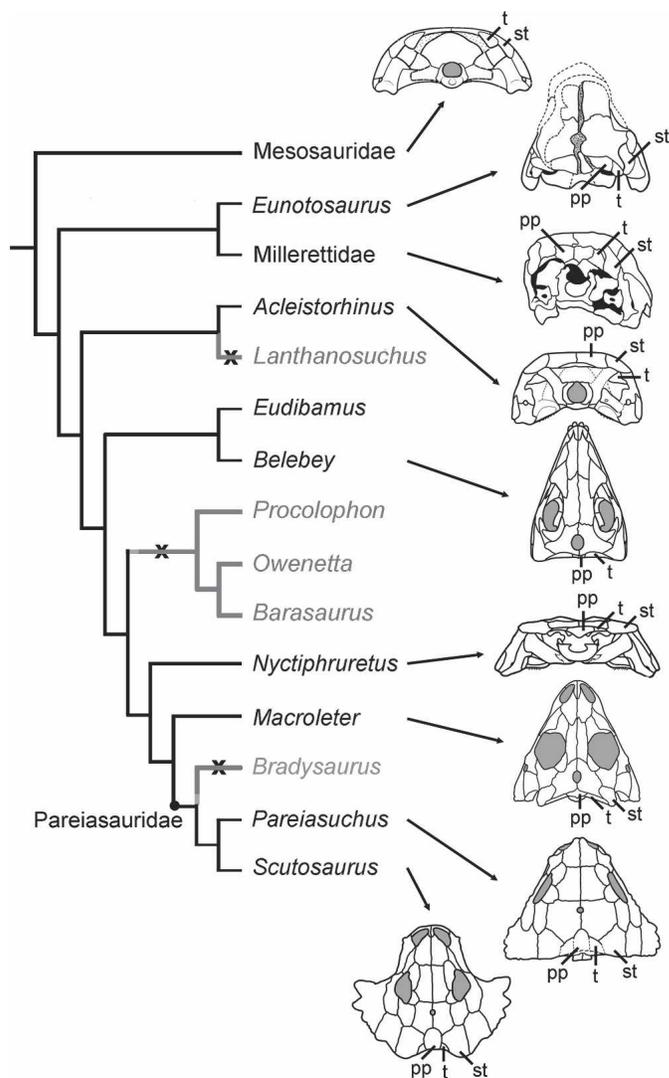


FIGURE 9. Phylogeny from this analysis indicating presence (in bold) and position of tabular, postparietal, and supratemporal. ‘x’ represents loss of tabular. Abbreviations listed in text. Outlines adapted from (top to bottom): Modesto, 2006; Gow, 1997; Carroll and Lindsay, 1985; de-Braga and Reisz, 1996; Reisz et al., unpubl. data; Carroll and Lindsay, 1985; this study; Lee, 1997a; Lee, 1997a.

*rhinus*, the tabular is always located posterolateral to the post-parietal and medial to the large supratemporal, the exact position of the ‘supernumerary element’ in pareiasaurs (Fig. 9). The topological relationship of the two elements in these two closely related taxa is the same, and allows for a primary assumption of homology (Rieppel and Kearney, 2002). Given that Hennig’s auxiliary principle states that homology must be assumed given the absence of evidence to the contrary (see Wiley et al., 1991), there is no evidence to suggest that pareiasaurs would have lost the tabular only to develop a new bone in a homologous position. Even if *Bradysaurus* and *Embrithosaurus* have lost this feature, it is still the more parsimonious solution to assume that the bone was lost in these taxa alone. Thus, the primary assumption of homology based on positional similarity, combined with information derived from the phylogenetic analysis, results in the conclusion that this element is in fact a tabular. A neomorphic bone appearing convergently in a position homologous with that of the tabular, in the skull of a group in which the fusion of skull elements frequently occurs seems highly unlikely. There appears

to be a trend towards cranial simplification in tetrapods in general, and the acquisition of neomorphic ossifications in amniotes is extremely rare (Sidor, 2001).

### CONCLUSION

An in-depth phylogenetic study of the cranial anatomy of *Macroleter poezicus* results in a tree showing a close relationship between the pareiasaurs and *Macroleter*, a relationship often postulated but only now supported by a phylogenetic analysis. It appears to be increasingly important to determine the relationships between the Russian nycteroleterids and nyctiphuretidids and the relationship of these taxa to other parareptiles, especially to pareiasaurs. The phylogeny of pareiasaurs in particular is an interesting issue, with very little description of known taxa, and few existing phylogenetic analyses of this significant, yet enigmatic clade. Further studies of poorly known parareptilian taxa will not only potentially help to shed light on the origins and relationships of turtles, but will also foster a greater understanding of amniote evolution.

