Oedaleops campi (Reptilia: Pelycosauria) New Genus and Species from the Lower Permian of New Mexico, and the Family Eothyrididae

by

WANN LANGSTON, JR.

THE UNIVERSITY OF TEXAS

AUSTIN, TEXAS

Table of Contents

List of Illustrations

Oedaleops campi (Reptilia: Pelycosauria) New Genus and Species from the Lower Permian of New Mexico, and the Family Eothyrididae

by

WANN LANGSTON, JR.[1]

ABSTRACT—A small Lower Permian pelycosaur, *Oedaleops* n. gen., is known from some skulls and associated dentary bones from the Cutler Formation of Rio Arriba County, New Mexico. The new species *O. campi* is almost certainly an ancestor of the later *Eothyris* and perhaps *Colobomycter*, which together with several less well known forms comprise the family Eothyrididae. This family appears to be antecedent to the Caseidae whose basic radiation occurred later than that of the Eothyrididae, and which may represent a fourth pelycosaurian suborder—Caseosauria of Williston. The Eothyrididae provide a route by which the caseid lineage could have passed through the Ophiacodontia from a time as remote as mid-Pennsylvanian. Although Edaphosauria of this age are unknown there is little doubt that the suborder was in existence prior to its first appearance in later Pennsylvanian rocks. Resemblances between edaphosaurs and caseids often noted by authors may have been inherited from similarly ancient ancestors.

Introduction

Among several interesting Permian vertebrate fossils discovered in the University of California's Camp Quarry[2] near Arroyo del Agua (Rio Arriba County) New Mexico, are two small skulls representing a new genus of Pelycosauria. These specimens were collected by Professor C. L. Camp in 1928. Subsequent excavations revealed several additional maxillae and some small dentary bones which for reasons given below may be referred to the same species. No other bones in the quarry can be positively identified with the species, but some associated postcranial elements may well belong to it and are described below.

This new genus appears to shed some light upon the relationships of the ophiacodont family Eothyrididae and its place in the ancestry of the caseid pelycosaurs.

[1] Texas Memorial Museum.
[2] For detailed account of this and nearby localities see Langston, 1953.

[5]

Class REPTILIA

Subclass PELYCOSAURIA

Family EOTHYRIDIDAE

Oedaleops, new genus[3]

Diagnosis.—Small and primitive eothyridid about the size of *Eothyris parkeyi*, but with longer face and tooth row, larger temporal fenestra, and more slender postorbital bar. Frontal enters orbit, lacrimal meets jugal, and inner narial wall is (presumably) better developed than in *Eothyris*. Dentition less aberrant than in *Eothyris*, with more, longer, slenderer, and smaller teeth; canine tusks slender, one pre-canine tooth in maxilla relatively larger than pre-canine of *Eothyris*.

Genotype.—Oedaleops campi

Oedaleops campi,[4] new species.

Type.—A slightly distorted skull, lacking palatal bones, braincase and some facial elements of the left side. U.C.M.P. No. 35758.[5]

Referred specimens.—Another skull, much distorted and incomplete, No. 40281. A nearly complete maxilla, No. 67222. Two incomplete maxillae, Nos. 67223 and 67224; two incomplete maxillae in a large block of matrix, No. 40095. Several isolated dentary bones prepared in shallow relief in large blocks of rock containing other specimens, Nos. 67225 and 40095.

Locality and horizon.—U.C.M.P. Loc. V-2814 (the Camp Quarry), on the southeast slope of a small butte, 410 yards south of New Mexico State Highway 96, about 940 yards southeast of the Rio Puerco bridge at Arroyo del Agua, section 8, T. 22 N., R. 3 E., Rio Arriba County, New Mexico. From soft brick-red clayey siltstone of the New Mexico Cutler Formation, about 125 feet below the top of the butte.

Age.—Early Permian (Wolfcampian).

Diagnosis.—Sole known species of *Oedaleops*.

Description

The type skull is complete except for the loss of the quadrates and other parts noted above. The posterior corners of the skull roof are damaged, and

[3] Οἰδαλέος = swollen + ὄψ = face, an allusion to the inflated appearance of the pre-orbital area as seen from above.

[4] Named for Professor Charles Lewis Camp of the University of California, discoverer of the Camp Quarry and other important Permian vertebrate localities in New Mexico.

[5] All specimen numbers in this paper refer to collections in the Museum of Paleontology, University of California, Berkeley.

the entire specimen has been a little flattened dorsoventrally by crushing. It has also been skewed to the left, flattening out the right side of the face. Most sutures are clearly seen. Some displacement of elements has occurred along sutural contacts; the whole right cheek region seems to have shifted forward and the squamosal has slipped upward beneath the supratemporal and parietal.

At first glance the referred skull shows little resemblance to the type. Not only is it less complete, but an unusual form of distortion has "rolled" it up anteroposteriorly into a nearly spherical mass. This specimen has been of little use in preparing the descriptions, which unless otherwise noted are based on the type specimen.

The referred dentary bones are well preserved, as are the isolated maxillae.

The type skull has the following principal dimensions: length as preserved, 76.0 mm.; greatest width, 56.0 mm. (estimated); least transverse diameter between the orbits, 18.0 mm.; postorbital length, 39.0 mm. (approximately); length of face from center of orbit, 37.0 mm.; length of upper tooth row, 43.0 mm. The height of the skull cannot be determined accurately owing to the post-mortem flattening. The referred skull was of about the same size.

The major features of the skull seen in dorsal aspect are shown in Figs. 1 and 5. The length/width index is approximately 141 (depending on one's ideas of the proportions of the undistorted specimen). Lateral inflation of the antorbital skull roof hides the tooth row in dorsal aspect, and the nasal bones overhang the nares, largely obscuring them from above. The posterior margin of the skull table is deeply but broadly emarginated by the depression of the parietal plate behind the pineal foramen. The apparent existence of posterolateral cornua is partly illusory as explained below.

All roofing bones are sculptured. On top of the skull the pattern comprises many low, semi-symmetrically arranged blister-like corrugations separated by shallow grooves of varying depth. The entire surface has a distinctively wrinkled or shriveled appearance (Plate I). The sculpture on the side of the skull is less pronounced except for some low "blisters" on the jugal and squamosal. The facial bones are marked only by insignificant anastomosing grooves and ridges. The roofing bones above the orbits, particularly near the edges of the openings, are marked by regularly alternating, short ridges and valleys whose longitudinal axes lie approximately radial to the center of the orbits. Medial to these circumorbital "corrugations" and approximately parallel to the dorsal edge of the orbit is a shallow groove strongly reminiscent of the lateral-line sulci of labyrinthodont amphibians. The groove can be followed forward on either side of the skull across the frontal and nasal where after some minor interruptions it finally turns laterally, passes to the side of the face and disappears at the posterodorsal corner of the naris. The sulcus also continues posteriorly, with some interruptions, across the post-

[7]
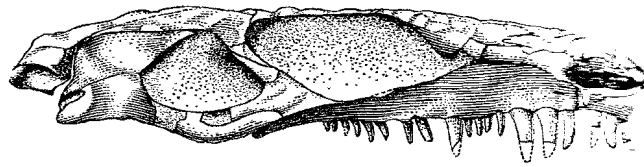
A

B
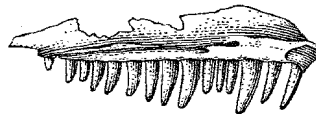
C

Fig. 1. *Oedaleops campi* n. gen., n. sp. A, type specimen U.C.M.P. No. 35758, lateral aspect; B, the same, dorsal aspect; C, left maxilla U.C.M.P. No. 67222, medial aspect. All × 1.

frontal and postorbital bones and gradually disappears toward the posterior end of the latter. On the whole the sculpture and sulci on the skull roof seem remarkably ordered and symmetrical. (See Plate 1).

