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THE EARLY PERMIAN REPTILE *ACLEISTORHINUS PTEROTICUS* AND ITS PHYLOGENETIC POSITION

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ABSTRACT—Restudy of *Acleistorhinus pteroticus* indicates that this Early Permian amniote from North America is the oldest known member of Parareptilia. Despite its stratigraphic position, *Acleistorhinus* is not a basal parareptile, and a phylogenetic analysis of parareptile interrelationships demonstrates that *Acleistorhinus* is a sister taxon to the Russian clade Lanthanosuchidae. This hypothesis of relationships is supported by eleven synapomorphies. The presence of an Early Permian parareptile in North American sediments provides strong support for the recent hypotheses of amniote phylogeny that propose an extensive evolutionary radiation for this group of reptiles.

INTRODUCTION

For more than a century (Cope, 1881, 1896), many of the taxa now referred to Parareptilia were considered to be "stem" reptiles (Cotylosauria) from which all other amniotes evolved. Case (1911) tried to resolve some of the outstanding issues surrounding the systematic position of many of these problematic taxa, but his systematic overview suffered from the precladistic era's indiscriminate mixing of plesiomorphic and apomorphic features for diagnosing taxa and determining relationships. Case's Cotylosauria included a plethora of taxa including pareiasaurs and procolophonids, presently assigned to Parareptilia (Laurin and Reisz, 1995), along with numerous other taxa including *Captorhinus, Bolosaurus,* and the currently recognized anamniotes *Diadectes, Seymouria,* and *Pantylus,* to name a few.

Later, in perhaps the most thorough attempt at understanding the phylogenetic position of many of these "stem" reptiles, Olson (1947) implied that reptiles had a diphyletic origin, and erected a new group, Parareptilia, within which he included seymouriamorphs, diadectomorphs, procolophonids, pareiasaurs, and chelonians. This diphyletic proposal did not meet with much support and was later overwhelmed by Romer's (1956) classification. Romer's taxonomy placed most of Olson's Parareptilia back into that enigmatic basal group collectively referred to as "stem" reptiles or Cotylosauria. Heaton (1980), after reviewing much of the earlier literature on Cotylosauria, concluded that all amniotes (his Reptilia) should be excluded from that group. He did, however, include the Russian nycteroleterids within his Seymouriamorpha, and hence within Cotylosauria and not Reptilia. Perhaps as a result of Romer's interpretation, or because of the formerly politically isolated locations (Russia, South Africa) where many of the key members of this assemblage are reposited, many of the parareptiles were ignored by North American paleontologists for much of the last four decades.

In a cladistic analysis of amniote interrelationships, Gauthier et al. (1988) identified parareptiles as a monophyletic group. More recently, Reisz and Laurin (1991) proposed that procolophonids were a sister-taxon to Testudines. Spurred on by these hypotheses, others have taken up the task of evaluating interrelationships among parareptiles, and their relationship to turtles (Lee, 1993). As a precursor to the present study, Laurin and Reisz (1995), re-examined the interrelationships of basal amniotes. Significantly, their analysis focused on evaluating parareptiles, a group which Gauthier et al. (1988) had found troubling, and concluded that parareptiles formed a monophyletic group. Contra Lee (1993), Laurin and Reisz have also restated the hypothesis of a sister-group relationship between procolophonids and turtles. However, Laurin and Reisz did not attempt to evaluate the phylogenetic position of many problematic taxa that have been frequently allied to Parareptilia (Ivakhnenko, 1987) because detailed anatomical data were not available.

One of these problematic taxa is *Acleistorhinus pteroticus,* from the Lower Permian Hennesey Formation of southwestern Oklahoma (Daly, 1969). Daly (1969) assigned her new taxon to Procolophonoidea (sensu Romer, 1956). This assignment was based on the overall shape of the skull and the orientation of the paroccipital processes, which according to Daly (1969) rose up to contact the enlarged supratemporals from below. Despite its obvious significance as the oldest known "procolophonoid" *Acleistorhinus* has been ignored since Daly's original description. Carroll (1988) appears to have doubted Daly's (1969) assignment of *Acleistorhinus,* and placed this taxon into the Captorhinomorpha incertae sedis. Additional preparation and restudy of the holotype and only known specimen of this enigmatic fossil has yielded a great deal of new information on its anatomy and phylogenetic relationships. Our work indicates not only that *Acleistorhinus* is the earliest known member of the Parareptilia, but also that it is the sister-taxon to the enigmatic Russian amniotes, the lanthanosuchids.

SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson, 1947

Definition—The most recent common ancestor of millerettids, *Acleistorhinus,* lanthanosuchids, *Macroleter,* Procolophonia, and all its descendants.

Emended Diagnosis—A reptilian clade diagnosed by the following autapomorphies: anterolateral maxillary foramen present and significantly larger than all other foramina in maxilla; foramen orbitonasale entirely surrounded by bone; temporal emargination formed by quadratojugal and squamosal; ectopterygoid teeth absent; paroccipital process-supratemporal contact present; sacral ribs only slightly in contact with one another or not at all; and iliac blade dorsally expanded into fan-like structure.

ANKYRAMORPHA, new taxon

Etymology—Ankyras, from the Greek for anchor, in reference to the anchor-shaped interclavicle.

Definition—The most recent common ancestor of Procolo-

phonia, *Macroleter,* Lanthanosuchidae, *Acleistorhinus,* and all its descendants.

Diagnosis—Members of Parareptilia exhibiting the following autapomorphies: dorsal process of premaxilla narrow; antero-dorsal process of maxilla high and extending to the dorsal limit of the external naris; posterior process of postorbital nearly as wide as long; jaw articulation anterior to occiput; dermal sculpturing on skull in the form of large tuberosities and pits; base of quadrate ramus of pterygoid deeply excavated posteriorly; ectopterygoid, if present, contributing to outer-most border of transverse flange; cultriform shorter than the body of the parasphenoid; paroccipital process antero-posteriorly expanded; quadrate condyle short and nearly flat antero-posteriorly; surangular short and not extending anteriorly beyond the coronoid eminence; prearticular short, terminating before coronoid eminence; trunk neural arches swollen but with narrow, high zygapophyseal buttresses; interclavicle with distinctive anchor shape (T-shaped); and anterior edge of transverse bar of interclavicle with deep groove for attachment of clavicles.

LANTHANOSUCHOIDEA Efremov, 1946

Definition—The most recent common ancestor of Lanthanosuchidae and *Acleistorhinus.*

Diagnosis—Ankyramorph reptiles diagnosed by the following autapomorphies: anterior margin of frontal sloping medially at an angle of no more than 70°; frontal with lateral lappets which separate prefrontal and postfrontal and occupy at least one-third of dorsal orbital margin; postparietal present but reduced to small occipital element; quadratojugal contributes to posterior margin of lateral temporal fenestra; lower temporal fenestra present; ectopterygoid large, at least one-half as wide as pterygoid; basicranial articulation long, extending along entire lateral margin of parasphenoid that is in contact with pterygoid; ventral exposure of basioccipital restricted to the condylar region; distinct basipterygoidal tubera absent; parasphenoid dentigerous; paroccipital process directed obliquely at 45° from occiput toward dorsolateral margin of skull; posttemporal fenestra small.

ACLEISTORHINUS Daly, 1969

ACLEISTORHINUS PTEROTICUS Daly, 1969

Holotype—Field Museum of Natural History, UR 1038.

Horizon and Locality—Lower Permian (Leonardian), Hennessey Formation, South Grandfield, Tillman County, Oklahoma.

Generic and Specific Diagnosis—Small lanthanosuchoid possessing the following autapomorphies: pineal foramen close to frontoparietal suture; lacrimal excluded from contact with nasal; postfrontal and supratemporal in contact; postorbital excluded from border of lateral temporal fenestra; dermal ornamentation of skull composed of shallow, circular pits; and cranio-quadrate space large.

GENERAL DESCRIPTION

The skull of *Acleistorhinus pteroticus* (Fig. 1) has a triangular outline in dorsal view. The surface is generally smooth except for small, shallow, circular pits. Anteriorly, the snout is gently rounded. Along its anterolateral margins are paired, oval external nares that have their long axes laying parallel to the long axis of the skull. Posterior to the nares the snout margins diverge until just anterior to the antorbital region. Beyond this point the skull is constricted then expands again as it proceeds beyond the mid-point of the orbit. Posterior to the orbit the skull margins run a parallel course until they form a tight 90° turn medially and converge along the occipital surface. Behind the orbit, and restricted to the lower half of the temporal region, the skull possesses a single lateral temporal fenestra bordered by the jugal anteroventrally, the quadratojugal posteroventrally, and the squamosal posterodorsally. The orbits are circular and are equidistant from either end of the skull.

Although there are some important differences in the present skull reconstruction when compared to Daly's (1969) original interpretation, much of the overall configuration of the skull table has remained essentially unchanged. However, due to more complete preparation, the interpretation of the occiput has been significantly altered. The most notable difference is in the composition of the quadrate which is here interpreted as a much smaller element; and the quadrate flange of the pterygoid which contributes an occipital flange to the region of the otic notch. Furthermore, it has not been possible to corroborate the unusual stapedial configuration presented by Daly (1969) and in the absence of any additional evidence the stapes has been reconstructed in a more conventional manner.

