Systematic Review

Order Pelycosauria Cope 1878

Primitive synapsid Amniota (Reptilia) with well developed inferior temporal fenestra, a broad anteriorly tilted occipital plate, reduced posttemporal fenestra bound by the paroccipital process of the opisthotic, lateral process of supraoccipital and tabular. On the occiput, there is a single median postparietal bone. On the palate the medial process of the jugal is sutured to the pterygoid but the ectopterygoid is still present.

The name Pelycosauria was originated by Cope, as was the name Theromorpha (Theromora). Prior to Romer and Price's review (1940), both terms were widely used. Case and several other writers used the former name; Williston, however, used the latter term for the group and preferred to use Pelycosauria in a rather restricted sense. Romer and Price (1940, p. 13) argued for the use of the name Pelycosauria because it is based on members of this group (*Clepsydrops* and *Dimetrodon*) and it has priority over the name Theromorpha (Theromora). In addition, the Theromorpha has been frequently used to include the early mammal-like reptiles as well as cotylosaurs, and hence its usage causes confusion (Romer and Price 1940, p. 14). For the last four decades, the term Pelycosauria has been generally accepted as representing all primitive, non-therapsid mammal-like reptiles.

In their discussion of pelycosaurian phylogeny, Romer and Price (1940) came to the conclusion that the presence of the inferior temporal fenestra was the only valid diagnostic feature of the group. In most pelycosaurs the margins of the inferior temporal fenestra are formed posteriorly by the squamosal, dorsally by the posterior process of the postorbital, anteriorly by the ventral process of the postorbital and the dorsal process of the jugal, and ventrally by the posterior process of the jugal. Inferior temporal fenestration is not restricted, however, to pelycosaurs and their descendants, but is also found in several other groups. In early diapsid reptiles, the inferior temporal fenestra is similar in configuration to that of pelycosaurs but different in the contribution of the quadratoju-

gal to the posteroventral border of the fenestra. This condition is seen only in caseids and the highly specialized varanopseids, and is considered to represent a feature derived within the Pelycosauria. Slightly different inferior temporal fenestrae are also present in such primitive reptiles as millerosaurs, mesosaurs and *Bolosaurus* (Romer 1956). However, pelycosaurs and their descendants can be distinguished from all other amniotes on the basis of a series of shared derived characters. The most readily recognizable of these characters is the presence of a broad anteriorly tilted occipital plate, formed mainly by the supraoccipital and opisthotic which are fused in most pelycosaurs. The large lateral extensions of these bones greatly restrict the posttemporal fenestrae. In addition, the postparietal is a single median occipital bone. No other true primitive reptile possesses these features. In both millerosaurs and captorhinomorphs, for example, the paroccipital process extends laterally either in cartilage or bone, but the supraoccipital does not extend far laterally to form a plate; further, the posttemporal fenestrae are relatively large and the postparietal bone is paired. In all pelycosaurs in which the septomaxilla is preserved, it appears as a highly distinctive, relatively massive, vertical piece of bone, located in the posterior portion of the external naris, consisting of a broad base which straddles the premaxilla and maxilla and a large dorsal process. In other primitive reptiles, the septomaxilla is a relatively simple curved sheet of bone (Heaton 1979). There are other cranial features that may be shared derived characters for pelycosaurs, but greater knowledge of the palate and braincase of other primitive reptiles is needed before the status of these characters is clarified (Reisz 1980).

In the postcranial skeleton, numerous primitive morphological features persist and there are no recognizable shared derived or advanced features that are restricted to this group. Most pelycosaurs in which an accurate presacral vertebral count is available possess 27 presacral

vertebrae, but some of the caseids apparently have as few as 24 (OLSON 1968). The presacral count of captorhinomorphs varies from 25 in captorhinids to 30 in protorothyridids (CARROLL and BAIRD 1972, CLARK and CARROLL 1973). In the early diapsid *Petrolacosaurus*, there are 26 presacral vertebrae (REISZ 1981). Furthermore, the vertebrae vary too much in shape and size among pelycosaurs to provide any shared derived characters for the group. Even within certain pelycosaurian families the vertebrae vary to a greater extent than in most primitive tetrapod groups. For example, within the Sphenacodontidae, *Haptodus* has short, narrow neural spines similar in proportions to the spines of protorothyridid captorhinomorphs, *Sphenacodon* has tall, blade-like spines that are slightly expanded distally, *Ctenospondylus* hat very tall, blade-like spines that are greatly expanded distally, and *Dimetrodon* and *Secodontosaurus* have very tall, narrow spines that are rounded in cross-section. The number of sacral vertebrae of pelycosaurs varies from two (ophiacodontids) to four (*Angelosaurus romeri*, a caseid pelycosaur); sphenacodontid and edaphosaurid pelycosaurs have three sacral vertebrae.