The transverse emargination of the skull table is accentuated by postero-lateral extensions of the supratemporal bones on either side. A strong median

[8]

nuchal ridge interrupts the smooth curve of the transverse occipital border. An almost insensible transverse crista parallels this edge just behind the pineal foramen, and from this the parietal plate descends gradually posteriorly toward the occiput. The crista is confluent laterally with a thick dorsal ridge that radiates posteriorly from near the center of parietal ossification (delineated by the sculpture pattern), and then passes onto the supratemporal where it becomes much more pronounced. The dorsal surface of the parietal thus enclosed is devoid of sculpture. A considerable area was thus available for attachment of the superficial dorsal neck muscles.

It is impossible to tell how steeply the occipital plate was inclined. In spite of the gradual descent of the parietals behind the transverse occipital crest, the nearly vertical position of the posterolateral edge of the squamosal suggests that the occiput may not have been strongly slanted. It is difficult to determine the normal inclination of the cheek plates, but a sharp separation between skull table and cheek on the right side suggests that the squamosal was more vertical in the uncrushed skull. It is impossible to know whether the lateral temporal fenestrae were visible from above, though this seems a logical inference.

The rostrum projects some distance beyond the end of the tooth row anteriorly, and although crushed, was obviously obtuse and high.

The jaw articulation probably occurred not far if at all below the level of the tooth row, but again distortion of the specimen injects a degree of uncertainty. The skull roof was not arched above the orbits.

The largest openings in the skull are the orbits which, as preserved, are longer than high (principal diameters of the right opening in the type are 23.7 mm. and 13.7 mm., respectively). The height was relatively somewhat greater in the undistorted skull. The orbit occupies about one-fourth of the skull length, and the center of the opening is approximately the anteroposterior midpoint of the skull. The orbits incise the skull roof broadly, greatly reducing the interorbital space. The narrowness here is accentuated by the expansion of the prefrontals.

The normal shape of the lateral temporal fenestra can only be inferred, but the opening was about half as large as the orbit. The postorbital bar, composed about equally of jugal and postorbital bones, is slender so the orbit and fenestra are not widely separated.

The nares were large openings for so small a skull, with a length of about 10.5 mm. in the type specimen. Probably the height was about the same. There is some suggestion of an inner narial wall on the nasal bones, and the openings are floored by a broad inward shelf formed by the premaxillae and maxillae.

The huge, round pineal foramen, almost one-third as wide as the orbit, lies at midlength of the parietal plate, but close to the posterior edge of the

[9]

subdermal skull surface. Its edges are slightly raised. The opening in the type specimen has a transverse diameter of 7.0 mm.

The premaxilla forms the ventral and anterior margins of the naris and projects forward and upward beyond the end of the tooth row. The dorsal processes of the united premaxillae appear on the superior surface of the skull where they extend between the nasal bones for a short distance.

The wide nasals curve downward onto the lateral surfaces of the face, and are broadly arched transversely across the top of the snout. Their relationship to the nares has already been described.

The long parallel-sided frontals have a narrow lateral process that projects into the orbital rim between the pre- and postfrontal bones. The part of the skull roof formed by these bones is flat, even a little depressed posteromedially.

The parietals form a very broad, flat leaf-shaped plate whose sharply irregular edges are in strong contrast with the smoothly parallel sides of the frontals. Broad parietal "lappets" with deeply serrated margins fore and aft are firmly integrated with the postorbitals and supratemporals, which separate the parietal from the squamosal surficially.

A relatively broad median interparietal element forms the nuchal ridge and about half of the dorsal occipital surface of the skull. It sends a strong "keystone" process upward and forward between the parietals to within a short distance of the transverse occipital crest but it fails to reach the subdermal surface of the skull table, and is unsculptured.

The large prefrontal has an inflated appearance in front of the orbit and occupies a large space on the side of the face. Above the orbit its edge is marked by the corrugated sculpture already described.

The postfrontal, similarly sculptured, seems small in relation to the prefrontal, and evidently appeared in lateral aspect only as a narrow band above the posterodorsal corner of the orbit.

In contrast, the postorbital bone is unusually large (but is likewise only narrowly exposed in lateral aspect). It extends almost to the posterior end of the skull and has a long squamous (or tongue-and-groove) union with the supratemporal bone posteromedially. Medially an irregular suture unites it with the parietal "lappet." The bone was in contact with the squamosal laterally at what appears to be a longitudinal tongue-and-groove suture. Farther posteriorly it seems to lie upon the dorsal surface of the squamosal. What is presumed to be a primitive line of weakness between skull table and cheek is well displayed here owing to post-mortem displacement of the squamosal forward along the suture.

The structure in the vicinity of the supratemporal and tabular bones is diffcult to interpret owing to the loss of much bone in the type and distortion of this region in the referred skull. The supratemporal which is clearly seen

[10]

in dorsal aspect in the accompanying illustrations is about twice as long as wide and appears exceptionally large. It carries a thick and rugose longitudinal ridge dorsally, somewhat reminiscent of the posterolateral *squamosal* ridges of eusuchian crocodiles. This terminates posteriorly in a low boss or irregular knob, and lends the impression of a hornlike protuberance at the posterolateral corner of the skull table. The supratemporal is inserted diagonally into the posterolateral corner of the skull table where it is lodged in an approximately parallel-sided notch, bounded laterally by the postorbital and (normally) the squamosal. Anteriorly this bone has a strong interdigitating union with the parietal. Posterolaterally its relationships are obscure; these will be considered further in the subsequent discussion.

A broad thin plate of bone medial to a long posterolateral process of the parietal and the supratemporal on the left side of the type is evidently a tabular bone. It is incomplete ventrally and its relationship to the postparietal is indistinct. But in the referred specimen a bone in the corresponding position shows a long sutural surface for the postparietal (which is displaced in the specimen and no longer has a contact with the tabular). Apparently the bone was entirely occipital in position and was not visible in lateral aspect. The pelycosaurian tabular normally impinges on the posttemporal fenestra, but no trace of this opening can be found on the incomplete bones preserved.

The long and low maxilla contains two sets of enlarged teeth. One, representing the usual "canines" of sphenacodonts and eothyridids, comprises two tusks and a slightly smaller tooth in front, at the anterior end of the maxillary series. A secondary peak is reached toward the end of the anterior third of the maxilla's length with a tooth only a little smaller than the posterior canine tusk. The greatest vertical expansion of the maxilla occurs above the last of the large anterior teeth and continues undiminished posteriorly to a point just anterior to the level of the secondary peak. The lateral surface of the maxilla behind the tusks is depressed so that the bone appears swollen around the bases of the tusks. It does not expand again around the bases of the teeth in the secondary peak. An elongate anterior process of the maxilla meets the premaxilla in a long diagonal suture beneath the center of the naris. This part of the bone is edentulous. Here the maxilla has an inwardly developed flange which enters the posteroventral part of the naris and with the premaxilla forms a broad floor in that opening. The lateral surface of the bone is penetrated here and there by tiny foramina. Above the base of the anterior tusk a larger foramen issues from the bone and continues a short distance anteroventrally as a shallow groove. A little above this a small slit-like foramen opens upward. There are two other small grooves in the same vicinity, but whether they issue from foramina is uncertain. The maxilla extends posteriorly in a long tapering process at least to the level of the postorbital

[11]

bar, and it may have reached the quadratojugal beneath the lateral temporal fenestra. The bone did not turn into the orbit from which it is excluded by a long infraorbital ramus of the jugal. It nevertheless appears to bound the opening anteroventrally in lateral aspect.

A referred left maxilla (No. 67222) is exposed from the medial side (Fig. 1c). There is a long sutural surface for the palatine bounded above by the thickened alveolar shelf. Anteriorly the roots of the tusks are surmounted by a thickened bulge, but this is not as strongly developed as in sphenacodonts. The vertical brace that occurs above the enlarged maxillary teeth of typical ophiacodonts (*Ophiacodon*) is not present. A foramen enters the supracanine bulge above the base of the third (and largest) tooth.