The jaws are in place and impossible to remove, but careful preparation has exposed the internal nares on the right side. As reconstructed, the lower jaws are not very different from the reconstruction proposed by Daly except that a suture between the angular and surangular is identified.

The sutural arrangement of the palatal elements was not well established by Daly (1969), but additional preparation has allowed most of the sutures to be identified. The palate possesses multiple rows of teeth arranged in a radiating pattern from the midline. An interpterygoid vacuity is present but is quite narrow. A short cultriform process extends into the vacuity. The parasphenoid is broad and there are small denticles present on the main body.

The marginal dentition is composed of conical teeth that are only slightly recurved. No canine region is evident although the second maxillary tooth is slightly larger than the rest. The tooth bearing portion of the maxilla extends posterior to the orbital margin.

DESCRIPTION

Skull

The elliptical external nares are each bordered by the maxilla posteroventrally, the nasal dorsally, and the premaxilla anteroventrally (Fig. 2A, D). Except for the distal ends, the nasal processes of the premaxilla are missing but, in contrast to Daly's interpretation, which concluded that they were never ossified, it is more likely that they were eroded away. The tooth-bearing portion of the premaxilla appears to be directed somewhat downward at its tip but it is not hooked as in captorhinids. Each premaxilla possesses spaces for four teeth. All the premaxillary teeth appear to be approximately the same size, and noticeably smaller than those on the maxilla.

The maxilla has a dorsal expansion immediately behind the nares forming the entire posterior border of the opening (Fig. 2D). This configuration resembles the condition exhibited by both procolophonids, turtles, and neodiapsids and results in the exclusion of the lacrimal from the posterior border of the nares. Immediately below the posteroventral narial margin, the maxilla possesses a large foramen, similar to that in procolophonids, pareiasaurs, nyctiphruretids, and millerettids. The maxillae has 11 and 13 teeth on the right and left sides respectively, but there is room for at least 17 teeth in each element.

The nasal contacts the anterodorsal margin of the maxilla and borders the nares dorsally (Fig. 2A). It has a rectangular outline and is bordered posteriorly by the frontal and posterolaterally by the prefrontal. The nasal has numerous randomly placed small pits on its surface as do all the dermal bones of the skull.

Slightly more than one third of the total length of the skull

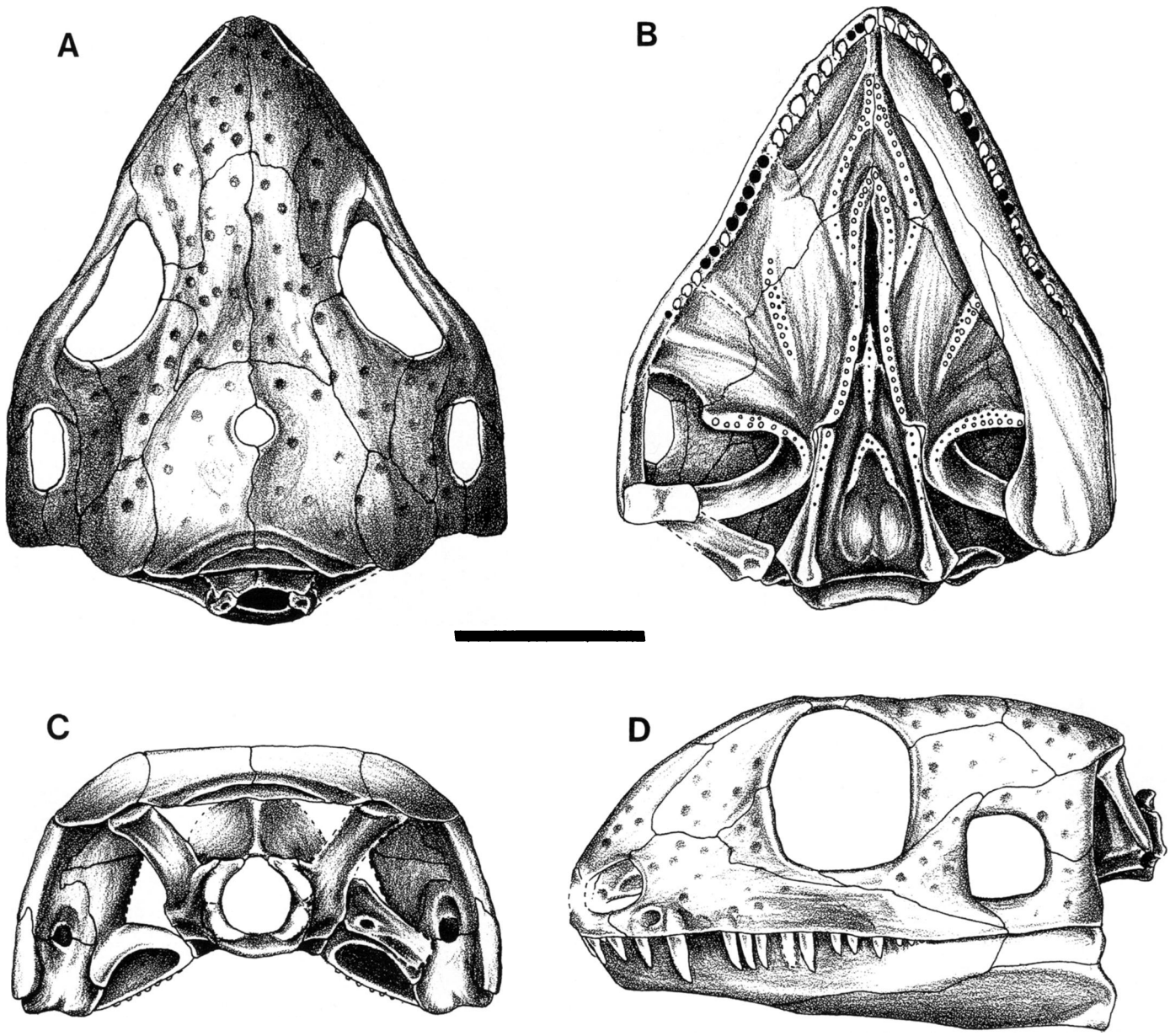

FIGURE 1. Skull reconstruction of *Acleistorhinus pteroticus* Daly. (**A**) dorsal view, (**B**) palatal view with left jaw omitted to show structures not otherwise visible, (**C**) occipital view with jaws removed, and (**D**) lateral view. Scale equals 1 cm.

is contributed to by the frontal (Fig. 2A). It is constricted anteriorly by the prefrontals, but is expanded above the orbits forming a lateral lappet that reaches the orbital margin. The right frontal, in particular, has had much of its surface obliterated, and a large, calcite-filled crack runs obliquely from the midline out to its lateral margin and continues through the prefrontal to the orbital margin. The left frontal is in somewhat better condition but it too has been subject to erosion posteriorly. The demarcation point from solid bone to eroded surface was initially interpreted by Daly (1969) as the region of the frontoparietal suture. That suture is now interpreted 3 mm further posteriorly. This new position is based on the assertion that a deep groove running horizontally across this region of the skull is the true frontoparietal suture.

The prefrontal does not differ from Daly's (1969) original description in any significant feature (Fig. 2A, D). The downward expansion of the prefrontal and subsequent contact with the maxilla precludes contact between the nasal and lacrimal.

The lacrimal is triangular in lateral view (Fig. 2D). Further preparation has shown that the bone is deep medially and forms a tight suture with the prefrontal antorbitally. A small foramen, possibly the lacrimal foramen, is present just medial to the anteroventral margin of the bone. A narrow splinter of the lacrimal overlies the maxilla posteriorly and forms an oblique suture with the jugal at mid-orbital length.

The triradiate jugal possesses a pair of short anterior and posterior processes, and a broad, tall dorsal process (Fig. 2D). The anterior process of the jugal overlies the maxilla, excluding it from the orbital margin, as in most tetrapods. The jugal tapers to a narrow sliver of bone anteriorly, in contrast to the broad process seen in procolophonoids.

