Eothyris and *Oedaleops*: Do These Early Permian Synapsids from Texas and New Mexico form a Clade?

Author(s) :Robert R. Reisz, Stephen J. Godfrey, and Diane Scott

ARTICLE

EOTHYRIS AND OEDALEOPS: DO THESE EARLY PERMIAN SYNAPSIDS FROM TEXAS AND NEW MEXICO FORM A CLADE?

ROBERT R. REISZ,[*,1] STEPHEN J. GODFREY,[1,2] and DIANE SCOTT[1]

[1]Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Road, Mississauga, Ontario, L5L 1C6, Canada,
robert.reisz@utoronto.ca;

[2]Present Address: Department of Paleontology, Calvert Marine Museum, P.O. Box 97, Solomons, Maryland, 20688, U.S.A.,
Godfresj@co.cal.md.us

ABSTRACT—The monospecific genera *Eothyris* (Petrolia Formation, Leonardian, Archer County, Texas) and *Oedaleops* (Abo/Cutler Formation, Wolfcampian, Rio Arriba County, New Mexico), known solely from cranial remains, are confidently assigned to the monophyletic Caseasauria based on cranial and dental characters. In addition, *Eothyris* and *Oedaleops* comprise the monophyletic Eothyrididae based on nine cranial and dental characters. In contrast to the medium to large sized herbivorous caseids, the small eothyridids exhibit dental features that indicate that they were faunivores. The presence of well-developed caniniform teeth suggests that they were predators. Both *Eothyris parkeyi* Romer and *Oedaleops campi* Langston exhibit a suite of plesiomorphic cranial characters that identify them as basal synapsids. Thus, the eothyridids are better representatives of the primitive synapsid cranial morphotype than the often-used ophiacodontids. Although they appear relatively late in synapsid evolution, both eothyridids are significantly older than all other caseasaurs, forcing the establishment of a long unrecorded lineage for caseids.

INTRODUCTION

The origin and initial diversification of Synapsida represents an important stage in the evolution of terrestrial vertebrates. Paleozoic synapsids include not only some of the oldest known amniotes (Reisz, 1986), but also the majority of Late Carboniferous and Permian taxa. The fossil record provides strong evidence that among Paleozoic amniotes, it is this clade that evolved rapidly, and diversified greatly to dominate the terrestrial ecosystems of the Permo-Carboniferous. Previous phylogenetic analyses (Laurin and Reisz, 1995) have shown that synapsids form one of the two branches of the basal amniote dichotomy, and that this clade has a long evolutionary history, extending from the Paleozoic to the present. Evolutionary events associated with the early history of this clade are therefore critical to our understanding of the initial phases of amniote evolution (Reisz, 1998).

It is generally recognized that caseasaurs are synapsids, and represent one branch of the basal dichotomy of this clade. The Caseasauria, represented entirely by Permian taxa, have been tentatively divided into the Caseidae and Eothyrididae (Reisz, 1986). Caseidae are composed of medium to large bodied herbivorous taxa from the upper part of the Lower Permian of North America and Western Europe, but the fossil record of this clade extends into the Middle Permian of northern Russia (Reisz and Laurin, 2001). Although reviewed by Olson (1965), this group is still poorly known despite the availability of interesting specimens (Maddin et al., 2008).

The family Eothyrididae was originally erected by Romer and Price (1940) as a sort of wastebasket to receive a number of 'primitive' synapsid taxa with large caniniform teeth: *Baldwinonus trux*, *Eothyris parkeyi*, *Stereophallodon ciscoensis*, and *Stereorhachis dominans*. Subsequently, *Baldwinonus dunkardensis* Romer, 1952, *Colobomycter pholeter* Vaughn, 1958,

Delorhynchus priscus Fox, 1962, and *Oedaleops campi* Langston, 1965, were also included within the family. In a systematic review of Permo-Carboniferous synapsids ('Pelycosauria'), Reisz (1986) removed all but *Eothyris* and *Oedaleops* from the family Eothyrididae, but the monophyly of the latter taxon was never tested.

Of the two currently recognized eothyridids (Figs. 1–8), *Eothyris parkeyi* was figured but only very briefly described by Romer (1937:90), at which time he noted, "In many respects it is by far the most primitive known member of the order." Later, Romer and Price (1940) reiterated its primitive appearance and provided additional anatomical information on its cranial elements, devoting most of their attention to the relative proportions of the skull. Watson (1954) added briefly to the description of *Eothyris* and provided restorations of the skull in dorsal view, right lateral view, and the first occipital view. *Oedaleops campi* was named and first described in some detail by Langston (1965), who noted the strong similarities between the two taxa. Although some isolated limb elements from the same quarry as the holotypic skull were tentatively assigned to *Oedaleops* by Langston, this association remains uncertain.

Despite their obvious significance, the anatomy and relationships of *Eothyris parkeyi* and *Oedaleops campi* have not been examined in detail. In addition, several recent phylogenetic analyses of Permo-Carboniferous synapsids have dealt with patterns of relationships (Reisz et al., 1992; Berman et al., 1995), but these dealt with eupelycosaurian taxa, and little is known about the phylogeny of the basal synapsids. The first phylogenetic analysis of caseid relationships (Maddin et al., 2008) provides valuable new information about this clade, but even a cursory examination of caseid cranial and postcranial anatomy shows that these synapsids possess numerous autapomorphic features that tend to obscure the primitive morphological pattern, in great part because of their adaptation to high-fiber herbivory. Thus, as putative basal members of this clade, the anatomy and relationships of *Eothyris* and *Oedaleops* are critical to both phylogenetic studies of synapsids, as well as to the
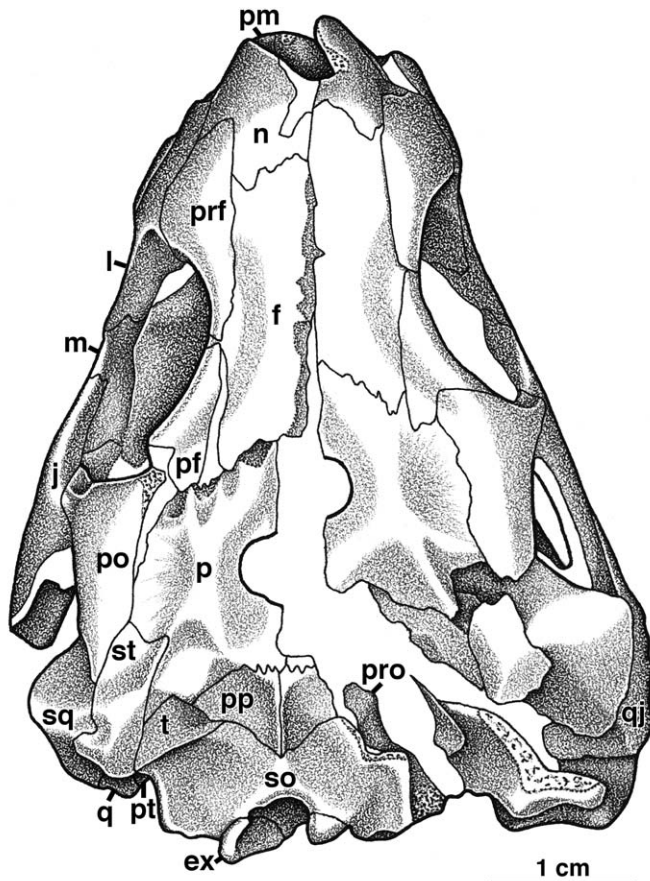
[*]Corresponding author.