The lacrimal is narrow and elongate. It extends from the orbit to the naris, increasing slightly in width anteriorly and there bending downward in concert with the dorsal edge of the maxilla. It bounds the naris completely behind, and sends a small process into the opening anteroventrally. This combines with the broad maxillary flange in the floor of the naris. Examination of the referred skull shows that the nasolacrimal canal is completely enclosed within the lacrimal bone. The canal apparently divides within the bone and emerges into the orbit through three foramina. Two, more dorsally placed, are subequal in size and considerably larger than the third, more ventral, opening. The lacrimal has an elongate posteroventral process that laps along the maxilla below the anterior part of the orbit. This branch of the lacrimal is not visible in lateral aspect, nor can the union with the jugal be seen. However, the bone appears long enough in the referred skull to have reached posteriorly to the anterior end of the infraorbital ramus of the jugal. The contact would have occurred within the orbit and would not have been visible laterally.

Exploration of the narial openings has failed to reveal a recognizable septomaxilla, but a tiny curved bit of bone lodged in matrix at the posterodorsal corner of the right naris may be part of this bone. Certainly the septomaxilla did not appear on the lateral surface of the face.

The three lateral rami of the jugal are long and slender. The ventral rami form, respectively, all of the lower margins of the lateral temporal fenestra and the orbit. The temporal ramus appears to have been wide in comparison to the slenderness of the postorbital ramus; the depth of the infraorbital ramus cannot be determined satisfactorily owing to post-mortem overlap by the maxilla. The jugal forms a distinct shelf within the orbit. This is continued backward and upward as a medially directed flange on the postorbital bar, which then continues onto the postorbital bone above. Posteromedially the shelf is deflected and becomes confluent with the pterygoid process of the jugal. The latter is large and lies mainly horizontal, at least as preserved.

The one squamosal preserved in the type has been displaced forward along

[12]

the lateral edge of the supratemporal bone, and has been much damaged ventrolaterally. Enough remains, however, to show that this was a very broad bone composed of three surfaces which stand at acute angles to each other. The lateral plate is perhaps twice as large as the occipital surface which nevertheless seems relatively large for a pelycosaur. It is uncertain whether the bone entered the subtemporal arcade, or was excluded from it by the jugal. It could not have contributed much in any case. At the posterodorsal corner of the lateral plate the surface of the bone is raised into a short thickened ridge whose posterior edge is roughened in sutural fashion. Below this expansion the posterior edge of the bone is broadly but shallowly emarginated vertically. Medial to the ridge, that is, on the occipital plate, there is a deep pit which in normal position doubtless received the tabular and (or) paroccipital process. Beneath the notch the occipital flange expands medially and descends as a broad plate toward its inferred surficial contact with the quadratojugal. During preparation part of the posterior roofing bones were temporarily removed revealing beneath them a relatively broad expanse of squamosal. This almost horizontal flange joins the lateral and occipital plates across the top of the bone. Its limits were not defined, but it was observed to extend medially for at least one-fourth of the width of the skull table. The dorsal surface of this plate is roughened but it does not show strong indications of a sutural union with the overlying parietal, postorbital, or supratemporal.

The displaced quadratojugal (not shown in Fig. 1) has a very long subtemporal ramus which evidently extended far enough forward to have contacted the maxilla. It appears largely to have underlain the other bones of the arcade and thus had only a limited lateral exposure at the posteroventral edge of the cheek. It evidently did not reach the edge of the lateral temporal fenestra, but was separated from this by union of the jugal and squamosal above. The quadratojugal is sharply deflected posteromedially where it was probably interposed surficially between quadrate and squamosal. No trace of a quadrate foramen has been detected on the quadratojugal.

I have assigned several small dentaries (Fig. 2) to *Oedaleops* on grounds of size, dental characters, the absence in the deposit of any other animal
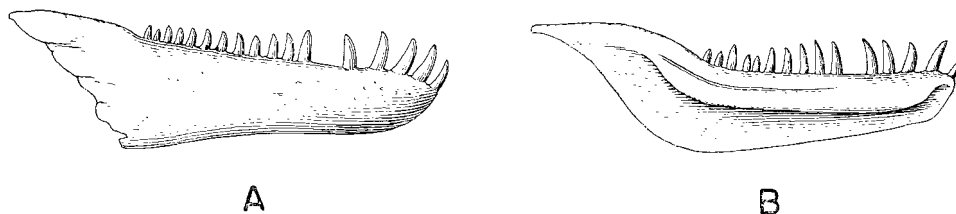

A   B

Fig. 2. *Oedaleops campi* Langston. Referred dentaries. A, U.C.M.P. No. 67225, lateral aspect; B, U.C.M.P. No. 40095, medial aspect. Both × 1.

[13]

with which such dentaries might more probably be associated, and a certain resemblance to the dentary of *Eothyris parkeyi* whose skull is closely similar to that of *Oedaleops*. One dentary (in block No. 40095) is 49 mm. long, 12 mm. deep posteriorly, with a tooth row about 30 mm. long. The bone is relatively deep, especially posteriorly. Posterodorsally a long slender process rises above the level of the tooth row. The dentigerous edge of the dentary slants downward toward the front, and the ventral edge of the bone is concave upward at about mid-length. The meckelian fossa is deep. No roughened symphyseal surface is seen on any of the dentaries. This and the widely open meckelian fossa suggest that the splenial was large and extended forward to the end of the jaw to participate broadly in the symphysis.

The teeth of *Oedaleops* are slender, semiconical, pointed, and moderately curved. Their relative sizes and arrangement are clearly shown in the illustrations. In the type skull the third maxillary tooth is the largest (in No. 67224 this tooth is 8.0 mm. long). The second is only a little smaller, and the first is almost as large as this. The big tusk has an oval basal section; all other teeth in the maxilla (No. 67222) are round at the base. Dental details are best seen in No. 67224. This is the largest of the referred maxillae with a length from the base of the first tooth to the eleventh of 24.2 mm. (this distance in the type skull is 20.8 mm.). Space for at least seventeen teeth is available; three replacement gaps exist (2, 4, 13). The sixth tooth has been broken just above the base. In this specimen the precanine is considerably smaller than the canine. The secondary peak occurs at the ninth tooth. All teeth have thickened bases seemingly fused to the maxillary bone. At the point of attachment the bone is penetrated by numerous tiny foramina arranged circumferentially around the base of each tooth. The crowns are capped with thin enamel which appears to grade proximally into softer material. No fluting is apparent, but on the lingual surfaces the enamel is finely and irregularly wrinkled, especially toward the tips of the crowns. Each crown bears a distinct carina on its anterior and posterior edges. These extend proximally to about mid-height of the teeth. In this specimen it can be seen that the tips of the crowns of all the teeth are turned a little inward. As in the other specimens they are slightly recurved anteroposteriorly.

The three premaxillary teeth seem relatively large. There is a gap between the premaxillary and maxillary dental series, but no "sphenacodont" notch occurs in the jaw margin at this place. Space is available for no more than 19 teeth in the maxilla of the type (the posterior part of the bone seems too thin to have borne teeth). Only 16 teeth are preserved, but there are only two gaps in the series resulting from replacement.

Space is available in the various dentaries for from 15 to 20 teeth, depending upon the length of the bone. The lower teeth vary from long slender cones with slightly blunt crowns to short, straight pegs. They are uncrowded

and regularly spaced with few replacement gaps appearing. The longest dentary teeth, more curved than the smaller ones, occur toward the front of the jaw although the first mandibular tooth is usually a little shorter than those immediately following. A slight tendency toward "prognathism" is seen where the labial edge of the dentary turns downward anteriorly.

Postcranial Elements Possibly Attributable to Oedaleops

Found scattered in the Camp Quarry with the skulls and jaws of *Oedaleops* were numerous postcranial elements which I strongly suspect belong to the genus. They are mostly of appropriate size, and repetition of elements occurs in the vicinity of some of the jaw bones. Most of the bones are demonstrably different from homologous bones of one associated pelycosaur, and only one other reptile recognized in the collection from skull material might possibly have contained them. They will be described without further consideration except to note that as a group the girdle and limb bones appear to belong to a pelycosaur (or pelycosaurs) of primitive grade, most probably an ophiacodont, edaphosaurian, or caseid. The fact that there seem to be strong resemblances to *Nitosaurus* may indicate the presence of that genus in the Camp Quarry. It might also indicate a closer relationship between *Oedaleops* to nitosaurids than is apparent from comparisons of the skulls alone. In any case the observations fit adequately into the concepts of eothyridid relationships to be discussed subsequently.