Restricted to the posteroventral corner of the skull, the qua-

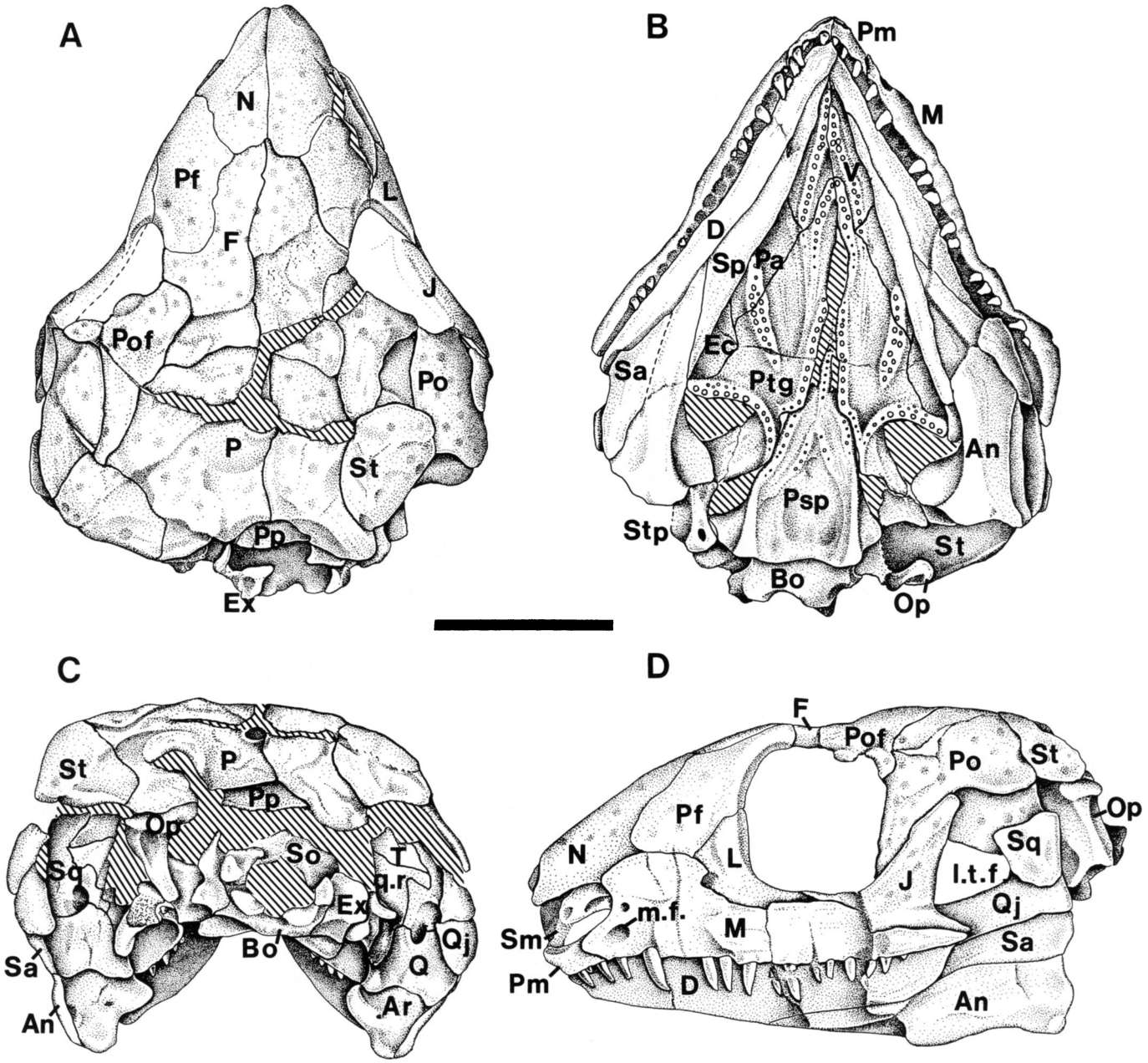

FIGURE 2. Specimen drawings of *Acleistorhinus pteroticus* Daly. (**A**) dorsal view, (**B**) palatal view, (**C**) occipital view, and (**D**) lateral view. Abbreviations: **An**, angular; **Ar**, articular; **Bo**, basiocciptal; **D**, dentary; **Ec**, ectopterygoid; **Ex**, exoccipital; **F**, frontal; **J**, jugal; **L**, lacrimal; **l. t. f.**, lateral temporal fenestra; **M**, maxilla; **m. f.**, anterolateral maxillary foramen; **N**, nasal; **Op**, opisthotic; **P**, parietal; **Pa**, palatine; **Pf**, prefrontal; **Pm**, premaxilla; **Po**, postorbital; **Pof**, postfrontal; **Pp**, postparietal; **Ptg**, pterygoid; **Psp**, parasphenoid; **Q**, quadrate; **Qj**, quadratojugal; **q. r.**, quadrate ramus of pterygoid; **Sa**, surangular; **Sm**, septomaxilla; **Sq**, squamosal; **St**, supratemporal; **Stp**, stapes; **T**, tabular; **V**, vomer. Scale equals 1 cm.

dratojugal is an L-shaped bone with a well-developed anterior process and a short dorsally directed process posteriorly (Fig. 2D). The anterior process overlies the posterior process of the jugal and forms the entire ventral border of the lateral temporal fenestra. The bone is well exposed occipitally and is sutured to the quadrate medially and the squamosal dorsomedially.

The squamosal has been displaced on both sides of the skull (Fig. 2D). On the right side it has been pushed forward underneath the postorbital. As a result of postmortem separation between the postorbital and postfrontal, a portion of the squamosal is exposed dorsally on the right side of the skull roof. The left squamosal is broken, and the lower half has telescoped over the upper half. Furthermore, the upper half has been displaced forward and underlies the postorbital and jugal. An undisturbed squamosal would appear as a triangular element in lateral view with its narrowest end directed ventrally and sutured to the dorsolateral margin of the quadratojugal. The anterior border rises obliquely underneath the postorbital, contributing to the dorsal border of the lower temporal fenestra, and sutured to the posterodorsal edge of the jugal. This is in strong contrast to the pattern depicted by Daly (1969), in which the squamosal did not contribute to the border of the temporal fe-

nestra. Occipitally, the squamosal is sutured to the quadrate ventrally, where it forms the dorsal border of the quadrate foramen (Fig. 2C). In addition, the squamosal makes contact with the occipital flange of the pterygoid medially, and a small triangular tabular dorsomedially.

Daly (1969) misinterpreted the supratemporal as the tabular and failed to recognize the real tabular as a discrete element. The tabular is instead an exclusively occipital element (Fig. 2C), as in most other amniote taxa where it is present. It is a wedge-shaped element that was sutured to the supratemporal and possibly the parietal dorsally, the occipital flange of the pterygoid ventrally, and the squamosal laterally.

A flat, broad, plate-like postorbital is exposed dorsolaterally on the skull roof and also extends far ventrally along the posterior orbital margin (Fig. 2A, D). It forms a tight suture with the postfrontal along most of its medial length; on the right side of the skull, the postorbital and postfrontal are separated, exposing the squamosal underneath. Posterodorsally the postorbital is in contact with the supratemporal.

Crushing and erosion have damaged the surface of the postfrontal (Fig. 2A, D). However, the left element retains sufficient detail to define its boundaries. The postfrontal contributes to the posterodorsal border of the orbit, and tapers posteriorly over the skull roof to fit between the parietal and the postorbital. It is bounded posteriorly by the supratemporal. The elongate configuration of the postfrontal in *Acleistorhinus* recalls the condition seen in *Owenetta,* but differs in being tapered posteriorly rather than broadly expanded. This reinterpretation of the postfrontal has also changed the relationships of this element to the parietals and supratemporals.

In the original description (Daly, 1969), the supratemporal was interpreted as a large element of the skull roof (Fig. 2A, C, D). Given the postmortem distortion and damage that has occurred in this region of the skull, it is difficult to determine its exact configuration. However, as a result of some additional preparation, a more likely configuration for the supratemporal is presented here. What was originally interpreted as the supratemporal-parietal suture is in reality a calcite-filled crack. The actual suture is clearly visible on the right side of the skull, and, although it is less clear on the left side, its outline can still be discerned. The supratemporal is here interpreted as being restricted to the posterolateral corner of the skull roof. Although the supratemporal is still a relatively large element, it is smaller, and encroaches less upon the median portion of the skull than in the original description (Daly, 1969).

Contributing to the majority of the skull roof in *Acleistorhinus* is the paired parietal (Fig. 2A). The present study confirms that the parietal is large and contributes significantly to the skull table. A great deal of surface damage has occurred, but the midline suture and lateral edge of the parietal are clear. A large pineal foramen is present but unfortunately it is continuous with a calcite filled crack that also transects the paired element. Posteriorly, the parietal is excavated slightly at the midline and lies superficial to a fused, median postparietal. Although Daly (1969) described the postparietal as a paired element, no evidence of a suture was found during this study. In fact, what had been interpreted as narrow, lateral extensions of the postparietal appear instead to be broken pieces of the parietal.

Occipital Region—Generally, in early amniotes the largest element of the occiput is the supraoccipital. In *Acleistorhinus* the supraoccipital is poorly preserved but it is evidently plate-like although not as massive as in synapsids (Fig. 2C). The reduction in the overall size of the supraoccipital allows for the development of relatively large posttemporal fenestra characteristic of Reptilia as most recently defined by Laurin and Reisz (1995). Unfortunately, beyond commenting on its general size, a detailed description of the supraoccipital is not possible.

Although the occipital condyle appears to be double (Daly, 1969), careful study of this specimen has revealed the presence of a depressed area between the two alleged condyles which is simply a region of poorly preserved bone (Fig. 2C). There is therefore no reason to suggest that such an unusual condyle, as proposed by Daly (1969), existed in *Acleistorhinus.* The suture between the basioccipital and exoccipital is difficult to see, but we have been able to determine that the basioccipital contributes to the ventralmost margin of the foramen magnum, and is sutured to the exoccipital laterally and dorsally at about the mid-height of the foramen magnum.

The opisthotics and exoccipitals appear to be indistinguishably fused (Fig. 2C). The right opisthotic is incomplete in lacking the paroccipital process, whereas on the left side the paroccipital process is present but is damaged. Daly's (1969) interpretation that the paroccipital process was inclined dorsally to the skull roof was the basis for her assertion that this taxon showed clear affinities to procolophonoids. The present study agrees with Daly's reconstruction with some reservation. The preservation is poor and as a result it is not possible to establish confidently whether the orientation of the paroccipital process is real or simply an artifact. However, an embayment on the posteromedial edge of the supratemporal and the posterolateral margin of the parietal may have served for the reception of the paroccipital process so that the present reconstruction of the element has remained as described by Daly (1969).