The appendicular skeleton of pelycosaurs is built upon the fundamental tetrapod plan seen in most primitive reptiles, and most of the osteological advances seem to occur within the group. In ophiacodonts, for example, the pelvic girdle is similar to that in captorhinomorphs and primitive diapsids in the following primitive features: a narrow, long, posterior process on the iliac blade, greatly thickened pubic symphysis and in early, smaller ophiacodontids, a lateral pubic tubercle. In sphenacodontids, edaphosaurids and caseids, the pelvic girdle appears advanced in the following features: broad iliac blade, the symphysis not greatly thickened on the pubis but of uniform thickness along the medial margin of the pelvis, no lateral pubic tubercle. These advanced features, which appear to have developed independently in these major pelycosaurian groups, are probably related to the development of an expanded vertebral-pelvic attachment formed by three sacral ribs. In varanopseids, although three sacral ribs are present, the primitive pelvic structure prevails. This is not unexpected, however, because the third sacral rib is very small. The herbivorous pelycosaurs, the caseids and edaphosaurids, retain the primitive limb proportions, whereas the advanced carnivorous pelycosaurs, especially the varanopseids and sphenacodonts, develop relatively slender, long distal limb elements and hence higher posture and a longer stride (REISZ 1980).

Suborder Caseasauria WILLISTON 1912

Primitive pelycosaurian reptiles that have anteroposteriorly elongated external narial openings, with an external narial shelf formed by the nasal and a pointed rostrum formed by the anteriorly tilted dorsal process of premaxilla. In these pelycosaurs the orbital margin is partially formed by the maxilla and the marginal dentition is reduced in number.

This group was erected for the reception of *Casea broilii* which WILLISTON (1912) considered, to be very different from other pelycosaurs. ROMER and PRICE (1940) abandoned this taxon and included the caseids with the edaphosaurids within the suborder Edaphosauria. This association was unfortunately based on a series of primitive pelycosaurian characters, such as low skull, low occiput, short paroccipital processes, lacrimal extending to the nares, primitive jaw articulation, apparently primitive atlas-axis complex, lack of ventral keels on the centra, lack of neural arch excavation, poorly developed rib tubercula, large ventral clavicular blades, short scapula, broad anterior coracoid plate and poorly developed triceps process on the posterior coracoid. This association was also based on a series of derived characters states that are probably related to adaptations to a herbivorous diet and to increase in size: small head, jaw articulation below the level of the tooth row, heavy lower jaw with deep symphysis, loss of caniniform teeth, small cervical vertebrae, three sacral ribs and large iliac blade. All of these derived features probably evolved in parallel and cannot be considered phylogenetically significant above the familial level (REISZ 1980).

Shared primitive characters of the Suborder Caseasauria that appear in derived form in all other pelycosaurs are: broad, plate-like supratemporal and skull width greater than height even in the snout region. In captorhinomorphs, millerosaurs and procolophonids, the skull retains the primitive cotylosaur (eg. *Limnoscelis*) pattern of a low profiled skull. This primitive pattern persists only in the members of this suborder of pelycosaurs; in other groups, the snout in the edaphosaurids, and the whole skull in ophiacodontids, varanopseids and sphenacodontids becomes narrow and deep. The broad supratemporal, a primitive reptilian and cotylosaurian char-

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acter state, persists as a broad sheet of bone in all caseasaurs, but is modified in all other pelycosaurs as well as in captorhinomorphs.

Among caseasaurian pelycosaurs, the postcranial skeleton is known only in caseids; despite certain specializations, the skeleton of primitive caseids is similar to that of other primitive reptiles. Evolutionary trends in the postcranial skeleton among the known caseids are mainly related to increase in size (OLSON 1968).

Fig. 34. Caseosaurian skulls (x1/4) in lateral view: (a) *Oedaleops campi* (after Langston 1965), (b) *Casea broilii* (after Olson 1968) and (c) *Casea rutena* (after Sigogneau-Russel and Russell 1974).

Family Eothyrididae ROMER and PRICE 1940

Small caseasaurid pelycosaurs with the jugals excluded from the ventral margin of the cheek by a long anterior process of the quadratojugal. The squamosal has a rounded posterior border that provides poor separation between the cheek and occipital surfaces of the skull.