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- APPENDIX 1. Description of characters used in the phylogenetic analysis.
- Narial shelf: absent (0); present (1). (Laurin and Reisz, 1995 no. 1)
  - Frontal orbital contact: present (0); absent (1). (Modified from Laurin and Reisz, 1995 no. 2)
  - Frontal lateral lappet: absent (0); large, occupies at least one-third of the dorsal margin of the orbit (1). (deBraga and Reisz, 1996 no. 7)
  - Pineal foramen position: in the middle of the body of the parietal (0); displaced posteriorly (1); displaced anteriorly (2); absent (3). (deBraga and Rieppel, 1997 no. 49)
  - Postparietal: paired (0); median (1); greatly reduced or absent (2). (Modified from Laurin and Reisz, 1995 no. 4)
  - Postparietal position: occipital (0); dorsally exposed, integrated into skull table (1). (Modified from Laurin and Reisz, 1995 no. 5)
  - Prefrontal-palatal contact: absent (0); weak (1); strong (2). (Laurin and Reisz, 1995 no. 6)
  - Prefrontal medial flange: narrow (0); wide (1). (Laurin and Reisz, 1995 no. 7)
  - Bulbous medial process of prefrontal: absent (0); present (1). (Laurin and Reisz, 1995 no. 8)
  - Lacrimal narial contact: present (0); absent (1). (Laurin and Reisz, 1995 no. 9)
  - Foramen orbitonasale: absent (0); represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (1); enclosed between prefrontal, lacrimal and palatine (2). (Laurin and Reisz, 1995 no. 10)
  - Jugal anterior process: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1). (Laurin and Reisz, 1995 no. 11)
  - Postorbital posterior process shape: increased width, parallelogram outline in lateral aspect (0); slender, half as wide as it is long (1). (Modified from deBraga and Reisz, 1996 no. 14)
  - Postorbital: close to occiput, posterior extent reaching at least 50% the length of the parietal (0); far from occiput, posterior extent not reaching the level of 50% the length of the parietal (1). (Modified from Laurin and Reisz, 1995 no. 13)
  - Posterolateral corner of skull roof: formed mostly by supratemporal (0); formed by parietal and small supratemporal or parietal alone (1). (Modified from Laurin and Reisz, 1995 no. 15)
  - Tabular and opisthotic: in contact (0); separated (1). (Laurin and Reisz, 1995 no. 16)
  - Tabular size: large and part of skull table (0); small and largely occipital (1); absent (2). (Laurin and Reisz, 1995 no. 17)
  - Supratemporal size: large (0); small (1); absent (2). (Laurin and Reisz, 1995 no. 18)
  - Premaxillary dorsal process: broad, narial opening faces predominantly laterally (0); narrow, narial opening faces anteriorly (1). (deBraga and Reisz, 1996 no. 1)
  - Anterodorsal process of the maxilla: absent (0); present (1). (Modified from Laurin and Reisz, 1995 no. 19)
  - Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0); larger than other foramina (1); the lateral surface of the maxilla lacks large foramina (2). (Laurin and Reisz, 1995 no. 20)
  - Maxilla and quadratojugal: separated (0); in contact (1). (Modified from Laurin and Reisz, 1995 no. 22)
  - Quadratojugal anterior extent: reaches posterior border of orbit (0); does not reach level of posterior border of orbit (1). (Modified from Laurin and Reisz, 1995 no. 23)
  - Caniniform region: present (0); absent (1). (Laurin and Reisz, 1995 no. 24)
  - Single caniniform maxillary tooth: present (0); absent (1). (Modified from Laurin and Reisz, 1995 no. 25)
  - Squamosal and post-temporal fenestra: separated (0); in contact (1). (Laurin and Reisz, 1995 no. 26)
  - Occipital flange of squamosal: gently convex all along the posterior edge of the skull (0); convex above quadrate emargination and concave medial to tympanic ridge (1); medial to tympanic ridge, facing posterodorsally (2); medial to tympanic ridge, concave, facing posterolaterally or ventrolaterally (3). (Modified from Laurin and Reisz, 1995 no. 27)
  - Quadratojugal shape: narrow, horizontal dimension exceeds vertical dimension by a factor of at least 3 (0); tall, greatest vertical dimension is at least 1/3 of or greater than horizontal dimension (1). (Modified from Laurin and Reisz, 1995 no. 28)
  - Quadratojugal ornamentation: confluent with the cheek and not ornate in any manner (0); ornamented, dermal protuberances project from its surface (1). (deBraga and Rieppel, 1997 no. 43)
  - Lower temporal fenestra: absent (0); present (1); distinct morphology—thin slit (2). (Modified from Laurin and Reisz, 1995 no. 30)
  - Postorbital contribution to lateral temporal fenestra: bordered by jugal, quadratojugal, squamosal, postorbital (0); no contribution by postorbital (1). (deBraga and Reisz, 1996 no. 20)
  - Quadratojugal-lateral temporal fenestra contribution: quadratojugal excluded from posterior border (0); quadratojugal contributes to lateral temporal fenestra (1). (deBraga and Reisz, 1996 no. 16)