Daly (1969) described the stapes of *Acleistorhinus* in some detail, but our study is unable to confirm most of her original interpretations. On the left side the stapes has been displaced, exposing a small pit on the ventral surface of the braincase (opisthotic-prootic) which is undoubtedly the fenestra ovalis (Fig. 2D). The right stapes is in place and displays a very unusual morphology (Fig. 2B, C). As mentioned above, during fossilization, much of the bone was replaced by calcite. It is likely that during preparation certain structures were damaged or actual boundaries were obliterated because of the calcite intrusion. This appears to have been the case with the stapes. For instance, the large, blade-like horizontal process and the paired ventral processes described by Daly (1969) is probably the result of poor initial preparation.

The most conservative reconstruction of the stapes in *Acleistorhinus* presents a structure that does not differ appreciably from that of other Paleozoic tetrapods. The stapes possesses a large foot-plate (otic process) and an incompletely ossified distal end (quadrate process). Daly (1969) described a tall, long, blade-like dorsal process, but unfortunately this process appears to be composed mainly of unattached bone fragments and matrix. Due to the apparent damage sustained in this region the presence or absence of a dorsal process cannot be established. In any event, it is clear that the relatively robust, stapedial morphology presented by this taxon resembles closely the morphology exhibited within early Amniota.

Palate—Preparation of the palate has allowed for identification of most of the palatal sutures with the possible exception of the vomerine margins (Fig. 2B). The palate possesses distinctive tooth-bearing ridges that extend in three directions from the region of the basicranial articulation. Two distinct, parallel tooth-bearing ridges extend anteriorly close to the midline, one tracking the border of the interpterygoid vacuity anteriorly and extending posteriorly onto the ventral surface of the braincase, while the second extends anteriorly onto the vomer. A shorter tooth bearing ridge extends from the basicranial region at an oblique angle to the long axis of the skull, and crosses onto the palatine. The third tooth-bearing region is along the transverse process of the pterygoid.

An anteriorly narrow vomer contributes to the medial border of the internal naris (Fig. 2B). Posteriorly, the vomer is separated from its pair along the midline by the pterygoid. The

lateral border of the vomer is not clear but the sutural contact with the palatine has been estimated to be at about the same level as the anterior boundary of the interpterygoid vacuity. Vomerine teeth are present as two distinct fields. Anteriorly a field of small denticles is located along the palatal midline. This field is not well preserved posteriorly but the tooth bases can still be discerned as the anterior margin of the pterygoid is approached. Radiating from the anterior field of denticles is an additional field that runs posteriorly at an oblique angle to the mid-line and continues beyond the anterior limit of the pterygoids. The paired tooth rows then continue posteriorly onto the pterygoid but appear to fade out gradually. The apparent loss of this tooth-bearing ridge may, however, be due to damage during the initial preparation, and it is conceivable that the tooth-bearing ridge extended posteriorly along most of the length of the pterygoid (Fig. 2B).

The palatine contributes to the posterior border of the internal naris and is sutured medially to the pterygoid and posteriorly to the ectopterygoid. Anteriorly, the palatine contacts the vomer. A portion of the large obliquely oriented tooth-bearing ridge that radiates outward from the basicranial area occupies a small section of the palatine immediately across from the pterygo-palatine suture.

The pterygoids are the largest bones of the palate. The sutural contacts with the vomer anteriorly, the palatine laterally, and the ectopterygoid posterolaterally are clearly defined. The overall appearance of each pterygoid is that of a triangular element with a generally flat anterior process, a transverse posterolateral process (transverse flange of the pterygoid), and a narrow, parasagittally deep posterior process (quadrate flange of the pterygoid).

Most of the transverse flange is directed laterally and is expressed as a tall, narrow ridge with a single row of well developed teeth along most of its surface. Smaller teeth are present on the sloping surface of the transverse flange, anterior to the row of large teeth. Medially, the flange curves strongly posteriorly through an arc of at least 90° to its transverse section. This region also possesses smaller teeth which are arranged on the surface of the flange and disappear posteriorly as the flange merges with the medial edge of the quadrate flange.

The quadrate flange of the pterygoid is deep vertically and is separated anterolaterally by a deep excavation from the transverse flange. The quadrate flange continues posteriorly where it sits on a slight protuberance on the medial surface of the quadrate (Fig. 2C). In addition, the quadrate flange of the pterygoid develops an occipital flange that spreads onto the surface of the "otic notch". This occipital flange is similar to that which is present in lanthanosuchids and some members of Procolophonia. The flange forms a sutural contact with the quadrate ventromedially, and rises obliquely, expanding laterally, as it contacts the squamosal dorsolaterally. It forms a tight suture with the tabular dorsally. An interesting feature of the pterygoid occipital flange is the development of a finger-like projection, or wing, that is directed laterally from its dorsolateral margin and encroaches upon the occipital flange of the squamosal.

The anatomy of the entire quadrate is difficult to describe because the jaws are in place. However, the anteroposterior length of the condylar region can be estimated, and it appears to be relatively short (Fig. 2B). This reduction in the anteroposterior length of the quadrate condylar region was presented as a procolophonian synapomorphy by Laurin and Reisz (1995). The quadrate is partially exposed occipitally. The quadrate contributes to the ventral half of the "otic notch" where it forms the ventral boundary of the quadrate foramen (Fig. 2C). The quadrate is sutured to the occipital flange of the pterygoid medially and the quadratojugal laterally. The quadrate is almost entirely an occipital element, except for a small portion that is exposed in lateral view below the quadratojugal.

A broadly triangular complex composed of the parasphenoid and basisphenoid occupies a little more than one third of the overall palatal length (Fig. 2B). The most remarkable feature of this complex is the great anteroposterior elongation of the basicranial articulation, encompassing nearly the entire length of the main body of the parasphenoid. Anteriorly the parasphenoid appears to possess a narrow, short cultriform process. However, its precise length remains uncertain because of poor preservation. The preserved portion of the cultriform exhibits broken tooth bases. Although heavily damaged, the parasphenoid plate also bears, immediately behind the basicranial articulation, two separate, paired rows of teeth diverging posteriorly. The lateralmost rows sit on a ridge that runs the length of the main body of the parasphenoid. The tooth bases on these ridges are evident anteriorly but appear to terminate at about the same level as the teeth on the posteromedial corner of the transverse flange of the pterygoid. The medialmost rows sit on paired, low ridges and run an obliquely oriented course posteriorly, merging imperceptibly with the lateral rows on either side of the parasphenoid. Posterior to the merging of the fields the tooth bases are no longer visible, but whether this absence is real or an artifact of preservation cannot be established.

Posterior to the tooth bearing region, the ventral surface of the parasphenoid appears to have been damaged during preparation. For instance, a small pit or foramen described by Daly (1969:683) is likely an artifact. Except for the paired ridges laterally, the posterolateral wings, and the deep sulcus medially, much of the bony surface is damaged and a detailed description of this region is not possible.

Mandible

Daly's (1969) description of the lower jaw is essentially accurate, but a few comments are necessary. We have been able to determine the suture between the angular and surangular (Fig. 2D). The suture is most clearly visible on the left side and presents a rather small surangular that is restricted to the posterodorsal corner of the lower jaw. In occipital view the surangular appears as a dorsolaterally directed projection, or wing, that hides the quadrate from lateral view when the jaws are closed. Below the surangular lies the articular, which can be most easily observed in posterior view and is correctly described by Daly (Fig. 2C). The angular, which is essentially a thin, laterally restricted bone, obscures all of the articular from lateral view and most of it from ventral view (Fig. 2B, D). The splenial is long and has most of its exposure on the medial surface of the jaw, as described by Daly (Fig. 2B). It is difficult to determine whether the splenial contributed to the mandibular symphysis.

RELATIONSHIPS

Methods

In order to determine the phylogenetic relationships of *Acleistorhinus* we analyzed a total of eight taxa using 60 characters (Appendix 1 and 2). All the coding for the taxa considered here has been done by the direct examination of specimens. This study follows the approach of Laurin and Reisz (1995) in establishing the primitive condition for synapsids. Mesosaurids were coded using data graciously supplied by S.P. Modesto. Eureptilia is considered here as defined by Laurin and Reisz (1995). The composition of Procolophonia and Milleretidae also follows their analysis and includes procolophonids, pareiasaurs, and Testudines within the former, and *Milleretta, Millerosaurus,* and *Milleropsis* in the latter. Lanthanosuchids are represented by two taxa *Lanthanosuchus,* and *Lanthaniscus* most recently described by Ivakhnenko (1980, 1987). *Macroleter* is the sole representative of the "nycteroleterids" (Carroll,

1988) and on the basis of new material represents the best available information pertaining to this group. The study of *Acleistorhinus* was restricted to the only known specimen which consists of a complete skull.

No weighting was assigned to any of the characters considered. All characters were left unordered and were optimized using the DELTRAN algorithm of PAUP 3.1 (Swofford, 1993). The DELTRAN option serves to minimize the number of synapomorphies at any given node. Character polarity was determined by the outgroup taxa. The resultant data matrix was subjected to a branch and bound algorithm (PAUP 3.1) which guarantees to find all of the most parsimonious trees.