FIGURE 1. Specimen drawing of *Eothyris parkeyi* Romer, MCZ 1161 in dorsal view. **Abbreviations**: **an**, angular; **ar**, articular; **bo**, basioccipital; **c**, coronoid; **d**, dentary; **ep**, epipterygoid; **ex**, exoccipital; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **pra**, prearticular; **prf**, prefrontal; **pro**, prootic; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **so**, supraoccipital; **sp**, splenial; **sph**, sphenethmoid; **sq**, squamosal; **st**, supratemporal; **su**, surangular; **t**, tabular.

phylogeny of amniotes. We therefore propose to test the monophyly of the Eothyrididae and its relationship to Caseidae as a first step in the large-scale reexamination of Permo-Carboniferous synapsid phylogeny and diversification.

Certain features of the cranial anatomy of *Eothyris* (Figs. 1–5) have become evident only after judicious mechanical preparation of the type specimen. The discovery of a new skull fragment of *Oedaleops* (Fig. 8) has also provided additional anatomical information. Except for a general description of the overall configuration of the skull, we will not redescribe those areas of the skulls that have already been treated previously.

Institutional Abbreviations—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; **UCMP**, University of California Museum of Paleontology, Berkeley.

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA
CASEASAURIA Williston, 1912

Definition—*Casea broilii* Williston, 1910, and synapsids related more closely to it than to either *Varanops brevirostris* Williston, 1914 or *Ophiacodon mirus* Marsh, 1878.

Diagnosis—Synapsid amniotes with the following cranial autapomorphies: in lateral view, the wedge-like dorsal process of each premaxilla forms an anteriorly pointed rostrum; the external narial shelf, an external flange formed by each nasal, is present beneath the dorsal margin of the narial openings; the external nares are anteroposteriorly elongate, occupying at least one-fifteenth of the skull length, or 25% of snout length; the external surface of each maxilla faces ventrolaterally rather than being oriented vertically; marginal dentition reduced to 22 teeth or fewer; in dorsal view, the antorbital width of the skull is greatest across the lacrimals, giving the antorbital region of the skull a broad appearance, the maxillae are therefore not visible in dorsal view and the lacrimals are visible above the maxillae in ventral view; parietal foramen unusually large, equal or larger in diameter than the foramen magnum; quadratojugal elongate, extending far anteriorly under the temporal fenestra; broad lateral wing of exoccipital, at least equal to the width of the foramen magnum. In addition, caseasaurs differ from all other synapsids in having a broad contribution of postorbital to skull table, maximum width greater than 50% of parietal width, and the supratemporal bone is broad, equal in width to nearly 25% of maximum parietal width, but is still associated with the posterolateral wing of the parietal. Overall the skull is low and broad, and this includes both the temporal region and the snout.

EOTHYRIDIDAE Romer and Price, 1940

Definition—*Eothyris parkeyi* Romer, 1937, and caseasaurians related more closely to it than to *Casea broilii* Williston, 1910.

Diagnosis—Caseasaurian synapsids characterized by the presence of the following cranial autapomorphies: maxillae do not contribute to the floor of external nares and premaxilla has long posterolateral process; two regions of enlarged teeth present on the maxillae, one far anteriorly (primary caniniform teeth), and a second midway along the maxillary tooth row just beneath the anterior margin of the orbit (secondary caniniform teeth); primary caniniform teeth greatly enlarged, more than twice the size of the immediate postcanine teeth; anterior position of the primary caniniform teeth, at most one precanine maxillary tooth being present in *Oedaleops* and none in *Eothyris*; jugals excluded from the ventral margin of the cheek by a long anterior process of the quadratojugals; posterior process of jugal long, forming ventral edge of temporal fenestra; squamosals having a broadly rounded posterior border that provides poor separation between the cheek and the occipital surface of the skull. Differs from all caseids in having dorsoventrally narrow, elongate lacrimals, maximum height being one-third or less than interorbital width.

EOTHYRIS Romer, 1937

Diagnosis—Small eothyridid caseasaur characterized by the greatly enlarged pair of canines that gives the snout a swollen appearance posterior to the external naris. Maxilla with distinct dorsal expansion above canines. No precaniniform teeth present in maxilla. Lacrimal slightly expanded laterally above the canines, and there is no lacrimal-jugal contact in the orbit. Therefore, maxilla contributes to the margin of the orbit.

EOTHYRIS PARKEYI Romer, 1937

Diagnosis—As for genus, monotypic.
Type Species—*Eothyris parkeyi* Romer, 1937.
Diagnosis—As for the genus.
Holotype—MCZ 1161 (Figs. 1–5), complete skull with mandibles, only slightly crushed along the midline of the skull table, allowing us to provide reconstructions in three views (Fig. 1).
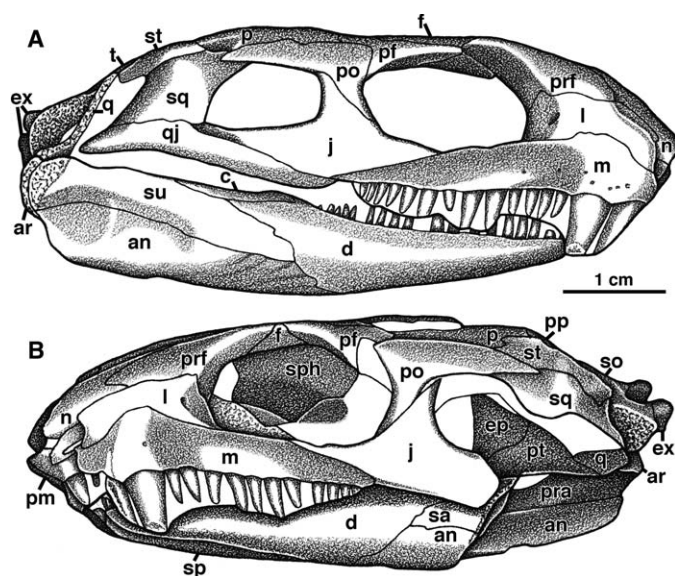
FIGURE 2.   Specimen drawings of *Eothyris parkeyi* Romer, MCZ 1161 in (**A**) right lateral, and (**B**) left lateral views, respectively. For anatomical abbreviations see Figure 1.

FIGURE 3.   Specimen drawing of *Eothyris parkeyi* Romer, MCZ 1161 in palatal view. For anatomical abbreviations see Figure 1.

Horizon and Type Locality—Petrolia Formation, Wichita Group, Leonardian, Lower Permian, from Tit Mountain, near Dundee, Archer County, Texas, USA.

OEDALEOPS Langston, 1965

Diagnosis—Small eothyridid caseasaur characterized by the presence of a single median postparietal that is excluded from the posterior edge of the skull table by a posteroventrally deflected occipital component of the parietal; frontal contribution to the orbit greater than in *Eothyris*. Differs from other caseasaurs in having a slender anteroventrally sloping postorbital bar, and a long tooth row, with at least 18 maxillary teeth, the highest number for any caseasaur.

OEDALEOPS CAMPI Langston, 1965

Diagnosis—As for genus, monotypic.
Type species—*Oedaleops campi* Langston, 1965.
Diagnosis—As for the genus.
Holotype—UCMP 35758, a partial skull, preserving much of the roof (Figs. 6, 7).
Referred specimens—UCMP 69679 three skull fragments, including a transverse section through the skull roof at the level of the orbit (Fig. 8), and part and counter-part of an incomplete skull table split through the spongiosum of the dermal bone. The latter is not illustrated but includes the poorly preserved posterior halves of the frontals, the postfrontals, part of the left postorbital, the parietals, and the postparietal.
Horizon and Type Locality—Abo/Cutler Formation, Wolfcampian, Lower Permian; Camp Quarry, near Arroyo de Agua, Rio Arriba County, New Mexico, USA.