Vertebra.—A complete neural arch (No. 67247) presumably is from a posterior cervical or an anterior dorsal vertebra. Its greatest height is 16.1 mm., and the transverse diameter across the diapophyses is 24 mm. This bone is very "un-pelycosaurian" in appearance, resembling the neural arches of cotylosaurs (*Limnoscelis*) and *Seymouria* more than *Ophiacodon* or *Casea*, for example. The "shoulders" of the postzygapophyses are moderately swollen and gracefully arched. The neural arch is wide, low, and the neural spine is a small ridge only a little higher behind than in front. The articular surfaces of the prezygapophyses are almost horizontal with a slight transverse arch. The transverse processes are strong and attached to the pedicle throughout their length. They were obviously continued on the sides of the centrum. Small forwardly-directed facets on either side of the neural canal show that as in *Seymouria* the neural arch contributed a small area to the intervertebral articulation.

Scapulocoracoid.—Several scapulocoracoids of the same form are present. One (No. 40282) has been separated from the matrix (Fig. 3a). No sutures are visible indicating that the animal was adult. The scapula seems exceptionally wide and low (if it is complete dorsally). Its superior and anterior
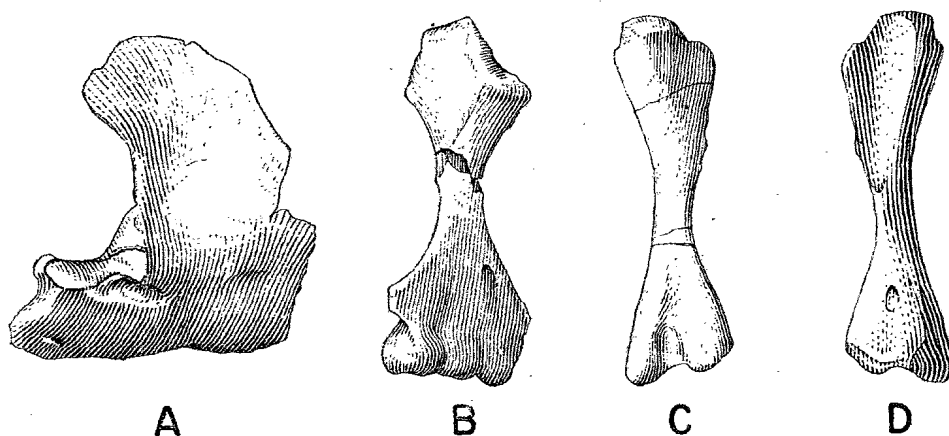
[15]

FIG. 3. Postcranial elements of a small pelycosaur, possibly *Oedaleops campi* Langston. A, right scapulocoracoid U.C.M.P. No. 40282, lateral aspect; B, right humerus U.C.M.P. No. 40283, ventral aspect, somewhat distorted; C, right femur U.C.M.P. No. 40284, dorsal aspect; D, the same, ventral aspect. All × 1.

edges are broadly curved and partly unfinished. A scar marking the area of overlap of the cleithrum is distinguishable on the visceral surface. This leaves the scapula in a direction that would have carried the cleithrum some distance forward above. Filling the gap that would have resulted from this anterior inclination of the cleithrum might have produced a scapular blade of more nearly edaphosaurian appearance. The supraglenoid buttress is narrow. There is no trace of a supraglenoid foramen. The posterior processes on the postcoracoid are strong. The coracoid foramen is relatively large, the ventrolateral sulcus at whose apex it lies, is wide. On the visceral side the subcoracoscapular fossa appears relatively very large. Its edge on the supraglenoid buttress is almost semicircular. The longitudinal bridge which roughly parallels the scapulocoracoid suture is thick and the longitudinally oval depression ventrolateral to it is deeply excavated. The specimen is 43.5 mm. high and has a length above the glenoid of 27 mm.

The absence of a suture between the postcoracoid and scapula, and the lack of a supraglenoid foramen are reminiscent of *Casea*. Except for the outline of the low scapular blade the structure seems fairly similar to such edaphosaurs as *Nitosaurus* and *Mycterosaurus*.

Ilium.—A right ilium (No. 67246) is among the most interesting bones in the entire Camp Quarry collection. One of a pair associated with two femora of the sort described below, it probably belonged to one of the individuals with scapulocoracoids described above. The bone is exceedingly thin and relatively flat, in part owing to post-mortem pressure. Its main features are clearly seen in Fig. 4. Notable is the great dorsal extent of the iliac blade and
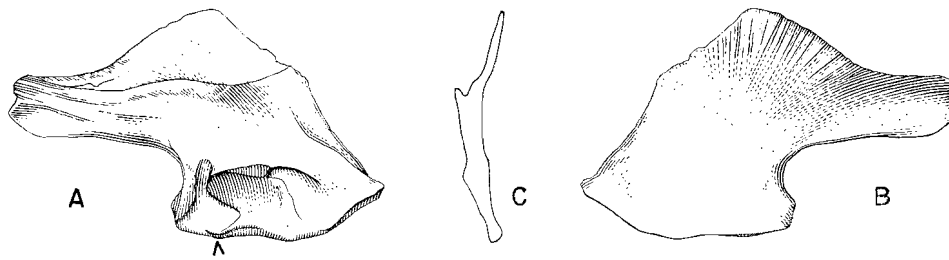
[16]

FIG. 4. Right ilium, possibly *Oedaleops campi* Langston, U.C.M.P. No. 67246. A, lateral aspect; B, medial aspect; C, vertical transverse section at A. × 2/3.

the elongate dorsolateral trough on the side which carried some dorsal axial muscles (Romer, 1956, p. 317). This trough opens directly upward and its lateral wall is raised and sharply defined for approximately three-fourths of the total length of the ilium. The iliac blade is not expanded anteriorly above the neck, but posteriorly it extends as a flattened process whose distal end is squarely truncated and unfinished. Longitudinal striae on both the lateral and medial surfaces mark areas of attachment for caudal ligaments. The iliac neck is high and relatively broad, with only a shallow constriction along its posterior edge. On the medial surface many strong ridges and grooves radiate from the central area of the blade toward its dorsal edge. There is no clear indication of a sacral articulation as occurs, for example, in *Ophiacodon*. The bone has a greatest length of 62 mm., and a height of 37.7 mm. The least anteroposterior diameter of the neck is 25 mm.

If this is a pelycosaur ilium it is surely the most primitive known in the whole order. The general structure is much more like that of the primitive (and near-contemporary) cotylosaur *Limnoscelis*, especially in the combined presence of the long posterior iliac process and the longitudinal trough (which is even more extensive than in *Limnocelis*). The ilium resembles *Ophiacodon* more than *Limnoscelis* only in the lack of any anterior expansion of the blade. It is not in the least similar to any edaphosaur, or *Casea*. Were it not for their association with postcranial material of more pelycosaurian nature these ilia would certainly have been regarded as "cotylosaurian." They are in any case of cotylosaurian grade.

Humerus.—A right humerus (No. 40283) has a long slender shaft, a moderately expanded distal end, and a relatively narrow head (Fig. 3b). All surfaces appear to be finished except the radial condyle. The deltopectoral crest is relatively strong. It terminates proximally in a heavy, posteriorly-turned bifid tuberosity, some distance from the head. The entepicondyle is thin and broadly expanded horizontally. Its posterior edge is slightly diagonal. The entepicondylar foramen is not unusual. The supinator process diverges mod-

[17]

erately from the shaft and is well separated from the ectepicondyle; the ectepicondylar foramen was not enclosed. The bone is 48.7 mm. long, 23.5 mm. wide (anteroposterior) at the distal end, and 13.2 mm. wide (dorso-ventral) at the head.