Results

Two equally parsimonious trees resulted from the search (Fig. 3) which required a total of 96 steps to resolve. The trees have an overall consistency index of 0.812 with a corrected index of 0.690 (when uninformative characters are excluded). This analysis indicates that *Acleistorhinus* is a parareptile and is closely related to the Russian lanthanosuchids. In addition, the results support, in general, the conclusions presented by Laurin and Reisz (1995), except that mesosaurids form an unresolved trichotomy with Eureptilia and the most recent common ancestor of Parareptilia. The present analysis increases the total number of taxa that can be assigned to Parareptilia by at least three. Only those nodes that are unique to this study will be evaluated below. The interrelationships within Procolophonia, including the phylogenetic position of Testudines, have been addressed elsewhere and will not be reevaluated below.

DISCUSSION

The results presented here show for the first time that the problematic Russian taxa (lanthanosuchids and nycteroleterids) are part of the crown group Amniota. Previously, published classifications had these taxa allied to various amphibian groups (Ivakhnenko, 1987; Carroll, 1988). The placement of these taxa, along with the North American taxon *Acleistorhinus,* within the monophyletic Parareptilia, has numerous implications.

This analysis supports the recent hypothesis that Parareptilia is a monophyletic group (Laurin and Reisz, 1995). We differ from Laurin and Reisz's analysis in the total number of synapomorphies diagnosing the clade, but the monophyly remains robust (only seven synapomorphies presently diagnose Parareptilia compared to 14 given by Laurin and Reisz [1995]). The recognition of *Acleistorhinus* and lanthanosuchids (Figs. 1, 3, 4) as sister-taxa presents a heretofore unrecognized clade between two parareptile taxa that are widely separated both geologically and geographically. This new evidence provides support for the hypothesis that parareptiles had a cosmopolitan distribution during the Paleozoic. This sister-group relationship, although not immediately apparent is supported by twelve synapomorphies (numbers in parentheses refer to characters in appendix 1 and 2; asterisk refers to ambiguous character; minus sign denotes a reversal): (6) anterior margin of frontal slopes medially at an angle of no more than 70°; (7) frontal with lateral lappet separating prefrontal and postfrontal and contributing to one-third of the dorsal orbital margin; (8) postparietal reduced or absent; (16) quadratojugal contributes to posterior border of lateral temporal fenestra; (17*) lower temporal fenestra present; (34) ectopterygoid very large, at least one-half as wide as pterygoid; (36) basicranial articulation long; (37) basioccipital ventral exposure restricted to condylar region; (38) basipterygoidal tubera absent; (40*) parasphenoid teeth present; (44) paroccipital process directed obliquely at an angle of 45° from occiput toward dorsolateral edge of skull table; and (−46) posttemporal fenestra small. Two (36 and 38) of the eleven characters are associated with the basicranial articulation and represent a unique morphology not previously recognized in any other taxa. Furthermore, the presence of *Acleistorhinus* in the Lower Permian of North America may indicate a Laurasian origin for the clade in the Permo-Carboniferous, with subsequent colonization of Gondwanaland in the Upper Permian. This scenario presents some interesting developments, most notably, the apparent incongruence between the earliest geological representative (*Acleistorhinus*) of the clade in North America and the earliest phylogenetically recognized member (Millerettidae) of the clade from South Africa. Notably the putative sister-group relationship between parareptiles and eureptiles proposed by Laurin and Reisz (1995), notwithstanding the possibility that either may share a closer affinity with mesosaurs, suggests that the common ancestor of these clades must be at least as old as the

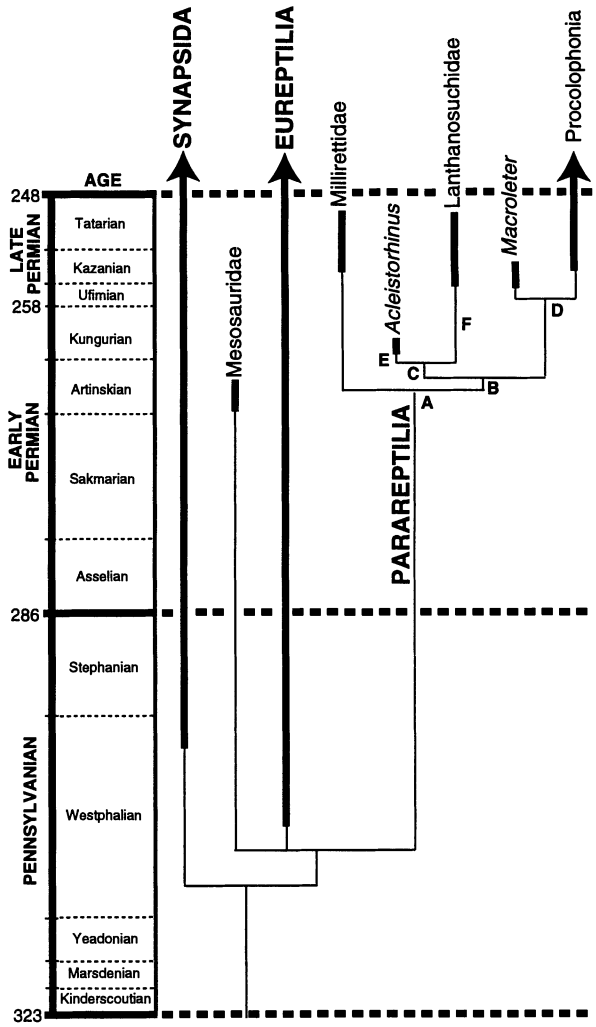

FIGURE 3. Cladogram of interrelationships and stratigraphic ranges among parareptiles. Character numbers describing nodes refer to characters enumerated in Appendices 1 and 2. In cases of a multistate character the derived state will be presented in parentheses. Ambiguous characters are denoted by an asterisk, and character reversals are preceded by a minus sign. Parareptilia (Node A), 3, 11, 19, 33, 46, 58, and 59; Ankyramorpha (Node B), *1, 2(2), 14, 23, 25, 29, 33, 41, 43, 47, 48, 50, 52, 53, and 54; Lanthanosuchoidea (Node C), 6, 7, 8, 16, *17, 34, 36, 37, 38, *40, 44, and -46; *Macroleter* plus Procolophonia (Node D), 9, *11, 13, 15, *27, *35, and 55; *Acleistorhinus* (Node E), *4, 9(2), 19, *20, 25(2), and *27; Lanthanosuchidae (Node F), 5, *11, 12, 13, *26, and -33. Stratigraphic ranges of taxa and geological dates are reconstructed from the following sources: Anderson and Cruickshank, 1978; Harland et al., 1989; and Hentz, 1988.

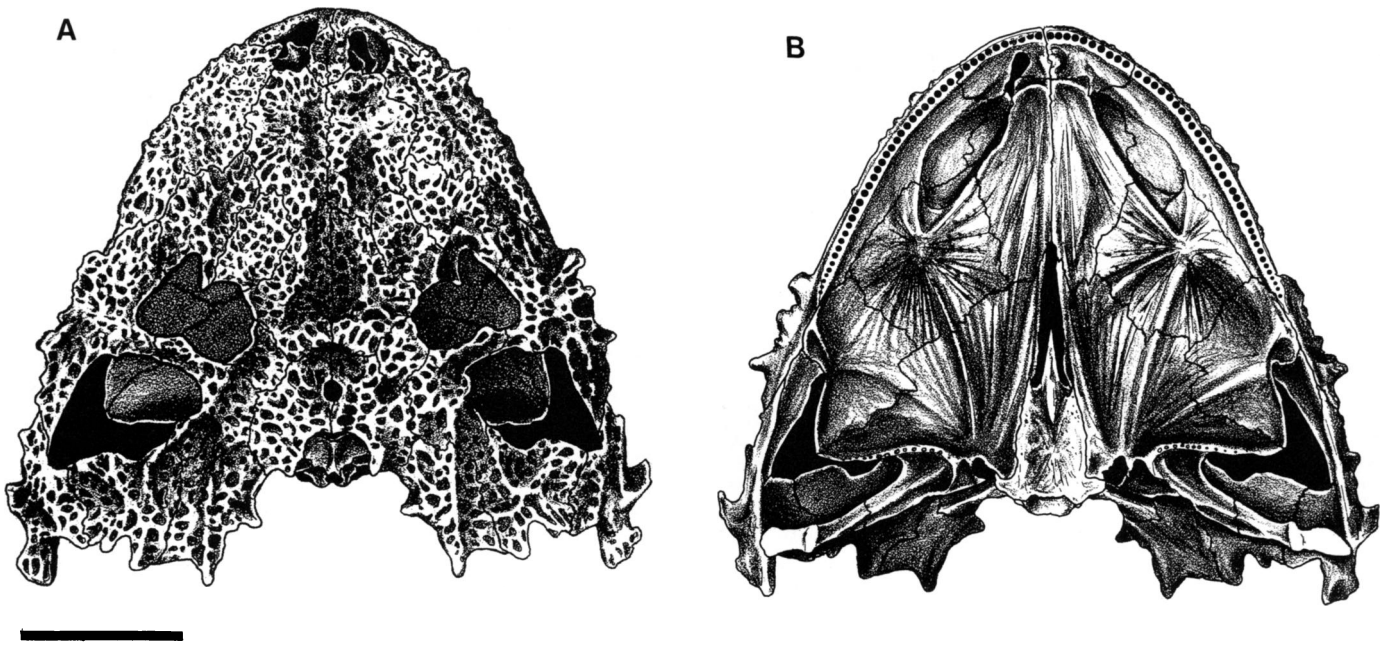

FIGURE 4. Specimen drawing of *Lanthanosuchus watsoni* Efremov. (**A**) dorsal view and (**B**) palatal view. Scale equals 5 cm.

earliest recognized member of the three groups. Using the tenet of minimum divergence time most recently discussed by Norell (1992) and Weishampel (1993), the earliest parareptile must extend into at least the Westphalian of the Upper Carboniferous. This suggests that representatives of all three major amniote clades (Diapsida, Synapsida, and Parareptilia) all diverged early in the evolutionary radiation of amniotes (Fig. 3). At the very least, parareptiles are much more diverse and possess a richer fossil record than previously recognized.