33. Temporal emargination: absent (0); with squamosal and supratemporal (1); with quadratojugal and squamosal (2); facing posteriorly and exposed on occiput, bordered by squamosal, quadratojugal, and quadrate (3). (Laurin and Reisz, 1995 no. 31)
34. Postorbital region of skull: long (more than 15% of skull length) (0); short (15% of skull length or less) (1). (Laurin and Reisz, 1995 no. 32)
35. Ventral margin of postorbital skull region: expanded below ventral extent of maxilla (0); rectilinear (1); emarginated (2). (Modified from Laurin and Reisz, 1995 no. 33)
36. Quadrate lateral exposure: absent (0); present (1). (Laurin and Reisz, 1995 no. 34)
37. Jaw articulation position: even with occiput (0); posterior to occiput (1); anterior to occiput (2). (Modified from Laurin and Reisz, 1995 no. 36)
38. Posterior extension of orbit: absent (0); present (1). (Laurin and Reisz, 1995 no. 37)
39. Dermal sculpturing: absent (0); tuberosities (1); tuberosities and pits (2); honeycomb pattern of ridges and pits (3). (Laurin and Reisz, 1995 no. 38)
40. Sculpturing involving circumorbital bumps: no distinctive ornamentation (0); circumorbital tubercles (1).
41. Posterior margin of skull roof: embayed bilaterally (0), with a single, median embayment (1); roughly straight (2). (Modified from Modesto, 1999 no. 125)
42. Interpterygoid vacuity: short, less than 15% of skull length (0); absent (1); long, at least 15% of skull length (2). (Laurin and Reisz, 1995 no. 39)
43. Interpterygoid vacuity anterior extent: reaches beyond posterior border of palatine (0); reaches level of palatine or less (1). (Modified from Reisz et al. unpublished data no. 127)
44. Choana: parallel to maxilla; palatine forms its posterior edge only (0); curved posteromedially; palatine forms its posterior and part of its lateral edge (1). (Laurin and Reisz, 1995 no. 40)
45. Alar flange of the vomer: absent (0); present (1).
46. Palatine contribution to palate: narrow, restricted to lateral margins of palate (0); broad, exceeds 50% of the width of the pterygoid (1). (deBraga and Reisz, 1996 no. 31)
47. Arcuate flange of pterygoid: present (0); absent (1). (Laurin and Reisz, 1995 no. 42)
48. Cranio-quadrate space: small, quadrate ramus of pterygoid and paraoccipital process of opisthotic converge posterolaterally (0); large, quadrate ramus of pterygoid and paraoccipital process of opisthotic are parallel to each other (1). (Laurin and Reisz, 1995 no. 43)
49. Pterygoid anterior extent: reaches level of posterior end of choana (0); posterior to choana (1). (Laurin and Reisz, 1995 no. 44)
50. Transverse flange of the pterygoid: large, approaches cheek, a noticeable lateral projection (0); small, does not approach cheek (1). (Modified from Lee, 1997 no. 19)
51. Transverse flange of pterygoid orientation: directed posterolaterally or transversely (0); directed anterolaterally (1); directed anteriorly (2). (Modified from Laurin and Reisz, 1995 no. 45)
52. Transverse flange of pterygoid dentition: shagreen of denticles, no ventral ridge (0); single row of large teeth, no ventral ridge (1); edentulous with ventral ridge (2). (Laurin and Reisz, 1995 no. 46)
53. Quadrate ramus of pterygoid: merges smoothly into transverse flange without distinctive excavation (0); deep excavation on posterolateral surface (1). (deBraga and Reisz, 1996 no. 29)
54. Ectopterygoid: large, anteromedial length at least 40% of anteromedially directed suture with pterygoid (0); small, anteromedial length less than 40% of anteromedially-directed suture with pterygoid (1); absent (2). (Modified from Laurin and Reisz, 1995 no. 47)
55. Ectopterygoid dentition: present (0); absent (1). (Laurin and Reisz, 1995 no. 48)
56. Ectopterygoid relationship to transverse flange: ectopterygoid distal to transverse flange, does not contribute to flange (0); ectopterygoid makes contact with tooth-bearing region of transverse flange (1). (deBraga and Reisz, 1996 no. 33)
57. Suborbital foramen: absent (0); present (1); fenestra present (2). (Laurin and Reisz, 1995 no. 49)
58. Basicranial articulation: kinetic/synovial (0); sutured and/or immobile (1). (Modified from Lee, 1997 no. 2)