This family was erected as a provisional group by ROMER and PRICE (1940) for the reception of the small pelycosaur *Eothyris*, known from a single nearly complete skull (fig. 6), and fragmentary remains of three large pelycosaurs, *Stereophallodon ciscoensis*, *Stereorhachis dominans* and *Baldwinonus trux*. These pelycosaurs were included within this family because they are "ophiacodont pelycosaurs, primitive in most known regards but paralleling the higher sphenacodonts in the development of much enlarged canines and showing a tendency toward elongation of the vertebral column" (ROMER and PRICE 1940, pp. 246–247). Both the presence of very large caniniform teeth and of long vertebrae represent slight modifications of the primitive pelycosaurian condition (REISZ 1980), and the dental and vertebral patterns seen in the specialized ophiacodont *Ophiacodon* represent derived conditions. Both *Stereophallodon* and *Stereorhachis* are, as indicated by ROMER and PRICE (1940), primitive ophiacodont pelycosaurs. They are therefore included here in the family Ophiacodontidae. *Baldwinonus trux*, however, appears to present a more difficult taxonomic problem. The holotype and only known specimen includes fragments of unusually long vertebrae, and a maxilla that appears to resemble closely that of *Stereophallodon*, but is

much smaller. It is certain that none of the materials associated with this species is an eothyridid pelycosaur. The specialized, pointed snout of *Eothyris* (fig. 6a) was not noticed in either the original or subsequent descriptions because the premaxilla was crushed posteriorly into the narial opening and the dorsal process was broken at the anterior tip. In his description of another small eothyridid, *Oedaleops campi*, LANGSTON (1965) indicated that this species is remarkably similar to *Eothyris*, and that these pelycosaurs are closely related to the caseids. *Oedaleops* has smaller caniniform teeth than *Eothyris*, similar in size to those found in early captorhinomorphs, but the former eothyridid is peculiar in that the supratemporal projects slightly beyond the posterior edge of the cheek. The exact configuration of the posterior end of the supratemporal in *Eothyris* is not known. This posterior projection of the supratemporal may represent another shared derived character of the family, but further materials are needed before this can be verified.

Eothyridids, represented by two species, *Eothyris parkeyi* and *Oedaleops campi*, are closely related to the caseid pelycosaurs as indicated by the shared derived characters listed above in the subordinal diagnosis. Shared primitive characters found in both caseids and eothyridids that appear in derived form in all other pelycosaurs are: skull width greater than the height, even in the region of the snout, (the frontal either excluded from the orbit *(Eothyris)* or the orbital margin of the frontal very short (*Oedaleops* and all caseids), broad, plate-like supratemporal. In captorhinomorphs, millerosaurs and procolophonids the skull retains the primitive cotylosaur pattern of a low profiled skull. This primitive condition persists among pelycosaurs only in caseids and eothyridids. In other pelycosaurs either the snout (edaphosaurids) or the whole skull (in ophiacodontids, varanopseids and sphenacodontids) becomes narrow and deep. Only in cotylosaurs *(Limnoscelis, Diadectes, Seymouria)* and the caseid and eothyridid pelycosaurs is the primitive pattern of the frontal retained: in other pelycosaurs and in early captorhinomorphs one-third of the dorsal orbital margin is formed by the frontal. The broad supratemporal, a primitive reptilian and cotylosaurian character, is modified in captorhinomorphs, diapsids and advanced pelycosaurs, but persists as a broad sheet in caseids and eothyridids.

Eothyris ROMER 1937, p. 89.

Type species *Eothyris parkeyi* ROMER

E. parkeyi is the only species that can be assigned to the genus *Eothyris*. The holotype and only known specimen is complete but most of the sculpturing originally present on the skull roof has been removed.

Eothyris is a small pelycosaur that possesses an unusually primitive skull pattern, but is specialized in the extreme development of canines and consequent reduction of pre-

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caniniform maxillary teeth. Significant characters in the skull include exclusion of the frontal from the orbital margin by the prefrontal and postfrontal, unusually narrow maxilla and extension of lacrimal to external naris despite great size of canines.

Eothyris parkeyi ROMER 1937, p. 89.
Holotype: MCZ 1161, a complete skull with mandibles from Tit Mountain, just northeast of Dundee, Archer County, Texas; Bell Plains Formation, Wichita Group, Lower Permian.
The skull (fig. 6) has been prepared by the use of a grinder, so that the pattern of sculpturing is preserved only on the orbital margin of the prefrontal and postfrontal bones. The suture pattern is somewhat unreliable because the outer layer of the dermal skull roof was removed upon grinding.