Within Parareptilia there is strong support for a distinct taxonomic unit which we have chosen to name Ankyramorpha. This clade includes all parareptiles exclusive of millerettids and is supported by fifteen synapomorphies (Fig. 3, Node B) only one of which is ambiguous: 1*, 2(2), 14, 23, 25, 29, 33, 41, 43, 47, 48, 50, 52, 53, and 54 (numbers refer to appendix 1 and 2, number in parentheses refers to a multi-state character).

Many of the synapomorphies diagnosing Ankyramorpha were previously diagnostic for Procolophonia. Indeed, Procolophonia was the most robust clade presented by Laurin and Reisz (1995) and included 29 synapomorphies. Only 19 of the original 29 are used in the present analysis. Those characters not considered were excluded because they could not be coded for the majority of taxa evaluated in this analysis. Furthermore, of the remaining 19 only six (4, 28, 30, 42(2), 51, and 59) presently diagnose Procolophonia. A seventh (31) is new to this study. The remaining thirteen characters, which are enumerated below, diagnose the more inclusive Ankyramorpha or the clade of *Macroleter* plus Procolophonia.

It is inevitable that in any particular analysis adding taxa that are nested within previously recognized clades will result in the effective reduction of the number of synapomorphies at any given node. Those synapomorphies presented by Laurin and Reisz (1995), and included in the present analysis, but which are no longer valid for Procolophonia are enumerated below (numbers refer to characters in appendix 1 and 2): 41, 43, 47, 48, 50, 52, 53, and 54 are now diagnostic for Ankyramorpha; 13, 15, 27*, 35*, and 55 diagnose the clade that includes *Macroleter* plus Procolophonia.

Some of the characters described above now represent synapomorphies between Procolophonia and the Russian taxon *Macroleter.* Additional study of nycteroleterids is currently underway by the authors and any further commentary on their exact relationship to Procolophonia must await the completion of that study. However, most of the other characters previously diagnostic of Procolophonia are presently diagnostic of Ankyramorpha.

CONCLUSION

There are three main points that can be considered when acknowledging that *Acleistorhinus,* lanthanosuchids, and *Macroleter* nest within Parareptilia. The first and most significant point is that Parareptilia as a monophyletic taxon sensu Laurin and Reisz (1995) is not only supported but its composition is augmented. In the phylogeny presented by Laurin and Reisz the Parareptilia was considered in a broader phylogenetic context, which focused more on establishing specific interrelationships within Amniota. Support for a monophyletic Parareptilia with a cosmopolitan and morphologically diverse composition is now well established. However, recent opposing views pertaining to the phylogenetic position of Testudines within Parareptilia are not addressed herein.

At present two competing hypotheses on turtle origins have been published with either procolophonids (Reisz and Laurin, 1991; Laurin and Reisz, 1995) or pareiasaurs (Lee, 1993) as sister-taxa to Testudines. It is clear that further work is required to resolve this controversy.

The second point is the identification of a parareptilian taxon in North America within the Paleozoic. Previously Paleozoic members of the clade were known to have only an Old World distribution. However, this is clearly no longer the case. In fact, not only is *Acleistorhinus* from North America, it is also the oldest known member of the clade. In addition, other material not previously recognized as parareptilian is also present in North America. Bolt (1980) described a nearly complete right maxilla (PR1089) from the Lower Permian locality at Richards Spur, near Fort Sill, which is undoubtedly parareptilian. The element has a high anterodorsal maxillary process and most

significantly possesses a large foramen directly below the narial margin.

The consequences of a parareptile presence in the Western Hemisphere during the Paleozoic are far-reaching. Until the present only Synapsida and Diapsida could trace their earliest known members to North America. Now parareptiles can also trace their earliest record from the same continent.

The final point pertains to the depositional environment associated with the locality in which *Acleistorhinus* was discovered. The locality of South Grandfield (Daly, 1973) is assigned to the Hennessey Formation of southwestern Oklahoma. This formation is believed to be contemporaneous with the Richards Spur locality near Fort Sill, Oklahoma. Both localities possess a mixed fauna, which is generally found as disarticulated and incomplete skeletal remains. In addition, of the over 500 specimens collected at South Grandfield, including over 200 skulls, only one specimen of *Acleistorhinus* is known. It is likely that this taxon is an erratic and it would not normally be preserved in the depositional environments that characterize the Lower Permian of North America.

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APPENDIX 1

Character Description:

The characters are enumerated below and presented in anatomical order. For precise distribution of characters among clades refer to appendix 2. To facilitate comparison, the primitive condition, for each character, and its distribution, is given immediately after the character name.

1. Premaxillary dorsal process: A broad dorsal process of the premaxilla (0) where the narial opening faces predominantly laterally is primitive for amniotes and is present in synapsids and captorhinids. A narrow dorsal process of the premaxilla, so that the nares face anterolaterally, (1) is present in all ankyramorphs. The character cannot be determined in millerettids.

2. Maxilla anterodorsal process: Primitively, the maxilla is low and does not reach up behind the nares to the dorsal limit of the narial margin (0). The present analysis indicates that the presence of an anterodorsal process of the maxilla (1) which excludes the lacrimal from the narial margin is found in all members of Ankyramorpha.

3. Anterolateral maxillary foramen: The absence of a distinct, large, maxillary foramen immediately behind the nares is primitive for amniotes (0). A large foramen (1) is present in all known parareptiles.

4. Pineal foramen: In general the pineal foramen is located in the center of the parietal (0). This is the case for all taxa coded here except Ankyramorpha. The derived condition places the pineal foramen at or very close to the frontoparietal suture (1). Both *Acleistorhinus* and Procolophonia possess the derived condition. However, the polymorphism present in lanthanosuchids, and the primitive condition present in *Macroleter* results in an ambiguous optimization for this character.

5. Prefrontal: In Paleozoic amniotes the prefrontal extends well beyond the anterior margin of the frontal (0) when viewed in dorsal aspect. This condition is true for all the taxa considered here except millerettids and lanthanosuchids. The latter two taxa have reduced the anterior extent of the prefrontal (1) or have conversely extended the anterior limit

of the frontal so that the former terminates prior to reaching the anterior margin of the latter.

6. Frontal: In most Paleozoic amniotes the anterior margin of the frontal is at an angle of 90° to its lateral margin (0). This is true of all of the taxa considered in this analysis except the clade comprised of *Acleistorhinus* plus Lanthanosuchidae. In this clade, the anterior border of the frontal is at an oblique angle of not more than 70° toward the mid-line (1).

7. Frontal lateral lappet: A lateral lappet of the frontal is absent (0) in all taxa considered here except *Acleistorhinus* and lanthanosuchids. A large frontal lappet which occupies at least one-third the dorsal margin of the orbit is diagnostic for Lanthanosuchoidea (Node C).

8. Postparietal: A large dorsally exposed postparietal is primitive (0) for amniotes and is present in all taxa except Ankyramorpha. The reduction or complete loss of the postparietal (1) appears to be a valid diagnostic feature of Ankyramorpha.

9. Lacrimal-nasal contact: A broad contact between the lacrimal and nasal (0) is considered primitive for amniotes. A marked reduction in the area of contact (1) between the two elements is here defined as a synapomorphy of the clade comprised of *Macroleter* plus Procolophonia. A separate derived condition whereby the lacrimal is entirely excluded from contact with the nasal (2) is an autapomorphy of *Acleistorhinus.*

10. Foramen orbitonasale: A foramen is not present (0) between the prefrontal, lacrimal, and palatine in synapsids (Laurin and Reisz, 1995) and eureptiles. A foramen (1) is present in millerettids and Procolophonia. Unfortunately, the condition in all ankyramorphs below the level of Procolophonia could not be determined.

11. Jugal anterior process: In most Paleozoic amniotes the jugal is excluded from the anterior margin of the orbit (0). Extension of the jugal so that it reaches the anterior orbital margin is present (1) in captorhinids, lanthanosuchids, and members of Parareptilia. The evolutionary history of this character is ambiguous because an increased anterior extent of the jugal may be a valid synapomorphy of Reptilia with independent reversals in both millerettids and *Acleistorhinus,* or it may be an autapomorphy of captorhinids and ankyramorphs, with a subsequent reversal in *Acleistorhinus.* One other scenario (DELTRAN) has the derived state independently acquired in captorhinids, lanthanosuchids, and Parareptilia.

12. Postorbital-supratemporal contact: Among amniotes, the presence of a postorbital-supratemporal contact is considered primitive (0), and is present in all taxa considered here except captorhinids where contact is absent (1).