DESCRIPTION AND COMPARISONS

This section refers to the anatomy of both *Eothyris* and *Oedaleops*, but with greater emphasis on the former because it is the more complete of the two. Because there is a well-preserved occiput, it has been possible to produce a skull reconstruction of *Eothyris* (Fig. 1), even though the palate is insufficiently exposed to be included. There is too little of the skull preserved in *Oedaleops* to permit a full skull reconstruction, nothing being
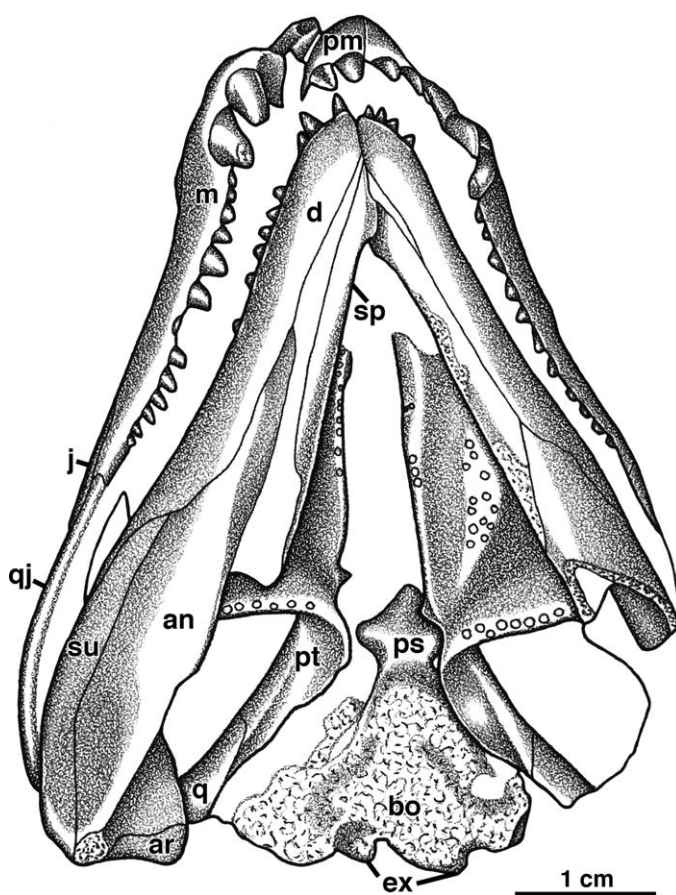
available from the occiput or the palate. It is therefore not possible to provide a precise outline of the skull in either dorsal or lateral views.

In cross-section, the gently convex skulls of *Eothyris* and *Oedaleops* are very low and broad by eupelycosaur standards (Berman et al., 1995). The midpoint in skull length lies just ahead of the posterior margin of the orbit. Caseids inherited this primitive cranial morphology and retained its general
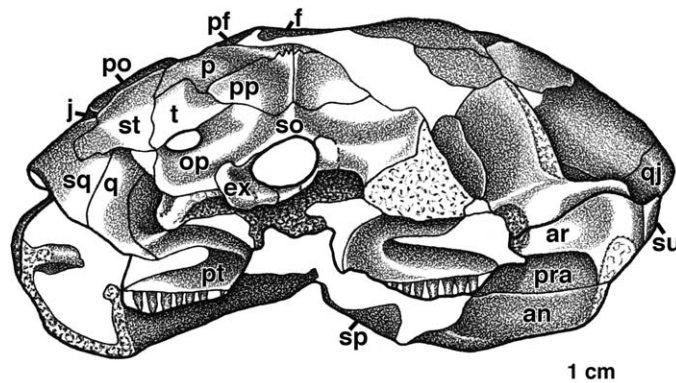
FIGURE 4.   Specimen drawing of *Eothyris parkeyi* Romer, MCZ 1161 in occipital view. For anatomical abbreviations see Figure 1.
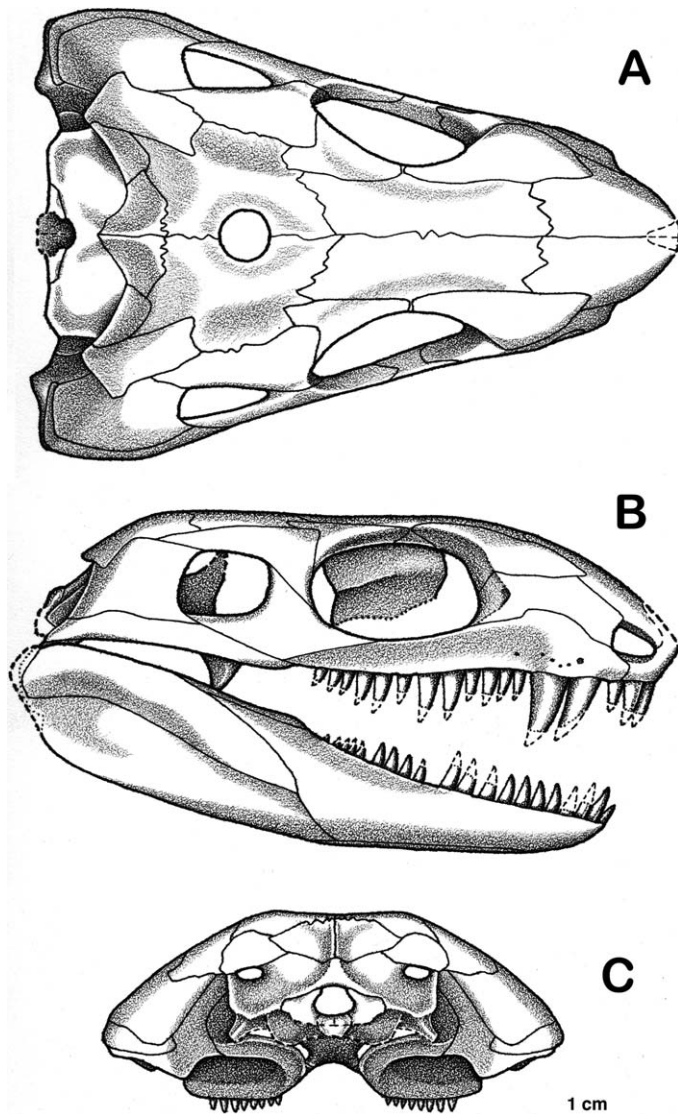
FIGURE 6. Specimen drawings of *Oedaleops campi* Langston, UCMP 35758, in (**A**) right lateral, and (**B**) left lateral views, respectively. **C**, the quadratojugal bone, which was attached to the ventral side of the skull. For anatomical abbreviations see Figure 1.

FIGURE 5. Restorations of the skull of (**A–C**) *Eothyris parkeyi* Romer, based on MCZ 1161 in **A**, dorsal; **B**, right lateral; and **C**, occipital views, respectively.

region (Figs. 1, 2). The large contribution of the postorbital to the skull table is also seen in other caseasaurs, and is considered to represent either the primitive condition for synapsids or another autapomorphy of caseasaurs.

In both *Eothyris* and *Oedaleops* the parietal bone has three distinct surfaces, a flat area that surrounds the large pineal foramen, a gently sloping lateral area in line with the medial sutures of the postfrontal and supratemporal bones, and a paired concave area on either side of the midline that is somewhat contiguous with the surfaces of the postparietal and tabular bones. *Oedaleops* differs from *Eothyris* and other caseasaurs in having an unusually large paired occipital concavity on the parietal (Fig. 6), one that extends from the posterior border of the pineal opening to the postparietal. The postparietal is a relatively large paired element in *Eothyris* that extends posteroventrally from the posterior edge of the skull table, as in all other caseasaurs, except *Oedaleops* where this bone is excluded from the posterior edge of the skull table, and there appears to be no midline suture between the two large, lateral wings.

Perhaps the most striking feature of *Eothyris* is the morphology of the maxilla, as it reflects its unique dental pattern (Figs. 1–4). The maxilla is a slender, elongate element and has

configuration while modestly evolving towards increasingly isometric proportions.