This humerus appears relatively more slender than any non-sphenacodont humerus figured by Romer and Price (1940). The narrowness of the distal expansion distinguishes it from humeri of most ophiacodonts, and the head is relatively narrower than in *Casea*. Otherwise the bone is about as close to *Casea* as to any other pelycosaur except possibly *Nitosaurus*.

Ulna.—In a large block of matrix (No. 40096) there is a small ulna which lies among a pair of scapulae and a humerus of the type described above. Little can be said of it except that it is about as long as the associated humerus and has a strong olecranon process. The sigmoid notch is deep. The distal end is moderately expanded. The bone is 39 mm. long, including the olecranon.

Femur.—One right femur (No. 40284) has been freed from the matrix (Fig. 3c,d); a number of others, all larger and more massive, remain in the rock. Number 40284 is slender, not much expanded at either end, and almost straight (a result of crushing?). The small head is terminal with a subtri-angular outline. It is continuous posteroventrally with the posterior edge of the intertrochanteric fossa, and is set off anteroventrally from the internal trochanter only by a shallow notch. The internal trochanter is well exposed in dorsal aspect and extends almost to the head of the femur. The fourth tro-chanter, not strongly developed, occurs below midlength of the adductor ridge. The posterior edge of the intertrochanteric fossa is sharp and the fossa is fully half as long as the entire bone. It seems unusually deep for so small a bone and is not clearly circumscribed distally. The condylar area is about equal to the proximal end in anteroposterior diameter. The posterior condyle is long, but seemingly unfinished ventrally. The dorsal edge is not distinctly separated from the rest of the condyle, nor is it greatly raised on the top of the shaft. The intercondylar fossa is deep above and shallow below. The condyles are not deeply divided. This bone is 49.3 mm. long. The greatest (anteroposterior) diameter of the distal end is 13.7 mm., that of the proximal end 13.3 mm.

This femur resembles that of *Nitosaurus* but is only half as large as the specimen figured by Romer and Price. Some of the other femora are a little longer, but much thicker, and resemble *Casea* more than *Nitosaurus*. The similarity to femora of *Ophiacodon* is slight. The larger femora are not unlike the bone in *Varanosaurus* in gross form, but the intertrochanteric fossa of the supposed *Oedaleops* femur extends much farther down the shaft.

[18]

Discussion

The presence in *Oedaleops* of a large lateral temporal fenestra bounded above by postorbital and squamosal bones immediately suggests affinities with the Synapsida. But a few of the late Permian millerosaurs (Millerosauria of Watson, 1957; Eosuchia of Romer, 1958, in part) show an analogous condition.[6] A cursory comparison of the illustrations of *Oedaleops* and the millerosaurs given by Watson (1957, Figs. 12, 13) and especially by Broom (1938, Figs. 1, 2) shows a striking coincidence in the arrangement of the roofing bones, the lateral inflation of the prefrontals, and even in the sculpture pattern.

There are in the millerosaurs certain features related to the middle ear which Watson (1957) supposed allied them more closely to diapsid than synapsid reptiles. Nothing is known about the fenestra ovalis, stapes, or quadrate in *Oedaleops*, so the possibility of a relationship to the millerosaurs must be considered on other, less direct grounds. In most millerosaurs the squamosal is recessed posterolaterally in connection with the development of a tympanic cavity, and the bone is structurally complex. There is only a limited occipital exposure of the squamosal, and the quadrate is widely exposed from the rear. In *Oedaleops*, although the quadrate is unknown, the squamosal has a wide occipital flange that must have largely obscured the quadrate in posterior aspect. And there is no suggestion on the squamosal of the existence of a tympanic recess. Although the posterolateral edge of the squamosal appears almost vertical in the *Oedaleops* specimen this is certainly artificial, and what little resemblance to millerosaurs exists here is only accidental. In millerosaurs the parietal lappets, formed somewhat as in *Oedaleops*, and pelycosaurs generally, are described as resting upon the upper surfaces of the squamosal and postorbital; whereas in *Oedaleops* the part of the lappet adjacent to the postorbital is integrated with it by suture. Overlap of the squamosal is best interpreted as retention of a primitive feature encountered also in captorhinomorph cotylosaurs such as *Limnoscelis* (Romer, 1946). Millerosaurs have paired postparietal elements; in *Oedaleops* there is but one median postparietal bone.

Oedaleops is not a millerosaur. Resemblances are probably a result of retention of a primitive reptilian skull roof pattern and (probably) a certain degree of convergence in ornamentation of the roofing bones, as discussed below.

Oedaleops resembles synapsids in most of the ways in which it differs from

---

[6] The striking parallelism in development of a lateral fenestra in *Milleretta rubidgei* and the pelycosaurs lead Broom (1938) to suggest that this millerosaur represented a group "somewhat intermediate" between cotylosaurs and the synapsids.

[19]

millerosaurs; it clearly fits the criteria of the Pelycosauria given by Romer (1958, p. 673). When compared with specific pelycosaurian genera the skull is seen (with one exception) to be relatively broader, the top flatter, and the head lower than in any of them. Its supratemporal bone is the largest known and occupies an area in the skull roof more comparable to labyrinthodont amphibians than most synapsid or captorhinomorph reptiles. The remnant of the otic notch as interpreted below and failure of the parietal to become firmly sutured to the squamosal posteriorly show about the least progressive conditions known in either of these reptile groups. The skull appears remarkably "cotylosaurian"; its structure in general is the most primitive known among pelycosaurs.

Oedaleops is not without specializations, however. The well-differentiated dentition is advanced in the development of canine tusks and in the presence of a clearly defined secondary peak in the maxillary series. The wide nares are more aberrant than in any pelycosaurs except the caseids. Possibly the rough and highly symmetrical sculpture should also be regarded as a specialization inasmuch as its form is entirely different from the usual pits and ridges found in many captorhinomorphs and some pelycosaurs. The symmetry of the pattern is not matched elsewhere among primitive reptiles so far as I am aware unless it be in the millerosaurs, where, unlike *Oedaleops*, the elevations are supposed to result from a fusion of osteoderms to the skull roof (Watson, 1957). Probably the unusual grooves which bear so strong a resemblance to amphibian lateral line sulci are only part of this remarkable sculpture pattern.

The enlarged tusklike anterior maxillary teeth of *Oedaleops* are paralleled elsewhere in pelycosaurs by the sphenacodonts and eothyridids. A cursory comparison of *Oedaleops* with these reveals a striking coincidence in gross form with the skull of *Eothyris parkeyi* Romer, and almost no similarities to sphenacodonts. *Oedaleops* must therefore be compared in some detail with *Eothyris* and its relatives.

Oedaleops *and the Eothyrididae*

Various (and often inadequately known) pelycosaurs have been placed with *Eothyris* in the family Eothyrididae, because like it they were neither sphenacodonts, edaphosaurs, nor caseids, but seemed to show ophiacodont qualities, and displayed a tendency toward the development in the anterior part of the maxilla of large canine teeth which sometimes would qualify as tusks. In some poorly known forms these tusks are the only distinguishing feature, and the family is possibly an artificial assemblage (Romer, 1952). Besides *Eothyris* and *Oedaleops* the Eothyrididae as presently constituted contains the late Pennsylvanian (Stephanian) genera *Stereorhachis* Gaudry

[20]

(1880) from Europe, and *Stereophallodon* Romer (1937) from North America; the early Permian *Baldwinonus* Romer and Price (1940), *Bayloria* Olson (1941), *Colobomycter* Vaughn (1958), and very doubtfully *Tetraceratops* Matthew (1908), all from North America. *Delorhynchus* Fox (1962) from the Lower Permian of Oklahoma is assigned to the family in this paper.

Oedaleops *and* Eothyris *compared.—Eothyris* is known by the unique holotype skull and jaws of *E. parkeyi* Romer, from the Belle Plains formation in Archer County, Texas (for illustrations and reconstructions of *Eothyris* see Romer, 1937, 1956; 1961b; Romer and Price, 1940; Watson, 1954). It is believed to occur a little later in time than *Oedaleops*.