Oedaleops LANGSTON 1965, p. 6

Type species *Oedaleops campi* LANGSTON
Small eothyridid pelycosaur that can be distinguished from *Eothyris* on the basis of slight differences in cranial morphology: smaller caniniform teeth, better developed precaniniform tooth, a small lateral process of the frontal that extends to the orbit between the prefrontal and postfrontal.

Oedaleops campi LANGSTON 1965, p. 6.
Holotype: UCMP 35758, a slightly distorted skull roof from Camp Quarry near Arroyo del Agua, Rio Arriba County, New Mexico; Abo/Cutler Formation, Cutler Group, Lower Permian.
O. campi is the only species that can be assigned to the genus *Oedaleops*. The holotype is a nearly complete skull roof, with parts of the cheeks missing. The distinctive feature of the skull roof (fig. 34a) is the well developed pattern of sculpturing present on the dorsal surface. Other specimens of the species add little to the data available on the holotype. Isolated dentaries attributed to this species are unusually deep dorsoventrally (LANGSTON 1965). Little is known of the postcranial skeleton of *Oedaleops*; the shoulder girdle, humerus and femur tentatively associated with *O. campi* are generally very primitive in design, but there is no evidence that this assignment is correct. The fragment of pelvis assigned to *Oedaleops* by LANGSTON (1965) probably belongs to a small cotylosaur.

Family Caseidae WILLISTON 1912

Small to very large caseasaurian pelycosaurs with greatly enlarged external narial openings, squamosals narrow anteroposteriorly, large pineal foramen located anterior to the midpoint of the interparietal suture, and jaw articulation slightly below the level of the tooth row. Maxillary and mandibular dentition is reduced in number, anterior premaxillary and mandibular teeth are largest in the jaw, and small terminal cusps are present on posterior marginal dentition; ribs are dorsolaterally expanded. Phalangeal formula is reduced, ranging from 2-3-4-4-3 to 2-2-2-3-2. These pelycosaurs have relatively small skulls, with large temporal fenestrae, barrel shaped bodies, have small cervical vertebrae and at least three sacral ribs even in the smallest forms.
This family has been recently reviewed by OLSON (1968). He demonstrated that such primitive reptilian features as large ventral clavicular blade, large head of the interclavicle, broad scapula, humerus with relatively short shaft and large ends, femur with large internal trochanter, broad epipodials much shorter than the propodials are present in early, small caseids, and that many of these features are exaggerated in the larger, later forms. In addition, the larger caseids are specialized in the presence of fully formed ectepicondylar foramen on the humerus and shortened, massive metapodials and phalanges. The unique construction of the ilium of *Casea*, with a narrow neck and large posterior and anterior flares represent a specialization of the genus. In later, larger caseids, there is either a slight or no anterior flare and only a moderate posterior flare on the iliac blade. Many of the specialized features, peculiar to the larger species, are also found in edaphosaurids, this clearly represents convergence.

Casea WILLISTON 1910b, p. 590.

Type species *Casea broilii* WILLISTON
A caseid of small size possessing an anteroposteriorly flared iliac blade, 12-15 marginal cheek teeth (fig. 34b and c). Posterior marginal teeth have serrated crowns. Members of this genus appear to represent the most primitive caseid pattern and lack the high degree of skeletal specialization present in other, more advanced caseids.

Casea broilii WILLISTON 1910b, p. 590.
Holotype: FMNH UC 656, skull and skeleton from Indian Creek, Baylor County, Texas; uppermost Arroyo or lowermost Vale Formation, Clear Fork Group, Lower Permian.
All the known specimens have come from a single fossiliferous lens, called the Cacops bonebed. This bonebed produced, in addition to this species, articulated skeletons of *Cacops* and *Varanops*. *Casea broilii* is the geologically oldest representative of the family and its first des-

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Table 1. The distribution of derived character states that formed the basis of the cladogram shown in Figure 40 (Modified from Reisz 1980, Table 1). The numbers of the character sets correspond to those shown at the nodes of the cladogram in Fig. 40.