The frontals and parietals are approximately equal in their midline length, but the nasals are shorter than the other paired elements, possibly because of the short length of the snout. Contrary to previous interpretations, the frontal of *Eothyris* (Figs. 1–3) has a slight contribution to the orbital margin, but smaller than that of *Oedaleops* (Figs. 6, 7). This tiny contribution to the orbit effectively prevents contact between the prefrontal and postfrontal bones. This condition can be seen clearly in the left side of MCZ 1161, where the skull has not been telescoped, and the spatial relationships between these three bones can be seen in both dorsal and lateral views (Figs. 2, 3). A similar pattern is seen in *Cotylorhynchus*, and appears to represent the primitive condition for Caseasauria because it is prevalent in that clade. The postorbital bone is very large in *Eothyris*, perhaps relatively the largest for any synapsid, with large lateral and dorsal contributions to the skull roof. Its large dorsal exposure increases the breadth of the skull table in this
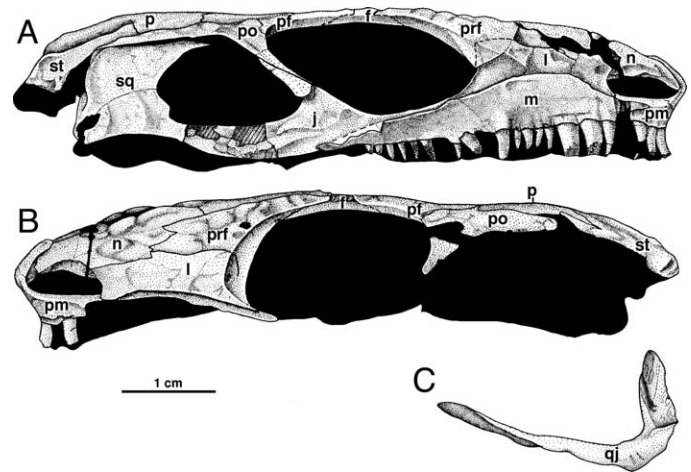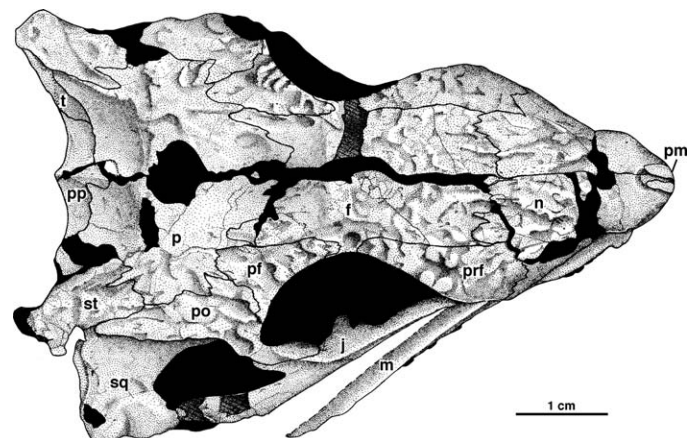

FIGURE 7. Specimen drawing of *Oedaleops campi* Langston, UCMP 35758, in dorsal view. For anatomical abbreviations see Figure 1.

an abrupt dorsal expansion in the area of the primary canine pair. This is different from the pattern seen in *Oedaleops*, where the modest dorsal expansion of the maxilla is smoothly convex in the region of the canines (Figs. 6, 7A). In addition, in *Eothyris*, the maxilla carries such huge canines that the anterior portion of the maxilla projects laterally, giving this area a swollen appearance immediately posterior to the external naris. Posterior to the canines, the maxilla has an orientation that characterizes all caseasaurs, its lateral surface being tilted slightly ventromedially (Fig. 3). In the orbital region, the maxilla contributes to the ventral margin of the orbit, bridging the space between the jugal and lacrimal bones. This is in contrast to the condition seen in *Oedaleops* and in caseids where this area can be discerned (i.e., *Casea rutena* and *Cotylorhynchus*), where the long, slender suborbital process of the lacrimal makes contact with the anterior process of the jugal (Figs. 6, 7A). However, as seems to be the case in all caseasaurs, the edge of the maxilla is either very close, or contributes directly to the ventral orbital margin. In both *Eothyris* and *Oedaleops*, the precaniniform process of the maxilla is extremely short, with that in the former carrying no teeth, and that in the latter carrying one tooth in front of the canines. Thus, the maxilla has little or no contribution to the floor of the external naris. This is in strong contrast to the condition found in all caseids, in which the maxilla contributes significantly to the floor of the narial opening.

The teeth of *Eothyris* and *Oedaleops* show none of the heterodont adaptations seen in caseids for herbivory. Although eothyridid teeth vary in size in relation to their position in the jaw, they retain the primitive sharply pointed conical morphology. Our designation of eothyridids as faunivores is based on their tooth morphology, the presence of well-developed caniniform teeth, small body size, and the premise that faunivory represents the primitive amniote dietary preference. A microwear analyses of eothyridid teeth might reveal whether they were hard-object faunivores (i.e., those that primarily consume hard-body invertebrates or actively comminute bone) or soft-object faunivores (i.e., caterpillar, or vertebrate flesh specialists).

The lacrimal is located directly above the anterior half of the maxilla, extends from the orbit to the posterior edge of the external naris and its lateral surface lies in the same plane as the maxilla, so that the snout has a distinctly swollen appearance in *Eothyris* (Figs. 1, 2). This bone is relatively slender, extending as a relatively narrow band of bone between the orbit and the external naris. It is difficult to determine if this is the primitive condition for synapsids, or a derived condition seen in these two taxa. The condition in caseids is highly autapomorphic with a relatively tall, anteroposteriorly short lacrimal, in keeping with their tall, large narial opening.

In *Oedaleops* (UCMP 69679, Fig. 8), a line of foramina is present on the orbital margin of each lacrimal immediately below the prefrontal-lacrimal suture. The line of openings approximately parallels the dorsolaterally directed suture between the two bones. On each lacrimal, two of these foramina are larger than the others. Two foramina like these may represent the primitive condition for amniotes (Modesto, pers. comm. Oct. 2007).

In both taxa, the premaxilla has the typical caseasaurian morphology with an anterodorsally directed process that creates the appearance of a short, pointed rostrum (Figs. 3, 4, 7). Each premaxilla has three tooth positions.

Despite being shorter than the frontal or parietal, the nasal is a broad element, extending far ventrolaterally on either side of the snout, where it forms the elongate dorsal border of the external naris. As in all caseasaurs, both taxa have well-developed external narial shelves on the nasals.

The prefrontals of both taxa are massive and make large dorsal and lateral contributions to the snout, giving the skull its typically broad caseasaurian appearance (Figs. 2, 6). In contrast
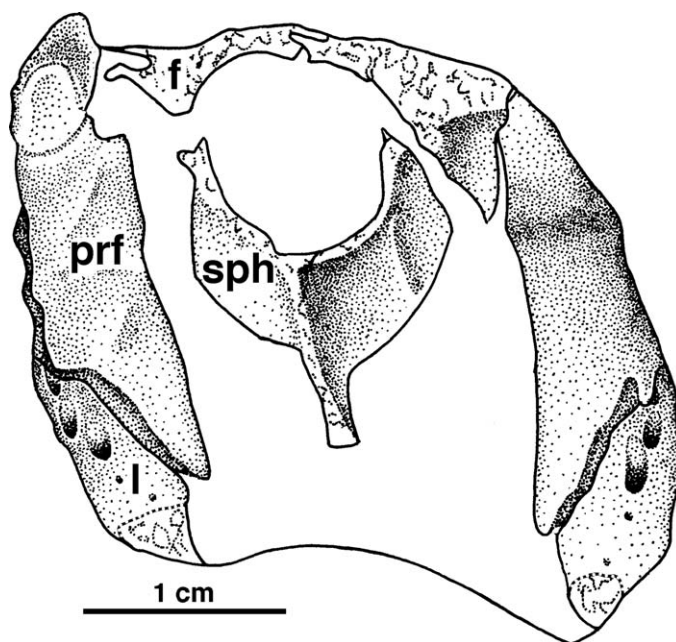

FIGURE 8. Specimen drawing of *Oedaleops campi* Langston: transverse section through the sphenethmoid of UCMP 69679 showing the anterior edge of the orbit.

to the highly modified condition seen in caseids, where the lacrimal is greatly shortened anteroposteriorly and the ventral process of the prefrontal is pinched off by the greatly enlarged external naris, the ventral process of the prefrontal is long, and forms much of the anterior orbital border. This is present in both taxa, but is particularly well represented in a skull fragment of *Oedaleops*, UCMP 69679 (Fig. 8). This partial skull also shows clearly the Y-shaped outline of the sphenethmoid, and its close association dorsally with the frontal.