13. Postorbital: Posterior margin of postorbital approaches occiput (0) or distant from occiput (1). In all amniotes except captorhinids, *Macroleter,* and Procolophonia the postorbital is located close to the occipital region of the skull. Lanthanosuchids appear polymorphic, but upon further inspection, it is clear that in *Lanthanosuchus* the derived configuration results only from the posterior expansion of the skull table. In fact, the postorbital is quite close to the occiput and may, therefore, be interpreted as primitive. The derived state is, therefore, an autapomorphy of Captorhinidae and Taxon D.

14. Postorbital: The posterior process of the postorbital is generally slender and always half as wide as it is long (0) in amniotes primitively. An increase in the width of the posterior process of the postorbital, resulting in a parallelogram outline in lateral aspect (1), diagnoses Ankyramorpha.

15. Tabular: The tabular is present (0) in all amniotes included here, except captorhinids and the clade which includes *Macroleter* and Procolophonia where the tabular is absent (1).

16. Quadratojugal-lateral temporal fenestra contribution: Primitively the quadratojugal is excluded from the posterior border of the lateral temporal fenestra (0). A contribution of the quadratojugal to the lateral temporal fenestra is present (1) only in Lanthanosuchoidea.

17. Lower temporal fenestra: Absence of a lower temporal fenestra probably represents the primitive condition for amniotes (0). The presence of a lower temporal fenestra (1) arises, apparently independently, in three of the four clades considered in this analysis. The derived state is well established in synapsids. A lower temporal fenestra is apparently also present within some millerettids, and in lanthanosuchids and *Acleistorhinus.* Personal examination of a well-preserved skull of *Macroleter* has also demonstrated the presence of a lower temporal fenestra. The optimization of the character must, however, remain ambiguous. A lower temporal fenestra may be primitive for amniotes with independent losses in mesosaurids, captorhinids, and Procolophonia, or it may represent an independent acquisition in synapsids and parareptiles with subsequent losses within millerettids and in Procolophonia.

18. Temporal emargination (otic notch): The absence of any embayment in the posterior margin of the skull is primitive for amniotes (0). All parareptiles show the presence of a temporal emargination (1) (Laurin and Reisz, 1995).

19. Postfrontal-supratemporal contact: All of the taxa considered here, except *Acleistorhinus,* lack a postfrontal-supratemporal contact (0). Contact between both elements (1) is an autapomorphy of *Acleistorhinus.*

20. Postorbital contribution to lateral temporal fenestra: Primitively, the lateral temporal fenestra is bordered by four bones: jugal, quadratojugal, squamosal, and postorbital (0). This is true of all taxa possessing a lateral temporal fenestra except *Macroleter* and *Acleistorhinus* where the postorbital is excluded (1).

21. Snout elongation: Primitively, in most Paleozoic amniotes the snout is short with the antorbital region equal to or only slightly longer than the postorbital region of the skull (0). The derived condition where the antorbital region is greatly extended (1) is present in mesosaurids.

22. Quadrate lateral exposure: The quadrate of Permocarboniferous amniotes is hidden from lateral view, representing the primitive condition (0). This is true for all taxa considered here except millerettids where the quadrate is exposed posterolaterally (1).

23. Jaw articulation: The position of the jaw articulation is here considered primitive if it is level with the occiput (0). This interpretation differs slightly from Laurin and Reisz's definition, which considered a posterior placement of the jaw articulation as primitive. The primitive state is true of all amniotes including millerettids contra Laurin and Reisz (1995) and the lanthanosuchid *Lanthaniscus* and can be identified by the equivalent posterior limit of the basioccipital in relation to the quadrate condyle. The derived states are manifested in *Acleistorhinus, Macroleter,* and Procolophonia where the position of the jaw articulation transects the main body of the parasphenoid-basisphenoid complex when an imaginary line is drawn from one quadrate condyle to the other (1), and within lanthanosuchids (*Lanthanosuchus*) where the jaw articulation is located well back of the posterior most limit of the basioccipital (2).

24. Posterior extension of the orbit: A generally circular orbit (0) which does not have its posterior margin reach the level of the pineal foramen represents the primitive condition for amniotes. Posterior extension of the orbit is hence derived (1). All taxa considered here are primitive for this trait except *Macroleter* and members of Procolophonia. Optimization is ambiguous because the condition in Procolophonia is here scored as polymorphic.

25. Dermal sculpturing: As demonstrated by most synapsids, mesosaurids, millerettids, and procolophonids amniotes primitively either lack or possess only weakly developed dermal ornamentation (0). In parareptiles, except *Acleistorhinus,* millerettids, and procolophonids the sculpturing manifests itself as deep pits in combination with prominent raised knobs (1). *Acleistorhinus* differs from both these patterns in having only shallow pits (2).

26. Arcuate flange of pterygoid: The presence of an arcuate flange on the pterygoid (0) is believed to be primitive for Amniota. The loss of this flange (1) occurs in mesosaurids and captorhinids where it probably represents cases of independent loss.

27. Cranio-quadrate space: A narrow space between the quadrate ramus of the pterygoid and the paroccipital process (0) was described by Lee (1993) as primitive for amniotes. An enlarged space (1) between these elements was shown to be derived for all members of Procolophonia (Laurin and Reisz, 1995). The present analysis demonstrates the derived condition to be present in *Acleistorhinus* and *Macroleter* as well. It is likely that this character is related to the position of the jaw articulation (character 17).

28. Pterygoid anterior extent: In all taxa considered here except Procolophonia, the anterior limit of the pterygoid reaches the posterior level of the choana (0). Failure of the anterior process of the pterygoid to reach the level of the choana (1) is considered derived.

29. Quadrate ramus of pterygoid: Primitively, the quadrate ramus of the pterygoid merges into the transverse flange of the pterygoid smoothly and without any distinctive excavation (0) along its posterolateral margin. This is the condition found in all amniotes except Ankyramorpha where a deep excavation develops on the posterolateral surface (1).

30. Transverse flange of pterygoid: A posterolaterally or laterally directed transverse flange of the pterygoid (0) is primitive for all amni-

otes. An anterolateral orientation of the transverse flange of the pterygoid (1) is an autapomorphy of Procolophonia.

31. Palatine contribution to palate: Primitively, in amniotes, the palatine is narrow and restricted to the lateral margins of the palate (0). This character can be quantified as the maximal width of the palatine, measured along an oblique axis relative to the mid-line, compared to the maximum width of the anterior process of the pterygoid measured along the same axis. The derived condition exhibits a palatine that is at least 50% broader than the pterygoid. Captorhinids, millerettids, and *Acleistorhinus* are primitive in retaining a narrow palatine. Possession of a broad palatine (1) that exceeds 50% the width of the pterygoid is scored as derived in Procolophonia, Synapsida, and Lanthanosuchidae.

32. Ectopterygoid teeth: Primitively amniotes possess a dentigerous ectopterygoid (0). All parareptiles except lanthanosuchids have lost their ectopterygoid teeth (1). However, assigning this derived condition as a diagnostic feature of Parareptilia must remain equivocal for the condition cannot be scored for captorhinids nor mesosaurids.

33. Ectopterygoid relationship to transverse flange: In all non-ankyramorphs for which the condition could be determined, the ectopterygoid is located distal to the transverse flange and does not contribute to the flange (0). In ankyramorphs the ectopterygoid approaches and makes contact with the tooth bearing region of the transverse flange (1) of the pterygoid.

34. Ectopterygoid: A small ectopterygoid, where it occupies less than one-third the total width of the pterygoid along its widest margin (0) is present in synapsids, millerettids, *Macroleter,* and Procolophonia. A large ectopterygoid where it is one-half as wide as the pterygoid (1) is found in the *Acleistorhinus*-lanthanosuchid clade. A second derived state is where the ectopterygoid is lost (2) as in captorhinids and mesosaurs.

35. Presence of a suborbital foramen: The absence of a suborbital foramen is primitive for amniotes (0). Its presence (1) has been shown to be a valid diagnostic feature of Reptilia (Laurin and Reisz, 1995). The present analysis indicates that the absence of this foramen in Lanthanosuchidae is a character reversal.

36. Length of basicranial articulation: The basicranial articulation or contact between the basipterygoid processes of the parasphenoid and their paired counterparts on the pterygoids is primitively restricted to the anterolateralmost margin of the parasphenoid (0). This condition is true for all the taxa considered here except the clade of *Acleistorhinus* and Lanthanosuchidae. In this clade, there is a long contact between parasphenoid and respective pterygoids that extends over much of the length of the main body of the parasphenoid (1).

37. Ventral exposure of basioccipital: Primitively, the basioccipital contributes extensively to the ventral surface of the braincase (0). This is true of all taxa considered in this analysis, except *Acleistorhinus* and lanthanosuchids. In these latter taxa the ventral exposure of the basioccipital is restricted to the condylar region (1).

38. Basipterygoid tubera: In all amniotes considered here except *Acleistorhinus* and lanthanosuchids, the basipterygoid tubera form paired processes extending laterally away from the main body of the basipterygoid (0). This configuration results in a distinct process that is bordered anteriorly and posteriorly by distinct notches. Lanthanosuchoids (Node C) are derived in having lost the posterior notch (1) so that the basipterygoid tubera are confluent with the main body of the basiparasphenoid.