Oedaleops and *Eothyris* show partial to complete agreement in the following respects.

1. They have among the smallest skulls known in pelycosaurs. (*Oedaleops* is slightly the larger.)
2. The relative proportions of the face to the postorbital cranium are comparable. (*Oedaleops* has relatively the longer face.)
3. The skulls are relatively the flattest among pelycosaurs.
4. The position of the jaw articulation is at about the same level (I suspect) as the tooth row.
5. The relatively large size of the orbits causes constriction of the skull roof between, which is unarched and even a little depressed.
6. A huge pineal foramen occurs near the center of the parietal plate.
7. The relative location of orbits and pineal opening is the same.
8. Enlarged nares and obtuse rostrum (perhaps too confidently assumed in some recent reconstructions of *Eothyris,* but certainly present in *Oedaleops*) are reminiscent of *Casea.*
9. Cheek plates (presumably) slope outward.
10. An unreduced lacrimal extends from orbit to naris; it contains within the orbit large foramina for the naso-lacrimal duct.
11. The shape and relationships of most of the roofing bones are very similar; the largest supratemporal bones known in pelycosaurs are wedged into the posterolateral corners of the parietal; parietal lappets are similarly developed.
12. There is an exceptionally long, tapering postorbital bone with wide supratemporal and squamosal contacts.
13. The prefrontal bones in front of the orbits are "inflated."
14. They show a common tendency toward differentiation of large canine tusks toward the front of the jaw, and a secondary peak in tooth size near the middle of the maxilla.

It is difficult to say how closely the sculpture patterns resembled each other owing to inferior preservation in the *Eothyris* specimen. In it the roofing bones seem to be roughened, but do not indicate presence of pits

and ridges of the type seen in caseids. The rugosity may well have been of *Oedaleops* character.

This is an imposing list even though the significance of the various similarities doubtless differs. The small size of the skulls is in itself probably the least important resemblance, and has influenced such characters as the relatively large orbits and pineal foramen. The resemblance in location of the foramen and the orbits is partly accountable on the ground that the position of the organs occupying them was controlled by the proportions of the brain case. In similarly small skulls of related animals the brain case was doubtless similar also. If there was a minimum size for the pineal organ in pelycosaurs below which it could not function adequately, perhaps the dimensions of the foramina in *Oedaleops* and *Eothyris* reflect this. Nevertheless its absolute size in these genera and *Casea broilli* is so similar that taken together with the other resemblances it is strongly suggestive of relationship.

The depression of the skull, position of the jaw articulation, slanting cheeks resulting (presumably) in a less angular transverse profile in the postorbital region, character of the lacrimal, large supratemporal, and broad parietal lappets appear to be primitive reptilian qualities that might be expected in generalized pelycosaurs close to the captorhinomorph ancestry of the group. The arrangement of the bones in the skull roof of *Oedaleops* and *Eothyris* conforms to a basic pattern in primitive reptiles and is shared by such disparate groups as millerosaurs and captorhinomorphs, as well as with ophiacodonts.

Individually some points of similarity between *Oedaleops* and *Eothyris* may signify no more than that both are small and primitive reptiles, but the extensive combination of many such characters must surely imply a fairly close relationship. If further proof is needed it is apparently provided by the presence in both animals of otherwise unique structure in the posterior skull roof and cheek region.

Watson (1954) refers to an "irregular knob" on the tabular bone in *Eothyris*. A similar knob occurs in *Oedaleops* on the supratemporal bone. Direct comparison between the specimens shows a strong resemblance in the gross form of this structure, but my examination of the *E. parkeyi* skull tends to confirm Watson's opinion that the knob is on the tabular instead of the supratemporal in this specimen. A faint line not previously reported in the *Eothyris* specimen may be a suture between supratemporal and tabular, however, and the suture shown by Watson may be only a crack. If this is so the supratemporal would be even larger than presently supposed, and the whole structure would appear almost identical to *Oedaleops*.

The knoblike process in *E. parkeyi* is tightly appressed to the slanting posterolateral edge of the squamosal in what seems to be a normal contact. In the type of *O. campi* the forward slippage of the squamosal may have rup-

[22]

tured a former union with the supratemporal and produced a wide gap in the side of the skull. This results in a gross but superficial resemblance to an otic notch of labyrinthodont form. The point at which the knob and squamosal were in contact is evidently represented by the low posterolateral ridge at the upper edge of the lateral squamosal cheek plate. A similar elevation of the squamosal occurs beneath the knob in *Eothyris*, and there forms part of the rim of a small matrix-filled depression near the posterolateral corner of the lateral squamosal plate. The tip of the supratemporal (of Watson) just enters this pit anterodorsally, and the knoblike process bounds it behind. One may imagine that comparable architecture would result if the squamosal of the *Oedaleops* specimen were shifted backward.

After examining the specimen I am unable to say whether the pit in *E. parkeyi* represents only a depression in the lateral skull surface, or is in fact a matrix-filled foramen in the side of the cheek. Edges of the squamosal in the critical area in *Oedaleops* appear smooth and it seems possible that these bounded a perforation in the side of the skull. The pit or foramen lies at about the spot where the remnants of a former otic notch might be expected, bounded above by supratemporal, below and anteriorly by the squamosal. Romer (1946, *et seq.*) has pointed out that a zone of weakness at the edge between skull table and cheek in *Limnoscelis* and other early reptiles including pelycosaurs probably derives from an ancestral otic notch. This zone would include the region of squamosal displacement, the knoblike process and the pit or foramen in both *Oedaleops* and *Eothyris*.

The potential significance of the possible existence of a foramen at this place is intriguing from the standpoint of early reptilian evolutionary theory (for example, see Hotton, 1960). That the structure was somehow related to an ancestral otic notch seems virtually certain. In any case its presence, if homologous in *Oedaleops* and *Eothyris*, is strong evidence of close relationship.

Differences between *Oedaleops* and *Eothyris* are fewer than the resemblances. *Oedaleops* shows the usual entry of the frontal bone into the orbital rim; failure of the frontal to reach the orbit in *Eothyris* is unique in the Pelycosauria. The jugal probably met the lacrimal in *Oedaleops* although the union was evidently not visible in lateral aspect. In *Eothyris* these bones are said to be separated by the maxilla (Romer and Price, 1940). The postorbital bar is decidedly more slender, and the lateral temporal fenestra is consequently larger in *Oedaleops* than in *Eothyris*. The facial region is relatively a little longer in *Oedaleops* than supposed in *Eothyris*; the ratios of rostral length (from anterior edge of orbit): total skull length are, respectively, .37 and .27.

The most outstanding differences are seen in the dentitions. Arrangement of the teeth is of the same pattern, but decidedly more aberrant in *Eothyris*.

[23]

The canines of *Oedaleops*, relatively large for a pelycosaur, are still smaller than the huge organs of *Eothyris*.[7] Although the tooth rows in both genera end at about the same level posteriorly, the maxilla of *Oedaleops* could have carried as many as 19 teeth whereas *Eothyris* had no more than 14 or 15, depending on the disposition of the precanine. If the *Eothyris* precanine is in the maxilla, the premaxillary teeth are two compared to a more usual number of three in *Oedaleops*. The jaw suspensorium was presumably longer in *Eothyris* than in *Oedaleops*.

Wherever differences are noted, except possibly the lateral processes of the frontal, *Oedaleops* appears to display the more primitive condition. Few alterations are required to derive the *Eothyris* skull from *Oedaleops*, and most of these appear related to the remarkable specialization of the *Eothyris* dentition. There the short deep mandible, long suspensorium (almost half the total length of the jaw) and massive anterior canine tusks, whatever their adaptational significance, bespeak a powerful jaw mechanism. Strengthening of the cheek by reduction of the lateral temporal opening, and thickening of the postorbital bar might be a natural consequence of increased stresses in this region. Parenthetically, Watson (1957), in discussing the small temporal fenestra of the millerosaur *Milleretta*, raises the question whether or not this is the first appearance of a temporal opening in sauropsid reptiles, or the "last stage of the closure of a formerly more extensive one."