1. Broad anteriorly tilted occipital plate
   Reduced posttemporal fenestra bound by paroccipital process of opisthotic, supraoccipital and tabular
   Septomaxilla comprised of a broad base and a massive dorsal process
   Inferior temporal fenestra
   ?Single median postparietal
2. Pointed rostrum formed by anteriorly tilted dorsal process of premaxilla
   Anteroposteriorly elongated external narial opening
   Ventral orbital margin partially formed by maxilla
   External narial shelf on nasal
3. Height of skull greater than the width in the region of the snout
   At least one third of the dorsal orbital margin formed by the frontal
   narrow, long supratemporal
   Pineal posterior to the midpoint of the interparietal suture
4. Nasal longer than the parietal at the midline
   Lateral extension of the skull table behind the orbits formed by the postfrontal and postorbital
   Jaw articulation behind the occipital condyle
   ?Skull table sharply separated from the cheek in the region of the snout
5. Excavated neural arches
   Ventral keel on dorsal vertebrae
   Supraglenoid foramen on scapular surface
   Tall narrow necked scapula
6. Small quadratojugal covered by squamosal
   Reflected lamina of the angular
   Retroarticular process turned downward
   Paroccipital process elongated and directed ventrolaterally

Table 2. The distribution of some of the derived character states that formed the basis of the cladogram shown in Fig. 40 (Modified from Brinkman and Eberth 1983, Table 2). The letters denoting the character sets correspond to those shown at three of the six nodes on the cladogram of Figure 40.

A. Humerus with secondary ridge leading from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus, with a fossa at the base of the crest
   Maxilla contacts the quadratojugal
   Basipterygoid process directed laterally and are mediolaterally elongate
B. Cheek margin concave
   Anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row
   Dorsal process of stapes articulating in a socket on the paroccipital process
   Angular with an extended ventral plate in the region of the articular

C. Articular surfaces of basipterygoid tubera differentiated into two flat areas at right angles to each other
   No shelf between basisphenoid wings
   Frontal with a lateral lappet
   Quadratojugal restricted to ventrolateral corner of skull
   Prearticular twisted
   Pterygoideus process of mandible formed entirely by articular
   Quadrate ramus of pyterygoid with rounded ventral edge

Dimetrodon proposed by Brinkman and Eberth (1983) is similar to that presented by Romer and Price (1940). This pattern of relationships is supported by new evidence provided by Brinkman and Eberth which indicates that seven cranial derived features shared by *Edaphosaurus* and *Dimetrodon* appear in primitive form in *Ophiacodon* (Table 2, C). This proposed pattern of relationships is preferred over the alternative interpretation of relationship proposed by Reisz (1980) for the families that include these genera because the latter is based only on four derived cranial features (Table 1, character set 4) that are shared by ophiacodontids and sphenacodontids and appear in primitive form in edaphosaurids. Of these four derived features two are general proportions that are of doubtful significance because they are in part a reflection of the manner in which the skull reconstructions were made.