39. Parasphenoid excavation for cervical muscles: Among amniotes deep pockets or excavations are present on the ventral surface of the parasphenoid (0) in both synapsids and mesosaurids and represents the primitive condition. The apparent loss of these pockets (1) was proposed as an autapomorphy for Reptilia as defined by Laurin and Reisz (1995). The present analysis agrees with this conclusion, but the condition in *Acleistorhinus* is not determinable due to the poor state of preservation of the ventral surface of the parasphenoid.

40. Parasphenoid teeth: As suggested by Laurin and Reisz, the absence of parasphenoid teeth (0) may be primitive for tetrapods. Synapsids and captorhinids are polymorphic and millerettids, lanthanosuchids, and *Acleistorhinus* are derived in possessing teeth (1). The presence of teeth may, therefore, be autapomorphic for millerettids and represent a synapomorphy uniting lanthanosuchids with *Acleistorhinus.* Alternatively, the development of parasphenoid teeth may be a synapomorphy of Reptilia with independent losses within captorhinids and for the *Macroleter*-Procolophonia clade. However, due to the numerous apparently independent acquisitions and losses of teeth on the parasphenoid, this character is best considered equivocal.

41. Length of cultriform process: A long cultriform process (0) is recognized as primitive for amniotes (Laurin and Reisz, 1995). A short cultriform processes (1) is present not only in Procolophonia, but in all members of Ankyramorpha.

42. Supraoccipital: Primitively, the supraoccipital is a broad plate (0) that occupies most of the dorsal region of the occiput as exemplified in synapsids and mesosaurs. The supraoccipital is narrowed (1) substantially in Reptilia, as in captorhinids, and is further modified in Procolophonia into a pillar-like structure (2) (Laurin and Reisz, 1995).

43. Paroccipital process: As presented by Laurin and Reisz (1995), the paroccipital process is primitively a deep dorsoventrally expanded blade (0) in amniotes. A separate, derived condition, where the paroccipital process is anteroposteriorly expanded (1) is present in Procolophonia and *Acleistorhinus.* Although, the condition of this character cannot be scored in lanthanosuchids and *Macroleter,* optimization makes this character an ankyramorph autapomorphy.

44. Paroccipital process orientation: Primitively the paroccipital process in amniotes is directed primarily laterally (0). In both lanthanosuchids and *Acleistorhinus* the paroccipital process is oriented obliquely from its base and extends dorsolaterally to contact the supratemporal (1).

45. Paroccipital-supratemporal contact: In synapsids, mesosaurs, and captorhinids the paroccipital process does not contact the supratemporal (0). The derived state is expressed in all parareptiles as a contact between the paroccipital process and the supratemporal (1).

46. Posttemporal fenestra: Primitively, the posttemporal fenestra is restricted to a small opening located between the opisthotic, supraoccipital, and tabular (0). This is clearly the condition in synapsids and appears to be redeveloped (character reversal) within Ankyramorpha, in the lanthanosuchids. The derived state, where the posttemporal opening is enlarged (1) may be a synapomorphy of Reptilia, but the character state optimization is ambiguous because the condition in mesosaurids cannot be determined.

47. Quadrate condyle: In synapsids, mesosaurs, millerettids, and captorhinids the quadrate condyle is primitively convex and elongate anteroposteriorly (0). In Procolophonia (Laurin and Reisz, 1995), the quadrate condyle is derived in being flat and short anteroposteriorly (1). The derived condition is also present in lanthanosuchids and *Macroleter.* In *Acleistorhinus,* the tightly adhered jaws prevent confirmation of the exact condylar configuration, but its length can be estimated and is here interpreted as "short." The derived character is, therefore, diagnostic of Ankyramorpha.

48. Surangular: Primitively, in millerettids, mesosaurs, and synapsids, the surangular extends well anterior to the coronoid eminence (0). A reduction in the anterior extent of the surangular (1) is derived for Procolophonia, *Macroleter,* and *Acleistorhinus.* The derived state diagnoses Ankyramorpha.

49. Total coronoid number: The only taxon which scores as primitive in having more than one coronoid (0) is Synapsida (Laurin and Reisz, 1995). All other taxa, where the character is known, are derived in having only one coronoid bone (1).

50. Prearticular: Primitively, the prearticular is long and continues anteriorly beyond the coronoid eminence (0). This is true of all non-ankyramorphs. A short prearticular (1) is present in procolophonians, *Macroleter,* and *Acleistorhinus*; the condition in lanthanosuchids cannot be determined. The character is nonetheless best interpreted as an autapomorphy of Ankyramorpha.

51. Retroarticular process: In all taxa considered in this analysis except mesosaurids and procolophonians, the retroarticular process is primitive in being small and dorsally convex (0). The derived state of having a broad, dorsally concave retroarticular process (1) is, therefore, a valid autapomorphy of mesosaurids and procolophonians respectively.

52. Trunk neural arches: The narrow neural arches (0) as represented by synapsids and eureptiles are considered to be primitive for Amniota. Swollen neural arches with both a dorsal and a ventral swelling associated with the zygapophyseal buttress (1) is derived for mesosaurids. A second derived condition is manifested in Ankyramorpha where, although the arch is broad as in anamniotes, such as seymouriamorphs, the buttressing is produced as a high, narrow zygapophyseal support, and the neural spine is tall (2).

53. Interclavicular head: Primitively, the interclavicle possesses a broad, diamond shaped head (0). This configuration is found in all non-ankyramorphs considered here. The derived state is represented by an anchor-shaped or T-shaped interclavicular head (1). This configuration

was recently used to diagnose Procolophonia, a conclusion which is emended here to include all ankyramorphs.

54. Clavicle-interclavicle attachment: Primitively, in all non-ankyramorph amniotes, the clavicles rest on the ventrolateral surface of the interclavicle (0). Laurin and Reisz (1995), have described the presence of a deep groove on the anterior margin of the interclavicle (1) in procolophonians, which served as sites of attachment for the paired clavicles. This derived character is presently extended to diagnose a more inclusive clade, the Ankyramorpha. Unfortunately, postcranial elements of *Acleistorhinus* are absent, and the presence of the derived state can only be confirmed in lanthanosuchids.

55. Scapular blade: Primitively, the height to length ratio of the scapular blade is approximately 3:1 (0). This is true of all taxa considered here except procolophonians and *Macroleter,* where the scapula is very tall, at least four times as tall as long (1). The condition is not known in *Acleistorhinus,* but Ivakhnenko (1980) indicates that the scapula of lanthanosuchids is short. The derived state is, therefore, best interpreted as a synapomorphy of the clade that includes *Macroleter* and Procolophonia.

56. Supinator process: Primitively, the supinator process is angled away from the humeral shaft (0) and contributes to a strong ectepicondylar groove (Laurin and Reisz, 1995). This is true only of Synapsida among the taxa considered here. A smaller, less pronounced supinator process (1) that extends distally is present in all sauropsids. A further derivation, where the supinator is greatly reduced to a small nubbin (2), is present in captorhinids.

57. Sacral rib contact: Primitively, the sacral ribs of amniotes are broad and are in contact with each other over a significant portion of their length (0). The derived condition presents a more slender rib configuration which is in contact only distally (1). This derived state was recently interpreted as a synapomorphy of Parareptilia (Laurin and Reisz, 1995). Unfortunately, the present analysis is unable to either confirm or refute their conclusion, for the sacral rib arrangement cannot be determined in either lanthanosuchids, *Macroleter,* or *Acleistorhinus.*

58. Configuration of the iliac blade: Primitively, in all amniotes the ilium possesses a long posterior process (0). This process is absent in parareptiles and instead a fan-shaped distal expansion (1) is present.

59. Acetabular buttress: A small overhang above the acetabulum (0) is primitive for amniotes and is present in the taxa considered here for which the condition can be determined. A very heavy acetabular buttress (1) was reported by Lee (1993) to be present in pareiasaurs and turtles. Recently work by the senior author indicates that a heavy acetabular buttress is also present in *Procolophon.* This derived condition, therefore, diagnoses Procolophonia.

60. Mediale centrale of pes: Presence of the mediale centrale in the pes (0) is considered primitive for amniotes (Laurin and Reisz, 1995). The only taxon in the present analysis that is primitive for this feature is Synapsida. Loss of the mediale centrale (1) is recognized as a diagnostic feature of Sauropsida.

APPENDIX 2. Data matrix used in analysis. Zero (0) denotes primitive state, all other numbers represent derived states for a given character. Polymorphism, when present, is given on a separate line below the relevant taxa.

Taxon	1111111111222222222233333333334444444444555555555556 12345678901234567890123456789012345678901234567890123456789012345678901234567890
Synapsida	00000000000000001000000000000010000000000000000000000000000000 1 1
Mesosauridae	000001000?00000?000?100001?0000??20?0?0000000?001?1100010001
Millerettidae	?0101000010000000100010000000001001000110100110010000000111?1 1
Macroleter	111000001?10111011010011101010011010001011?0111111021?11?101
Acleistorhinus	111101112?000101111100102010100111011?111111011?10?????????
Lanthanosuchidae	11?011110?1001011100000010001010110111111?1101????2110?????
	1 2
Procolophonia	11110000111011?010?001000111111101000101210111110121111111
	1 11 1 2
Eureptilia	00000000001110000000000001000000000000100100010010000001000
	1 2