The differences noted seem qualitatively comparable to the criteria often used to distinguish genera in the Pelycosauria and some other reptile groups. But the resemblance between *Oedaleops* and *Eothyris* is so strong that there can be no doubt that they belong in the same family.

Oedaleops *and other eothyridids compared.*—*Colobomycter pholeter* Vaughn (1958), from the early Permian fissure fillings near Lawton, Oklahoma, was hitherto the second best understood eothyridid. *Oedaleops* agrees with it in:

1. The small skull showing a tendency toward abbreviation of the face (less extreme in *Oedaleops*).

2. The general architecture of the cranium. The proportions and relationships of individual skull bones are fairly similar except for differences to be noted below. The parietal is comparably broad and parietal lappets were probably about equally developed. Vaughn suspected the presence of a large supratemporal element in *Colobomycter*; if confirmed this would be a strong suggestion of relationship to *Oedaleops* (and *Eothyris* too as pointed out by Vaughn). The lacrimal and jugal meet beneath the orbit, more broadly apparently than in *Oedaleops*. Like *Oeda-*

[7] The tiny precanine of *Eothyris* was apparently overlooked in earlier descriptions, and later was placed in the maxillary series by Romer and the premaxillary by Watson. Examination of the specimen leaves me undecided on its position, but there is no question that the precanine of *Oedaleops* is in the maxilla.

[24]

leops, Colobomycter appears to have had no facial exposure of the septomaxilla.

3. The large orbits and pineal foramen. Vaughn suspects the anteroventral corner of the lateral temporal fenestra was acute and fairly sharp in *Colobomycter*, a condition which he notes is rare in pelycosaurs, but occurs in *Varanops*. This is certainly also the case in *Oedaleops.*

4. The eothyridid tendency toward differentiation of large canine tusks.

5. The maxilla which bounds the naris posteroventrally and sends a shelflike flange into it. A peculiar groove on the side of the maxilla above the tusks in *Colobomycter* may issue from a supracanine foramen as in *Oedaleops.*

The similar arrangement of dorsal longitudinal roofing bones in *Oedaleops* and *Colobomycter* may be explained in the same way as the concomitant resemblance between *Oedaleops* and *Eothyris*. As would be expected, *Colobomycter* resembles *Eothyris* about as closely as *Oedaleops* in the pattern of the roofing bones. As between *Oedaleops* and *Eothyris*, it is the extensive integration of several similar characters into a comparable whole that leads to the conclusion that *Oedaleops* and *Colobomycter* are related. The supracanine foramina are uncommon in pelycosaurs and if homologous in these genera would strongly support the inferred relationship.

But differences are extensive also.

1. The skull of *Oedaleops* was probably lower and certainly broader behind. Proportional differences in reptile skulls are so subject to adaptational influences that comparisons of gross form may have little meaning at a supergeneric level. Between genera and species, however, they are more significant. The depression of the *Oedaleops* skull is a primitive feature; the greater width suggests a closer relationship to *Eothyris* than to *Colobomycter.*

2. The frontals in *Colobomycter* have a wider lateral process entering the orbit. Frontal participation in the orbital rim is a normal pelycosaurian trait. Presence of this character in *Colobomycter* and *Oedaleops* suggests that failure of the frontal to reach the orbit in *Eothyris* may be an aberrant development rather than a relict character in that genus, and not a distinctive feature of the Eothyrididae.

3. There is a wider contact between the parietal and postfrontal in *Colobomycter*, and the parietal appears to have formed much more of the skull table there than in *Oedaleops*. No mention is made of a transverse occipital crest in *Colobomycter* and the illustration (Vaughn, 1958, Fig. 1) suggests that there was a relatively broad expanse of parietal behind the pineal foramen. The reduction of the subdermal area of the parietal posteriorly in *Oedaleops* is perhaps an advancement seen neither in *Eothyris* nor *Colobomycter*, but paralleling the emargination of the skull table in more advanced ophiacodonts, and perhaps also the structure found in caseids (see below).

4. Perhaps the most striking difference between these genera is the abbreviation of the lacrimal and the consequent union of the maxilla and nasal on the side of the face in *Colobomycter*. This condition occurs elsewhere in non-sphenacodont pelycosaurs only in *Mycterosaurus* and (presumably) *Delorhynchus*. Some greater

[25]

expansion of the maxilla would of course be expected in *Colobomycter* in connection with its larger canine tusks. *Oedaleops* is distinctly more generalized in this regard.

5. Equally singular is the great expansion of the postorbital bar in *Colobomycter*. A similar condition is known elsewhere in pelycosaurs only in *Bayloria*, and to a lesser degree in *Eothyris*. *Oedaleops* is of usual construction.

6. Although the length of the maxilla appears to be about the same in relation to its posterior termination, there is little further resemblance in this bone. In *Colobomycter* it forms much more of the posterior narial rim and as noted occupies a larger area of the face than in either *Oedaleops* or *Eothyris*.

7. There are fewer maxillary teeth in *Colobomycter*, and the canines were larger than in *Oedaleops*, indicating a higher grade in the Eothyrididae. The "secondary peak" in the dental series occurs farther back in *Colobomycter*, a point probably of no great importance.

8. The sculpture pattern of *Colobomycter* comprises irregular pits in an otherwise smooth roofing surface. It is very different from the heavily corrugated pattern of *Oedaleops*. The pits in the skull of *Colobomycter* may suggest a relationship to Casea.

Oedaleops seems to lie much closer to *Eothyris* than to *Colobomycter*.

The tiny *Bayloria morei* Olson, from the Arroyo formation in Baylor County, Texas, is the smallest known pelycosaur. It shows the usual pelycosaurian morphology associated with small size and agrees with *Oedaleops* accordingly. Also in partial or complete agreement are:

1. Short face
2. Broad depressed cranium
3. Presence of an unreduced lacrimal which enters the naris anteriorly, and contacts the jugal behind
4. Entry of the frontals into the orbits
5. Depression of much of the parietal plate posteriorly, below the general level of the skull table
6. A deep transverse emargination of the skull roof posteriorly, occupied at the occipital edge by a broad postparietal bone
7. The position of the parietal foramen posteriorly in relation to the subdermal skull roof
8. Large supratemporal bones
9. Position of the jaw articulation at the level of the tooth row
10. A tendency toward enlargement of some anterior maxillary teeth.

Some of these resemblances are qualified or are so incomplete as to be almost meaningless. The relatively insignificant development of an eothyridid type of dental specialization and the abbreviation of the face simply suggest that *Oedaleops* and *Bayloria* belong in the same family of pelycosaurs. The position of the jaw articulation is a primitive condition shared with other generalized pelycosaurs. The depression of the *Bayloria* skull is

greater in front than behind and the lateral profile is thus distinct from *Oedaleops* where the top of the skull is more on one level. Frontal participation in the orbit of *Bayloria* appears to result from enlargement of the openings and not through development of a lateral process on the frontal bone. The transverse emargination of the skull table is accentuated in both *Oedaleops* and *Bayloria*, but in *Bayloria* this is a result of the posterolateral attenuation of the parietal bones instead of an extension of the supratemporals, as in *Oedaleops*. The pineal opening in *Bayloria*, though comparable in its position relative to the parietal plate, occurs *posterior* to the transverse occipital crest and appears to open below the level of the subdermal skull roof!

The nares bear little similarity to the wide openings in *Oedaleops* and there is no suggestion of an obtuse overhanging rostrum in *Bayloria*. The end of the snout is broadly curved in dorsal outline rather than acute as in *Oedaleops*, and the nares open as much to the front as laterally. There is a wide lateral exposure of the septomaxilla on the face in *Bayloria*; in *Oedaleops* this bone is not even seen in lateral aspect. The postorbital bar is reminiscent of *Colobomycter* and is very much wider than in *Oedaleops*. The postorbital bone has not the posterior attenuation seen in *Oedaleops*. The maxilla is relatively slender, doubtless in correlation with the relatively small size of the teeth. *Bayloria* differs markedly from *Oedaleops* in the presence of four premaxillary teeth, three maxillary pre-canines and the relatively small size of the single canine tusk.