The jugal has a particularly 'archaic' appearance in *Eothyris*, perhaps because the anteroventral indentation for the lateral temporal fenestra is not strongly emarginated (Figs. 1–3). The postorbital bar is broad and massive. In these features, *Eothyris* seems more primitive than *Oedaleops* because the jugal in the latter has a deep anteroventral temporal emargination (Fig. 7), and forms a relatively more slender postorbital bar than in either *Eothyris* or *Casea*. In addition, in both *Eothyris* and *Oedaleops*, the posterior process of the jugal is long, and makes contact with the squamosal, excluding the quadratojugal from the temporal fenestra. The same condition is also present in *Casea broili*, the varanopid *Mycterosaurus*, as well as in ophiacodontids, indicating that this is probably the primitive condition for synapsids. Other caseids show the derived condition of the quadratojugal entering the temporal fenestra, which is attributed to the greatly enlarged temporal fenestra in the large caseids.

In both taxa, the quadratojugal is an exceedingly long, slender element that appears to lack a dorsal process (Figs. 1–4, 6, 7). This bone extends anteriorly to form the ventral edge of the skull along nearly one-third of the skull length, from the posterior edge of the skull to the level of the intertemporal bar. In fact, the anterior tip of the bone extends nearly to the level of the posterior orbital border, and underlaps the maxilla for a short distance. This great length of the quadratojugal appears to be an autapomorphy of eothyridids because in both basal caseids and varanopids, where the quadratojugal makes contact with the maxilla, the latter bone extends posteriorly beyond the posttemporal bar, resulting in a relatively shorter quadratojugal.

Although the quadratojugal is elongate in caseids, it rarely extends to the level of the anterior border of the temporal fenestra (*Cotylorhynchus*), and never under the postorbital bar. The occiput is only preserved completely in *Eothyris* (Figs. 1, 5), and has the outline of a low trapezoid, not at all box-like as seen in eupelycosaurs. The squamosal of both taxa extends far medially onto the occiput without forming a distinct boundary between the temporal and occipital surfaces. Despite its large contribution to the occipital region, the squamosal does not make contact with the paroccipital process of the opisthotic in *Eothyris* (Fig. 5). This condition is also seen in caseids, ophiacodontids, as well as in varanopids, and probably represents the primitive synapsid condition. In addition, *Eothyris* appears distinct from other synapsids in not having a contact between the squamosal and the supraoccipital. As in other caseasaurs, both the supratemporal and the paroccipital processes of the opisthotic extend posteriorly beyond the edge of the skull. In addition, the posterior process of the supratemporal has a shallow lateral notch in both *Eothyris* and *Oedaleops*. Although the occipital condyle is only known in the former, where it is poorly preserved, it seems to be a relatively small structure, similar in proportions to those in caseids; however, it does not seem to have the distinct ventral tilting of the condylar surface that characterizes caseids. Both the postparietals and tabulars are relatively large occipital elements in contrast to the thin, narrow elements in *Cotylorhynchus*. The postparietal in *Eothyris* does not contribute to the dorsal border of the posttemporal fenestra (Fig. 5). As in caseids, the exoccipitals have broad lateral wings that form a relatively long sutural border with the supraoccipital-opisthotic complex.

The jaw articulation, preserved only in *Eothyris* (Figs. 3, 5), is at the same level as the occipital condyle in a vertical transverse plane, and level with the marginal dentition in a horizontal plane. The quadrate condylar articulation surface is transversely very broad, similar in proportions to that in caseids.

On the palate, only preserved in *Eothyris*, the parasphenoid forms a large, broad plate and the basicranial articulation is located ventrally, close to the transverse flange of the pterygoid (Fig. 4). The ventral surface of the parasphenoid-basioccipital complex is poorly preserved, and only its broad outlines are discernable. The three dental fields on the pterygoid can be seen, and it appears that those on both the transverse flange and along the anteromedial edge are composed of single rows, whereas the anterolateral field consists of a broad, unorganized swath of small teeth.

In lateral view of the lower jaw in *Eothyris* (Fig. 3), the dentary, angular, and surangular present roughly equal surface areas. A shallow concavity develops at the posterior end of the mandible between the angular and surangular. At the dorsal end of the suture between the dentary and surangular, the coronoid overlaps both bones to gain an elongate exposure visible in lateral view. There is almost no development of a retroarticular process in *Eothyris*.

The dermal ornamentation seen in *Oedaleops* is particularly well developed on the bones that form the dorsal edges of the orbit, as well as on the nasals, frontals, and along the lateral portions of the parietal. It is not possible to determine if this pattern of sculpturing, which is different from that in caseids, is a diagnostic feature of this genus, or of both taxa because the bone surfaces of *Eothyris* are not as well preserved as in *Oedaleops*, and was probably prepared with a grinder, eliminating surface detail of the relatively soft bone.

DISCUSSION

Phylogenetic Position of the Eothyrididae

The monophyly of the Eothyrididae was tested by analyzing a data matrix of 13 taxa and 69 morphological characters (Appendices 1, 2) using parsimony PAUP* (Swofford, 2000). The ingroup is comprised of 11 synapsid taxa, Reptilia and Diadectomorpha forming the outgroups. The purpose of this analysis was also to test the monophyly of Caseasauria and Caseidae. Six eupelycosaur taxa were included in the data matrix in order to test the relationships between caseasaurs and varanopids, a sister-taxon relationship that has been proposed previously (Brinkman and Eberth, 1982). All characters have the same weight, and all multistate characters were unordered. The monophyly of the Eothyrididae is confirmed by this analysis, and the results are shown in Figure 9. A single most parsimonious tree was found. Tree statistics, bootstrap values, and decay indices are given in Figure 9. *Oedaleops* and *Eothyris* cluster as sister taxa outside of Caseidae.