59. Length of basicranial articulation: restricted to anterolateral margin of the parasphenoid (0); extends over much of length of main body of parasphenoid (1). (deBraga and Reisz, 1996 no. 36)
60. Parasphenoid pocket for cervical musculature: present (0); absent (1). (Laurin and Reisz, 1995 no. 50)
61. Parasphenoid wings: present, parasphenoid broader posteriorly than long (0); absent, parasphenoid narrower posteriorly than long (1). (Modified Laurin and Reisz, 1995 no. 51)
62. Cultriform process: longer than the body of the parasphenoid (0); shorter than the body of the parasphenoid (1). (Laurin and Reisz, 1995 no. 52)
63. Parasphenoid teeth: absent (0); present (1). (Laurin and Reisz, 1995 no. 53)
64. Supraoccipital: plate-like, no sagittal crest (0); body constricted at midline, forming sagittal crest (1). (Modified from deBraga and Rieppel, 1997 no. 56)
65. Paraoccipital process: vertically broad (0); anteroposteriorly expanded (1); narrow (2); tubular, composed of opisthotic (3). (Laurin and Reisz, 1995 no. 56)
66. Paraoccipital process orientation: directed primarily laterally (0); oriented obliquely, at an angle of at least 45 degrees from the horizontal plane of the skull (1). (deBraga and Reisz, 1996 no. 44)
67. Contact between paraoccipital process and dermatocranium: to tabular and squamosal (0); to squamosal and supratemporal (1); to supratemporal (2) to squamosal and quadrate (3); ends freely (4). (Modified from Laurin and Reisz, 1995 no. 57)
68. Medial wall of inner ear (made of prootic): unossified (0); ossified with acoustic nerve foramina (1). (Laurin and Reisz, 1995 no. 59)
69. Post-temporal fenestra: small, diameter less than half the diameter of foramen magnum (0); large, diameter at least equal to foramen magnum (1). (Modified from deBraga and Rieppel, 1997 no. 59)
70. Osseous contact between basioccipital and basisphenoid: present (0); absent (1). (Lee, 1993 #A3, scored as per Laurin and Reisz, 1995 no. 61)
71. Occipital condyle shape: reniform to circular (0); transversely broad (1). (Laurin and Reisz, 1995 no. 62)
72. Ventral exposure of basioccipital: contributes extensively to ventral surface of the braincase (0); restricted to condylar region (1). (deBraga and Reisz, 1996 no. 37)
73. Ventral braincase tubera: absent (0); present and restricted to basioccipital (1); present, very large and restricted to basisphenoid (2); median (3). (Modified from Laurin and Reisz, 1995 no. 63, and deBraga and Rieppel, 1996 no. 65)
74. Lateral flange of exoccipital: absent (0); present (1). (Laurin and Reisz, 1995 no. 64)
75. Quadrate condyle articular surfaces: strongly convex, anteroposteriorly longer than they are wide (0); nearly flat, anteroposteriorly shorter than they are wide (1). (Modified from Laurin and Reisz, 1995 no. 65)
76. Stapedial dorsal process: ossified (0); unossified (1). (Laurin and Reisz, 1995 no. 67)
77. Morphology of marginal dentition: single cusp (0); two or more cusps (1). (Modified from Lee, 1997 no. 59)
78. Foramen intermandibularis: anterior symphyseal foramen (0); two foramina, a symphyseal and a posterior foramen located anterior to coronoid process (1); two foramina, a symphyseal and a posterior foramen located posterior to or at level of coronoid process (2). (Laurin and Reisz, 1995 no. 69)
79. Meckelian fossa orientation: faces mediodorsally, prearticular narrow (0) faces dorsally, prearticular broad (1). (Laurin and Reisz, 1995 no. 70)
80. Fossa meckelii: long, occupies at least 20% of lower jaw length (0); short, occupies less than 20% of lower jaw length (1). (Laurin and Reisz, 1995 no. 71)
81. Surangular length: extends beyond coronoid eminence (0); does not extend beyond coronoid eminence (1). (Laurin and Reisz, 1995 no. 72)
82. Accessory lateral shelf on surangular anterior to articular region: absent (0); present (1). (Laurin and Reisz, 1995 no. 73)
83. Coronoid number: two or three (0); one (1). (Laurin and Reisz, 1995 no. 74)
84. Prearticular extends: beyond the coronoid eminence (0); does not extend beyond coronoid eminence (1); prearticular very long (2). (Laurin and Reisz, 1995 no. 75)
85. Retroarticular process: absent or small and narrow (0); transversely broad, dorsally concave (1). (Laurin and Reisz, 1995 no. 76)
86. Retroarticular process composition: articular body (0); three or more