The proposed relationships of varanopseids to other pelycosaurs represent the most radical departure from the hypotheses of Reisz (1980), and Romer and Price (1940). This is based on the interpretation that *Ophiacodon*, *Dimetrodon* and *Edaphosaurus* share four derived cranial features (Table 2, B) that appear in primitive form in *Varanops* and *Aerosaurus*, and on the interpretation that *Casea*, *Varanops* and *Aerosaurus* share three derived skeletal features (Table 2, A) that appear in primitive form in *Ophiacodon*, *Dimetrodon* and *Edaphosaurus* (Figure 40b). Examination of the four cranial features (Table 2, B) that formed the basis for the first of these two theories proposed by Brinkman and Eberth (1983), reveals that their interpretation of the polarity of the character states in two of these features is probably invalid. One of these morphological features is the outline of the cheeck margin, the other is the slope of the dorsal process of the premaxilla. The outline of the cheek margin in *Casea*, *Varanops* and *Aerosaurus* was interpreted by Brinkman and Eberth as convex and therefore represents the primitive condition, whereas the outline in *Ophiacodon*, *Edaphosaurus* and *Dimetrodon* is concave and therefore represents the derived condition. This polarity was determined through the use of *Diadectes* as the outgroup. If, however, another cotylosaur, *Limnoscelis*, is used as the outgroup, then the concave outline becomes the primi-
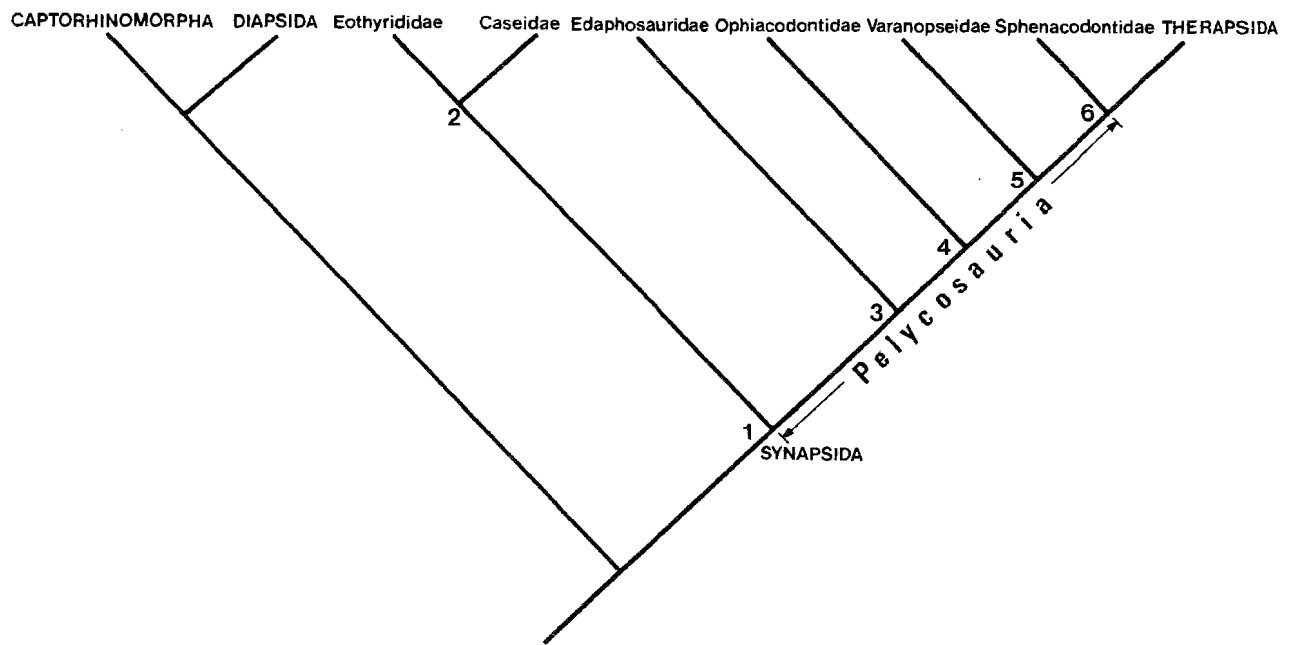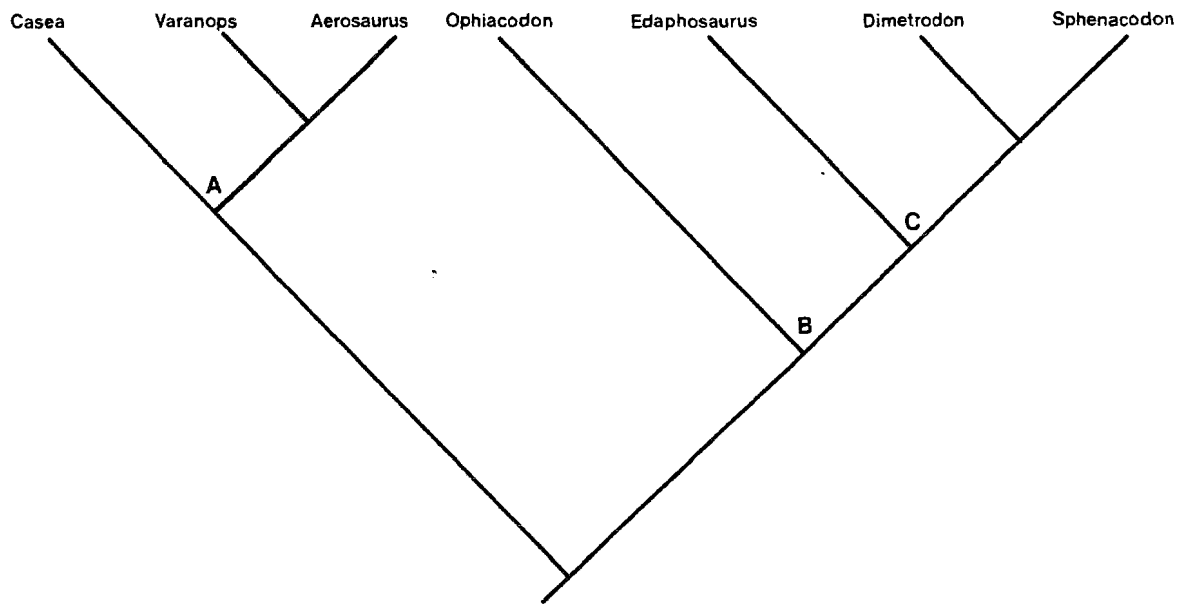
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Figure 40. Hypothesis of relationships for selected genera of pelycosaurs (modified slightly from Brinkman and Eberth 1983, Figure 14). The capital letters located at three of the nodes refer to lists of shared derived characters given in Table 2.
Hypothesis of interrelationships of the families of pelycosaurian reptiles (Reisz 1980, Figure 17). The numbers at the nodes of the cladogram refer to lists of shared derived characters given in Table I.