In a systematic review of Permo-Carboniferous synapsids (Pelycosauria) Reisz (1986:89) was able to show that *Eothyris* and *Oedaleops* share a number of characters with caseids to form the monophyletic Caseasauria, but this hypothesis was first proposed in a previous cladistic analysis (Reisz, 1980). Interestingly, the following modified list of characters supporting the monophyly of Caseasauria includes numerous features of the snout: 1) in lateral view, the wedge-like dorsal process of each premaxilla forms an anteriorly pointed rostrum; 2) the external narial shelf, an external flange formed by each nasal, is present beneath the dorsal margin of the narial openings; 3) the external nares are anteroposteriorly elongate, occupying at least one-fifteenth of the skull length, or 25% of snout length; 4) the maxillae either contribute to or are only narrowly separated by a band of the lacrimal and jugal bones from the ventral margin
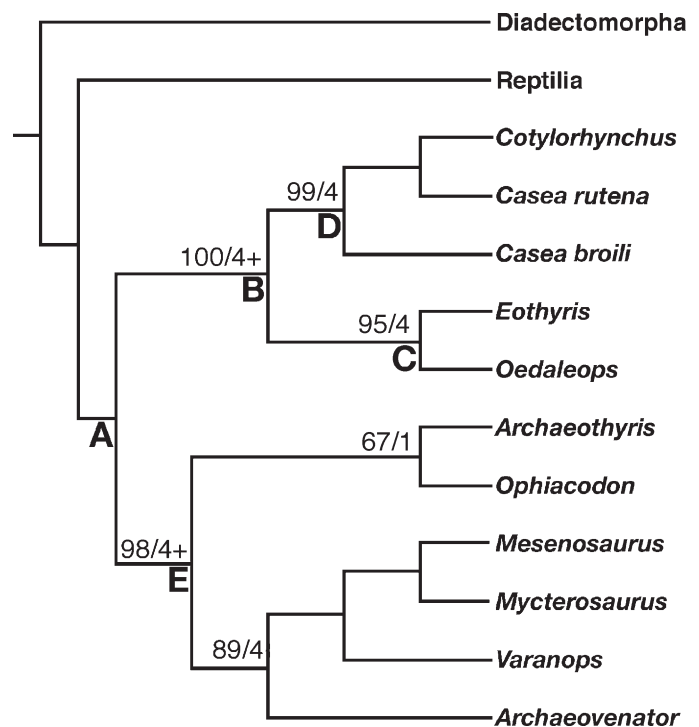

FIGURE 9. Synapsid phylogeny. The monophyly of the Eothyrididae was tested by submitting a data matrix of 13 taxa and 69 morphological characters (Appendix 1) to a phylogenetic analysis using parsimony (PAUP*, Version 4.0b10). The morphological characters were polarized in 13 taxa according to the outgroup criterion. Reptilia and Diadectomorpha have been chosen as outgroups. All characters have the same weight, and all multistate characters were unordered. Tree length 140 steps, CI 0.701, HI 0.3429, RI 0.8093, RC 0.5723. The numbers at selected nodes indicate bootstrap values and decay indices, respectively. Major Nodes: **A**, Synapsida; **B**, Caseasauria; **C**, Eothyrididae; **D**, Caseidae; **E**, Eupelycosauria.

of the orbits (an orbital maxilla may be an autapomorphy of *Eothyris parkeyi*; Fig. 1); 5) the external surface of each maxilla faces ventrolaterally rather than being oriented vertically; 6) the marginal dentition is reduced to 22 teeth or fewer; 7) in dorsal view, the antorbital width of the skull is greatest across the lacrimals, giving the antorbital region of the skull a broad appearance; consequently, the maxillae are not visible in dorsal view and the lacrimals are visible above the maxillae in ventral view. There are additional caseasaur characters in the skull: 8) broad contribution of elongate postorbital to skull table, maximum width greater than 50% of parietal width; 9) parietal foramen unusually large, equal to or larger in diameter than the foramen magnum; 10) supratemporal bone broad and long, equal in width to nearly 25% of maximum parietal width, but still part of the skull table; 11) quadratojugal elongate, extending at least 35% of the skull length or to the level of the postorbital bar; 12) broad lateral wing of the exoccipital, at least equal to the width of the foramen magnum.

The numerous postcranial features of caseids, many of which are clearly associated with herbivorous feeding behaviour on high fiber food, could not be evaluated at this taxonomic level because neither *Eothyris* nor *Oedaleops* is known from postcranial remains.

Reisz (1986) redefined the family Eothyrididae as a monophyletic taxon united by the following two synapomorphies: the jugals are excluded from the ventral margin of the cheek by a long anterior process of the quadratojugal (also present in caseids); and the squamosals have a rounded posterior border that provides poor separation between the cheek and the occipital surface of the skull. Although the latter character has a questionable evolutionary history, we have been able to identify additional synapomorphies of *Eothyris* and *Oedaleops* that are seen in the primitive condition in caseids and varanopids, as well as in sauropsids (reptiles): 1) two maxillary tooth peaks occur at roughly the same positions along the length of the bone (Langston, 1965), one far anteriorly (the primary canines), and a second midway along the maxillary tooth row, just beneath the anterior margin of the orbit (the secondary caniniform teeth); 2) an unusually large pair of primary caniniform teeth is present in both taxa, at least twice as large as the first pair of postcanine teeth; 3) the primary caniniform teeth occupy an anterior position, with at most one precanine maxillary tooth being present in *Oedaleops* and none in *Eothyris*. This provides strong evidence that these caniniform teeth evolved independently from those of other, more crownward synapsids. In addition, 4) the maxillae do not contribute to the floor of the external nares, being largely replaced by the posterolateral process of the premaxilla; and 5) the posterior process of the jugal is long, forming the ventral edge of the temporal fenestra. Other unusual cranial characters, like the dorsoventrally narrow lacrimals, with their maximum height being one-third or less than the interorbital width of the paired frontals, has been difficult to evaluate because of its apparent link with characters 2 and 3 listed above, but may be a valid eothyridid autapomorphy. Another potential eothyridid autapomorphy is the nasals being distinctly shorter than the frontals or parietals. Although they are approximately equal in length to the frontal and parietal in *Cotylorhynchus*, they are short in both *Casea rutena* and *Casea broili*. Thus, the distribution of this character among basal caseids is not well known at this time.

These eothyridid autapomorphies confirm that these two small faunivorous caseasaurs form a natural clade—the Eothyrididae—which is the sister taxon to the more numerous, and younger Caseidae (Fig. 9). However, a more detailed cladistic analysis of caseasaurian relationships requires a thorough review of all known caseids. A preliminary analysis of caseid phylogeny has been undertaken using the better-known members of that clade (Maddin et al., 2008) as part of a detailed description of the Russian caseid *Ennatosaurus tecton*.

The fossil record of Eothyrididae is dramatically different from that of its sister taxon, the Caseidae. In contrast to the presence of numerous caseid taxa in the Permian of North America, at least three caseids (of which two remain undescribed) from western Europe (Berman et al., 2000, 2001; RR, pers. obs.), and with at least one member being found in the Middle Permian of Russia (Maddin et al., 2008), eothyridids are extremely rare components of the Early Permian terrestrial vertebrate community. *Eothyris* and *Oedaleops* are restricted to individual localities in Texas and New Mexico, respectively. The rarity of these finds prevents any discussion of the evolutionary history of this clade, except that its earliest known appearance near the Permo-Carboniferous boundary greatly predates the oldest known appearance of its sister taxon, the Caseidae. Thus, the fragmentary fossil record of eothyridids does provide evidence that caseids must have had a long, hidden history before their appearance in the latter part of the Early Permian. Of course, the ghost lineage of caseasaurs, as the sister taxon to eupelycosaurs or all other synapsids is also spectacularly long, extending from at least the Permo-Carboniferous boundary well into the Middle Pennsylvanian, when the first synapsids and reptiles appear in the fossil record (Reisz, 1972; Reisz and Modesto, 1996).

LITERATURE CITED

Berman, D. S, R. R. Reisz, J. R. Bolt, and D. Scott. 1995. The cranial anatomy and relationships of the synapsid *Varanosaurus* (Eupelycosauria: Ophiacodontidae) from the Early Permian of Texas and Oklahoma. Annals of the Carnegie Museum 58:99–138.

Berman, D. S, R. R. Reisz, T. Martens, and A. C. Henrici. 2001. A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside of North America. Canadian Journal of Earth Sciences 38:803–812.

Berman, D. S, R. R. Reisz, D. Scott, A. C. Henrici, S. S. Sumida, and T. Martens. 2000. Early Permian bipedal reptile. Science 290:969–972.

Brinkman, D., and D. A. Eberth. 1983. The interrelationships of pelycosaurs. Breviora 473:1–35.

Fox, R. C. 1962. Two new pelycosaurs from the Lower Permian of Oklahoma. University of Kansas, Publications of the Museum of Natural History 12:297–307.