- elements (articular, prearticular, angular and surangular) (1). (Laurin and Reisz, 1995 no. 77)
87. Lateral shelf on articular region: absent (0); on articular (1); on surangular (2). (Laurin and Reisz, 1995 no. 78)
88. Coronoid process: small or absent, composed of several elements (0); high process composed of coronoid only (1); high, composed primarily of dentary (2). (Modified from Laurin and Reisz, 1995 no. 79)

89. Splenial: contributes to symphysis (0); excluded from symphysis (1). (Laurin and Reisz, 1995 no. 80)

Notes: Characters 40 and 45 are new to this study. The majority of characters were adapted from Laurin and Reisz, 1995, but many were also independently used in subsequent or contemporaneous studies (including Lee, 1995; 1997a; deBraga and Rieppel, 1997).

APPENDIX 2. Data matrix used in this study.

Taxon	1	2	3	4	5
	1234567890	1234567890	1234567890	1234567890	1234567890
Synapsida	A00B000000	0000000000	00A0000001	0000A00000	0C00000000
Mesosauridae	0000000000	?0?0001000	0101110000	??01100000	1000001?00
<i>Eumotosaurus</i>	?00000????	?0100110?1	?011111100	??20212010	120??????0
Millerettidae	0000001000	2010001000	111A10110A	0020112010	1200000000
<i>Eudibamus</i>	000????2100	?0011??210	0?01110?02	1101?01?00	201?????11
<i>Belebey</i>	0001202100	20011?0210	0101110002	1101000100	2010010?11
<i>Acleistorhinus</i>	001210???1	?001011011	1110010101	1130102010	1200000100
<i>Lanthanosuchus</i>	001C201001	?0010?1011	?011112111	1130101020	1200010100
<i>Macroleter</i>	0002A02101	2101001011	1100103111	1120002121	1011110100
<i>Nyctiphruretus</i>	0001102101	?0010?2011	1101103100	??20002120	1211100110
<i>Bradysaurus</i>	0102111000	?1010?2011	1001102110	??30002021	11111101?0
<i>Scutosaurus</i>	0102111000	?101011011	1101102110	??30002021	10111101?0
Procolophon	10022?2111	21010?1011	1001103100	??20202100	2010010110
Owenetta	1002012111	?10?0?2011	1000103100	??20202100	?210010110
<i>Barasaurus</i>	100201?110	?0010?2011	1001103100	??20202100	?210010110
Captorhinidae	000C001000	11011?2100	0110010000	??00100030	0200001000

Taxon	6	7	8	9
	1234567890	1234567890	1234567890	1234567890
Synapsida	010000000A	00A0000000	00C0000D00	AA00000000
Mesosauridae	0102????000	000000??1?	000?000??0	001?1000?
<i>Eumotosaurus</i>	01?????001	000010????	?0???10???	0?????0??
Millerettidae	0101101001	1010001011	0000010?00	0010000000
<i>Eudibamus</i>	22111??000	1?0??0????	11????02???	???200?20
<i>Belebey</i>	2211110000	100??0???0	???00?0201	10120?021
<i>Acleistorhinus</i>	011011111?	1010012??0	1100100???	1011010?1
<i>Lanthanosuchus</i>	0110110111	1010012?0?	11?11?0???	??????????
<i>Macroleter</i>	0111?01100	1101101?1?	0001??02?1	11111?111
<i>Nyctiphruretus</i>	01?0011001	110?101011	00001?0???	??1?????1
<i>Bradysaurus</i>	1111101101	1101101110	0001101?11	10111?110
<i>Scutosaurus</i>	1111111101	1101101110	0001111211	10111?110
Procolophon	1211111001	0101102011	001011021?	111111011
Owenetta	1211111001	1101103?1?	00100?0211	101111011
<i>Barasaurus</i>	12?1111001	1101103?1?	00100?0???	??????????
Captorhinidae	0002??1001	10A0204?10	0000000100	0010000000

Polymorphism is indicated by letters, such that A = 0&1, B = 1&2, C = 0&2, D = 0&1&2.