Caseidae   Eothyrididae   Varanopseidae   Ophiacodontidae   Edaphosauridae   Sphenacodontidae   THERAPSIDA
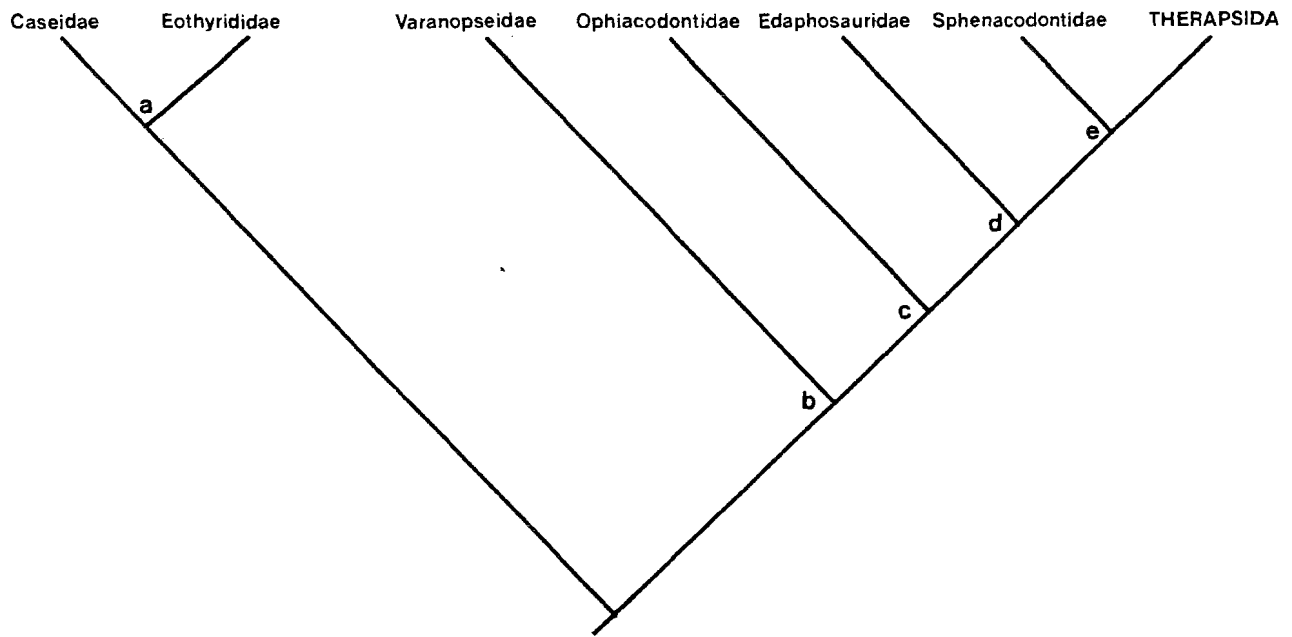
Figure 41. Hypothesis of relationships for families of pelycosaurian reptiles. This cladogram shows a certain pattern of pelycosaur relationships which is the result of integration and reevaluation of the hypotheses presented by Reisz (1980) and by Brinkman and Eberth (1983). The letters at the nodes refer to shared derived characters given in Table 3. See text for discussion.

are mediolaterally elongate and extend far laterally from the sides of the para-basisphenoid. This condition was interpreted by BRINKMAN and EBERTH (1983) as derived, while the anteroventrally oriented short processes seen in sphenacodontids and edaphosaurids was considered primitive. This polarity was determined through the use of *Diadectes* and *Archeria* as outgroups. If another cotylosaur such as *Limnoscelis* is used as the outgroup, then the laterally oriented elongate processes become the primitive pelycosaur condition, and the anteroventrally oriented processes can be interpreted as derived. This alternative interpretation is supported by the distribution of this character among primitive reptiles, because in protorothyridids, mesosaurs, milleretids and primitive procolophonids the basipterygoid processes are oriented laterally and extend far from the sides of the para-basisphenoid.