Langston, W. 1965. *Oedaleops campi* (Reptilia: Pelycosauria) new genus and species from the Lower Permian of New Mexico, and the Family Eothyrididae. Bulletin of the Texas Memorial Museum 9:5–47.

Laurin, M., and R. R. Reisz. 1995. A reevaluation of early amniote phylogeny. Zoological Journal of the Linnean Society 113:165–223.

Maddin, H. C., C. A. Sidor, and R. R. Reisz. 2008. Cranial anatomy of *Ennatosaurus tecton* (Synapsida: Caseidae) from the Middle Permian of Russia and the evolutionary relationships of Caseidae. Journal of Vertebrate Paleontology 28:160–180.

Marsh, O. C. 1878. Notice of new fossil reptiles. American Journal of Science 15:409–411.

Modesto, S., C. A. Sidor, B. S. Rubidge, and J. Welman. 2001. A second-varanopseid skull from the Upper Permian of South Africa: implications for Late Permian 'pelycosaur' evolution. Lethaia 34:249–259.

Olson, E. C. 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. Oklahoma Geological Survey Circular 70:3–70.

Reisz, R. R. 1972. Pelycosaurian reptiles from the Middle Pennsylvanian of North America. Bulletin of the Museum of Comparative Zoology 144:26–60.

Reisz, R. R. 1980. The Pelycosauria: a review of phylogenetic relationships; pp. 553–592 in A. L. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates. Academic Press, London and New York.

Reisz, R. R. 1986. Pelycosauria; pp. 1–102 in O. Kuhn (ed.), Handbuch der Palaoherpetologie, vol. 17A. Gustav Fischer Verlag, Stuttgart, Germany.

Reisz, R. R. 1998. The origin and early evolutionary history of amniotes. Trends in Ecology and Evolution 12:218–222.

Reisz, R. R., and D. W. Dilkes. 2003. Archaeovenator, a small varanopseid synapsid from the Upper Pennsylvanian of Kansas. Canadian Journal of Earth Sciences 40:527–539.

Reisz, R. R., and M. Laurin. 2001. The reptile Macroleter: the first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. Geological Society of America Bulletin 113:1229–1233.

Reisz, R. R., and M. Laurin. 2004. A reevaluation of the enigmatic Permian synapsid Watongia and of its stratigraphic significance. Canadian Journal of Earth Sciences 41:377–386.

Reisz, R. R., and S. P. Modesto. 1996. Archerpeton anthracos from the Joggins Formation of Nova Scotia—a microsaur, not a reptile. Canadian Journal of Earth Sciences 33:703–709.

Reisz, R. R., D. S. Berman, and D. Scott. 1992. The cranial anatomy of Secodontosaurus obtusidens, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the Lower Permian of Texas. Zoological Journal of the Linnean Society 104:127–184.

Reisz, R. R., D. W. Dilkes, and D. S. Berman. 1998. Anatomy and relationships of Elliotsmithia longiceps Broom, a small synapsid (Eupelycosauria: Varanopseidae) from the late Permian of South Africa. Journal of Vertebrate Paleontology 18:602–611.

Romer, A. S. 1937. New genera and species of pelycosaurian reptiles. Proceedings of the New England Zoological Club 16:89–96.

Romer, A. S. 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh-West Virginia Region. Annals of the Carnegie Museum 33:47–112.

Romer, A. S., and L. W. Price. 1940. Review of the Pelycosauria. Geological Society of America, Special Papers 28:1–538.

Swofford, D. L. 2000. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinaeur Associates, Sunderland, Massachusetts.

Vaughn, P. P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and the origin of the family Caseidae. Journal of Paleontology 32:981–991.

Watson, D. M. S. 1954. On Bolosaurus and the origin and classification of reptiles. Bulletin of the Museum of Comparative Zoology 111:199–249.

Williston, S. W. 1910. New Permian reptiles: rhachitomous vertebrae. Journal of Geology 18:585–600.

Williston, S. W. 1912. Primitive reptiles. Journal of Morphology 23:637–666.

Williston, S. W. 1914. The osteology of some American Permian vertebrates, II. Walker Museum Contributions 1:107–162.

APPENDIX 1.   List of characters and character states used in the phylogenetic analysis and to construct the cladogram shown in Figure 9. The numbers in brackets refer to the state for a character. Most characters are taken from Reisz et al. (1998), unless otherwise indicated. Character descriptions that have been modified are also indicated. All the characters have the same weight.

(1) Skull ornamentation with circular pits: absent (0); present (1).
(2) Premaxillary rostral process: absent (0); present (1). Reisz (1986).
(3) Relative size of first premaxillary tooth: not largest in series (0); largest in tooth row (1).
(4) Premaxillary tooth number: two (0); three (1); four or greater (2) Modified from Reisz and Dilkes (2003).
(5) Premaxillary narial shelf: narial shelf of external naris separated from sculptured lateral surface (0); rounded narial shelf that extends smoothly to ventral edge of skull (1).
(6) External narial shelf on nasal: absent (0); present (1). Reisz (1986).
(7) Nasal length: distinctly shorter than frontal (0); roughly equal to frontal (1); nasal markedly longer than either frontal or parietal (2). Berman et al. (1995).
(8) External naris length: short, less than 25% of preorbital length (0); moderate, equal or greater than 25% of preorbital length (1); long, more than 50% of preorbital length (2).
(9) Narial posterodorsal expansion: absent (0); present, but modest, pinched between nasal and maxilla (1); greatly enlarged, between nasal and lacrimal (2). Reisz and Dilkes (2003).
(10) Septomaxilla shape: curled in external naris (0); pillar in external naris (1); on surface (2).
(11) Septomaxilla: lateral, sheet-like exposure absent (0); present (1). Reisz and Dilkes (2003).
(12) Maxilla dorsal process: absent (0); present, extending to level of dorsal narial margin (1). Modified from Reisz et al. (1998).
(13) Lateral buttress of maxilla: external dorsally oriented maxillary buttress absent (0); present (1).
(14) Maxilla lateral surface: slopes dorsomedially or is vertical (0); slopes dorsolaterally, overhanging tooth row (1).
(15) Maxilla tooth bearing region: extends anterior to posterior edge of orbit (0); stops under postorbital bar (1); extends posterior to postorbital bar (2).
(16) Precaniniform maxillary tooth number: no canines (0); none or one precaniniform (1); two or more precaniniforms (2).
(17) Caniniform region: absent (0), present (1); caniniform tooth at least twice as large as all other maxillary teeth (2). Modified from Reisz and Dilkes (2003).
(18) Secondary caniniform region: absent (0); present (1).
(19) Maxilla-premaxillary suture: diagonal in area of external naris, premaxilla and maxilla forming floor of external naris (0); greatly elongated with long posterolateral process of premaxilla, maxilla excluded from floor (1).
(20) Maxillary tooth number: 8–17 teeth (0); 22–28 teeth (1); more than 35 teeth (2).
(21) Marginal dentition: serrations absent (0); serrations present (1); leafy serrations on crown (2). Modified from Modesto et al. (2001).
(22) Marginal dentition lateral compression: present distally (0); present over two-thirds of tooth (1). Reisz and Dilkes (2003).
(23) Marginal dentition shape: conical and slightly recurved (0); strongly recurved and mediolaterally compressed (1); spatulate, with lingual curvature (2). Modified from Reisz et al. (1998).
(24) Maxilla–prefrontal contact: absent (0); present (1).
(25) Lacrimal duct: opening on posterior edge of lacrimal (0); opening laterally near posterior edge of lacrimal (1); opening laterally on concave surface of lacrimal (2).
(26) Prefrontal contribution to orbit: restricted to anterodorsal corner of orbit (0); long ventral process of prefrontal extending ventrally to reduce lacrimal contribution to orbit (1). Modified from Reisz et al. (1998).
(27) Antorbital region: broad antorbital region, nasal largely dorsal element (0); antorbital region narrow and tall, nasal has nearly vertical contribution to snout (1).
(28) Frontal: posterolateral process short or absent (0); posterolateral process long and narrow, matching length of postfrontal, and between parietal and postfrontal (1).
(29) Frontal orbital border: frontal contribution to orbit absent or narrow (0); frontal contribution to orbit broad, forming most of dorsal edge (1).
(30) Circumorbital ornamentation: tuberous ornamentation on prefrontal and jugal absent (0); present (1). Modified from Reisz et al. (1998).
(31) Postorbital process: short and broad (0); posterior process elongate and broad occupying more than one-half of temporal length (1); posterior process long, narrow (2). Modified from Reisz et al. (1998).
(32) Dorsal and lateral surfaces of postorbital: forming smooth rounded curve (0); sharply divided – angular (1).
(33) Postorbital lateral process: absent (0); enlarged, forming tubercle (1). Modified from Reisz and Dilkes (2003).
(34) Parietal: anterior extension between orbits absent (0); present (1). Modified from Reisz et al. (1998).