The alternative hypothesis of relationships that takes into account the morphological evidence provided by the eothyridids *Eothyris* and *Oedaleops* and a resolution of the contradictions in the two recent cladistic analyses (REISZ 1980, BRINKMAN and EBERTH 1983) is presented in Fig. 41. The list of shared derived characters for this cladogram is given in Table 3. It is important to emphasize that nodes b, and especially c of the cladogram represent aspects of the theory of relationships that are not well supported and analyses of character polarities of

other osteological features are needed to resolve the interrelationships of the pelycosaurs included in this clade. As suggested by BRINKMAN and EBERTH (1983) these testable hypotheses serve as a framework for continued interpretation of pelycosaur relationships through detailed taxonomic and morphological revisions of individual genera and families.

It is generally accepted that therapsids or advanced mammal-like reptiles arose from pelycosaurs. Most authors (ROMER and PRICE 1940; BOONSTRA 1972; CURRIE 1979) consider therapsids to be a natural group whose origin should be sought among sphenacodontid pelycosaurs. OLSON (1962), however, proposed that the therapsids represent a grade of organisation, with multiple origins from pelycosaurs and suggested that the morphological features found in common in early therapsids may have evolved independently in different groups. One aspect of this proposal, that the dicynodonts and their primitive therapsid relatives arose from caseid pelycosaurs, represents the greatest departure from the generally accepted theories of therapsid origins and relationships. OLSON (1974) subsequently modified his interpretation of the origins of therapsids through the evaluations of their early distribution patterns. In this updated model OLSON suggested that the evolution of the sphenacodontid pelycosaurs towards the therapsid level may have occurred in many areas, and that a few of the evolv-

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Table 3. Distribution of derived character states that formed the basis of the cladogram proposed in this study (Figure 43). The letters in front of the character sets correspond to those shown at the nodes of the cladogram in Fig. 43.

a. Pointed rostrum formed by anteriorly tilted dorsal process of premaxilla
External narial shelf on nasal
?Ventral orbital margin partially formed by maxilla
Anteroposteriorly elongated external narial opening
b. Height of skull greater than the width in the region of the snout
At least one third of the dorsal orbital margin formed by the frontal
Narrow, long supratemporal located in a groove formed by the parietal and squamosal
Pineal posterior to the midpoint of the interparietal suture
c. Dorsal process of stapes articulating in a socket on the paroccipital process
Angular with an extended ventral plate in the region of the articular
Cheek margin concave
?Nasal longer than parietal at the midline
d. Zygomatic arch formed by jugal and squamosal
No shelf between parasphenoid wings
Frontal with a lateral lappet
Quadrate ramus of pterygoid with rounded ventral edge
Prearticular twisted
?Pterygoideus process formed entirely by articular
e. Small quadratojugal covered laterally by squamosal
Reflected lamina of the angular
Retroarticular process turned downward
Paroccipital process elongated and directed ventrolaterally

ing taxa could have passed the therapsid threshold to give rise to the major groups of therapsids.

The presence in primitive therapsids of a series of shared derived cranial features gives credence to the hypothesis that therapsids form a monophyletic group (Kemp 1982). These derived characters include loss of supratemporal bone, reduction in the size of the interpterygoid vacuities, development of a boss around the pineal foramen, great dorsal expansion of the maxilla, enlargement of the reflected lamina of the angular.

Among pelycosaurs the haptodontines and sphenacodontines are the most likely candidates for sister-group status with therapsids. Romer and Price (1940) proposed that of all the known sphenacodontids, *Haptodus* is the most likely ancestor. They indicated that the skulls of therapsids could be more readily compared with those of sphenacodontines, but postcranial specializations seen in members of the latter group would bar them from direct ancestry. They concluded that *Haptodus* is a reasonable common ancestor of therapsids and sphenacodontines. In a detailed analysis of haptodontine sphenacodontids Currie (1979) suggested that haptodontines and sphenacodontines are more closely related to each other than either is to any known therapsid. Currie also proposed that cranial similarities between sphenacodontines and therapsids may be the result of convergence, correlated with only one feature, the increased development of canines. Slight differences in the snout region, such as the pattern of the lacrimal-maxillary suture and the relationship of the septomaxilla to the maxilla and nasal reinforce the theory of independent acquisition of similar derived features.