(35) Pineal foramen: located on anterior or mid-region of midline parietal suture (0); located in posterior region of midline parietal suture (1).

(36) Pineal foramen: smaller in diameter than foramen magnum (0); equal to or larger in diameter than foramen magnum (1). When foramen magnum size unknown, pineal size to parietal width ratio is used.

(37) Supratemporal: broad, long element of skull roof, extending onto lateral surface (0); large, in parietal and squamosal trough of skull table (1); elongate, slender in parietal and squamosal trough (2).

(38) Squamosal lateral surface: with short anterodorsal process and not extending along entire length of posterior process of postorbital, expanded ventrally (0); with long anterodorsal process extending to corner between posterior and anteroventral processes of postorbital, expanded ventrally (1); sub rectangular in outline, with short anterodorsal process, no ventral expansion (2).

(39) Squamosal occipital shelf: occipital process of squamosal present, broad, contributing to occipital surface of skull (0); narrow (1); absent (2).

(40) Squamosal posterodorsal process: absent (0); present (1). Modesto et al. (2001).

(41) Squamosal contact with jugal: absent anterodorsally (0); present on postorbital bar (1).

(42) Lateral temporal fenestra: absent (0); present (1). Modified from Reisz et al. (1998).

(43) Temporal fenestra shape: oval, height equal to or greater than length (0); posteroventral expansion resulting in triangular outline of fenestra (1); oval, length greater than height (2). Modified from Reisz et al. (1998).

(44) Lateral temporal fenestra height vs temporal skull height: equal to or less than 0.5 (0); greater than 0.5 (1). Absence of temporal fenestra is interpreted as state 0.

(45) Lower temporal bar: zygomatic arch or subtemporal bar tall, occupying at least 30% of skull height (0); bar narrow, occupying less than 20% of postorbital skull height (1).When fenestra absent, height of jugal is used.

(46) Quadratojugal–maxilla contact: absent (0); present, quadratojugal long (1); present, maxilla long (2).

(47) Quadratojugal anterodorsal process: absent (0); present, covered by squamosal (1); present and superficial (2). Modified from Reisz and Dilkes (2003).

(48) Anterior extent of quadratojugal: equal to anterior extent of ventral portion of squamosal (0); longer, extending anterior to ventral portion of squamosal underneath temporal fenestra (1); much longer, extending to level of temporal fenestra (2).

(49) Jugal posterior process: short, extending along up to half of postorbital region (0); long, forming more than half of postorbital region (1). Condition not affected by presence or absence of fenestra.

(50) Quadrate and occipital edge: nearly vertical or vertical occipital margin (0); occipital edge with moderate anterior slope, 10 degrees or greater (1). Modified from Reisz and Laurin (2001).

(51) Tabular: large, sheet-like (0); narrow, slender (1); slender medially, broad laterally (2). Modified from Reisz and Dilkes (2003).

(52) Exoccipital lateral wing: tall and narrow (0); broad, extending under paroccipital process (1).

(53) Dimensions of paroccipital process: tall, blade-like, taller than supraoccipital at midline (0); tall, blade-like, equal or less than supraoccipital (1); narrow, rod-like, and unattached (2).

(54) Parasphenoid dentition posterior to level of transverse flange: absent (0); present along edges (1); present on edges and posterior body (2). Reisz and Dilkes (2003).

(55) Basal tubera: short, broad, with short articulating facets facing anterolaterally (0); long, wing-like, with long articulating facets facing anteriorly (1).

(56) Teeth on transverse flange: single row on edge (0); additional teeth anterior to single row (1).

(57) Lower jaw shape: symphysis is thinnest portion of jaw (0); symphyseal region nearly as deep as mid-tooth row (1).

(58) Angular posteroventral edge: ridged, or keeled (0); ridge or keel elongate, more than half of bone (1); rounded (2). Modified from Reisz and Dilkes (2003).

POSTCRANIAL CHARACTERS

(59) Hyoid: short, directed to quadrate region (0); long directed posteriorly beyond skull (1). Reisz and Dilkes (2003).

(60) Vertebral neural spine excavation: absent (0); present (1). Reisz (1986).

(61) Neural spine height of presacral vertebrae from base of zygapophysis vs maximum centrum height: less than 1.5 (0); 1.5 or greater (1). Modified from Reisz et al. (1998).

(62) Dorsal centra midventral margin: rounded (0); ridged but without keel (1). Reisz and Dilkes (2003).

(63) Sacral ribs: two, unequal (0); two, equal (1); three or more (2). Reisz (1986).

(64) Supraglenoid foramen: present (0); absent (1). Reisz and Laurin (2004).

(65) Clavicular head: large (0); small (1). Reisz and Laurin (2004).

(66) Dimensions of femur: broad and short, maximum length/distal width ratio less than 3/1 (0); long and slender, length to distal width ratio more than 3/1 (1).

(67) Radiale maximum width to length ratio: subequal or < 1(0); > 1(1). Reisz and Laurin (2004).

(68) $5^{th}/4^{th}$ metacarpal length ratio: 0.65 or more (0); less than 0.65 (1). Reisz and Laurin (2004).

(69) Distal phalangeal length to width ratio: < 1.5 (0); 1.5 or greater (1). Modified from Reisz and Laurin (2004).

APPENDIX 2. Data matrix of selected taxa showing the states for the characterslisted in Appendix 1.

Diadectomorpha	0002001000 0000000001 0000000000 0000000000 00?0000000 001?0000?0 000000000?
	1 1 1
Reptilia	0002001000 0000000001 0000000010 0000000000 ?0?0000000 0010000000 000001011?
	1 1
Cotylorhynchus	1111011201 0101100000 2020000000 1000011211 0121111110 2100011000 002100001?
Casea broili	1111010201 0101100000 2020000000 1000011011 0120011100 2100001020 002100?00?
Casea rutena	1111010201 0101100000 2020000000 1000011211 0121011110 210? 0?1000 002??01?0?
Eothyris	?101010101 0011012110 0000000000 1000011001 0120011200 01000100?? ??????????
Oedaleops	0101010101 0001012111 0000000000 1100011001 012111120? 0??00?0 ??? ??????????
Archaeothyris	000??02001 ?0000210?1 0000001110 210010201? 01200?1?10 00??000??0 1100?0????
Ophiacodon	0002002001 0000021002 0100001110 21001?2010 0100001111 0010000100 110010001?
	1
Mycterosaurus	000210111? ?100221000 1111111111 211110201? 010112?001 10111?0?11 111111??1?
Mesenosaurus	0002101111 0100221001 1111111111 211110201 0101101101 1011101110 111 ?1111?
Varanops	0002101022 11102210?1 0110201110 01?1102120 1111122101 1012110211 112011110?
Archaeovenator	0002101222 10000000?? 0000011110 210110201? 010110?000 10?00001?0 011111??0?