Oedaleops seems less closely related to *Bayloria* than to *Eothyris*, or even to *Colobomycter*.

Baldwinonus trux Romer, known only from the scrappy type specimen, is from New Mexico Cutler beds at El Cobre Canyon and hence potentially interesting for comparison with *Oedaleops*. The only part preserved that can be compared is a section of the maxilla containing a large "tusk," but the five or so pre-canines readily distinguish *B. trux* from *Oedaleops* which has only one. From material available the (seeming) eothyridid tendency toward development of canine tusks is the only suggestion of relationship between these genera.

Baldwinonus dunkardensis Romer, from the Washington group (Lower Permian) in eastern Ohio, was assigned to *Baldwinonus* with reservation (Romer, 1952). Although this species is only known from an incomplete maxilla it seems to have teeth arranged more as in *Oedaleops*, with one comparatively large pre-canine, followed by two larger tusks. The second tooth seems to have been larger than the third—a point probably of no great significance owing to the factor of dental succession. Unlike *Oedaleops*, a heavy finger-like buttress surmounts the canine region on the inner surface of the maxilla, in *Ophiacodon* fashion. Whether the elevation of the maxilla at this place was great enough to have met the nasal between the lacrimal and naris

[27]

is uncertain. It is, however, higher than the length of the preserved tusk whereas in *Colobomycter* the dorsal expansion of the maxilla appears less than the length of the canine (see Vaughn, 1958, Fig. 1A). On the other hand, where no brace or unusual vertical expansion of the maxilla occurs in *Oedaleops*, the bone is still higher than the longest tooth. The canines of *B. dunkardensis* are more massive than those of *Oedaleops*, and presumably greater reinforcement was needed by the maxilla. The individual was about half as large as *B. trux*, but still four times as big as *Oedaleops campi* or *Eothyris*. Its relationships with these forms are obscure, but the maxilla seems morphologically as close to *Oedaleops* and *Eothyris* as to *Baldwinonus trux*.

Stereophallodon ciscoensis Romer, from the Pueblo formation (Cisco group) in Archer County, Texas is poorly known. Enough of the skull has been recovered, however, to show that resemblance to *Oedaleops* is slight: the animal was much larger, the tusk (or tusks) was exceptionally strong, the rostrum was elongate in *Ophiacodon* fashion, and there was a deep depression in the prefrontal where in *Oedaleops* there is inflation. Perhaps *Stereophallodon* is related to *Baldwinonus*, but any affinity to the better-known eothyridids, *Oedaleops*, *Eothyris*, and *Colobomycter* seems remote.

Stereorhachis dominans Gaudry is the oldest known European pelycosaur. Romer and Price (1940) found ample evidence for allying it with the comparably ancient *Stereophallodon*. A fragmentary maxilla and the dentary can be compared with *Oedaleops*. The former does not appear very similar—the ventral edge of the maxilla in *Stereorhachis* is convex downward, and rises considerably anteriorly. The dentary is long and more slender than that of *Oedaleops*. It has heavier teeth; one anterior tooth is tusklike. A maxilla referred to this genus by Thevenin (1910) as *Stereorhachis? cynodus* (Gervais) has sabre-shaped teeth unlike the relatively simple cones in *Oedaleops*. The arrangement of the teeth, however, suggests the eothyridid condition. Again the tendency toward enlarged canines is the only common denominator with *Oedaleops*.

Romer and Price (1940:260) observe that the dental apparatus of the early Permian *Tetraceratops*, "may be derived from that seen in eothyrids, and no features seen in *Tetraceratops* would debar it from a position in the family." On the other hand I find nothing to suggest a relationship to *Oedaleops*, beyond its small size, short face, large orbit, etc. Even the dentition is so aberrant that little similarity to *Oedaleops* exists.

Delorhynchus priscus Fox is based on three incomplete maxillae of *Colobomycter* size, from the same fissure deposits that produced the type of *C. pholeter*. The animal had a large naris with some sort of inner wall, an ex-

[28]

ternally pitted maxilla, and an "infraorbital canal" issuing forward from a foramen above the anterior maxillary teeth. These are features met with in the Caseidae and in part at least in eothyridids.

Fox notes resemblances to *Colobomycter*, but rejects the possibilty of a close relationship to it on the basis of certain reported differences. These, however, include the presumed absence of pitting on the maxilla of *Colobomycter* which Vaughn states (1958, p. 984) is so poorly preserved as not to "permit any statement as to whether it was pitted." The "infraorbital" canal described in *Delorhynchus* is contrasted with the supracanine groove in *Colobomycter*, which Vaughn believes may contain a foramen at its apex. As shown previously *Oedaleops* has both a groove (not as well developed as in *Delorhynchus* or *Colobomycter*) and one or more associated foramina in the same region and surely homologous with the structure described in *Delorhynchus*. The naris of *Delorhynchus* is reported to be much wider than that of *Colobomycter*, but I am unable anywhere in Vaughn's paper to find the figure of 1.7 mm. given as the height of the opening by Fox. On the contrary, Vaughn emphasizes repeatedly (pp. 984, 986) the large size of the naris of *Colobomycter*. Hence the only positive known difference between *Delorhynchus* and *Colobomycter* appears to be the absence of an eothyridid dentition in the former.

Fox referred *Delorhynchus* to the Nitosauridae because of supposed differences from *Colobomycter* and the eothyridids, and the existence of some features that occur in *Mycterosaurus*. Among these is the exclusion of the lacrimal from the naris by dorsal continuation of the maxilla (inferred in *Delorhynchus*). But this also occurs in *Colobomycter*. On the other hand the maxilla of neither *Mycterosaurus* nor *Nitosaurus* is sculptured. The maxilla of *Delorhynchus* has an anterodorsal process that extends some distance above the naris. There is a suggestion of such a process in *Colobomycter* (see Vaughn, 1958, Fig. 1A), and it is possible that the nasal bone is displaced downward to cover part of a more extensive process of the maxilla. Nothing of the sort appears in the reconstruction of *Mycterosaurus* by Romer and Price (1940, Pl. 21). And *Mycterosaurus* shows no suggestion of *Casea*-like nares which is evidently present in *Delorhynchus*. An "infraorbital" canal is unreported.

Thus, not only does *Delorhynchus* resemble some eothyridids, it also shows some suggestion of a structure that is currently thought to be an exclusive caseid property, and which is found in no nitosaur. In view of this, resemblance in dentition between *Delorhynchus* and the nitosaurs—based after all on only four teeth—seems insufficient grounds for placing the genus in the Nitosauridae. It is much more likely to be an eothyridid of *Colobomycter* form. Comparisons with *Oedaleops* are impossible except to note that both

[29]

animals have unusual *Casea*-like narial structure, and the dentitions appear to be different.

Relationships of the Eothyrididae

Eothyridids as ophiacodonts.—Ever since appearance of *Review of the Pelycosauria, Eothyris* has been accepted as a primitive ophiacodont with an aberrant dentition. Romer and Price (1940) have presented evidence of the ophiacodontoid construction of the postcranial skeleton in the other eothyridids where this is known. Gaps in our knowledge of the eothyridid structure still exist, however. Re-examination of the palate in the type specimen of *E. parkeyi* has revealed further morphology that can be interpreted as ophiacodontoid. A short basicranial process arises from the pterygoid (the epipterygoid cannot be distinguished) a little above and anterior to the main axis of the transverse pterygoid flange. This flange is moderately developed and bears a single transverse row of small teeth. The palatal ramus of the pterygoid is broad and its median edge is fairly straight. This ramus carries two regular rows of small teeth, one medial, the other along the lateral edge. Although differing in position from the pterygoid teeth of *Ophiacodon* the tendency toward a linear arrangement of these teeth is stronger in ophiacodonts than sphenacodonts. The character of the bone surface in the area between the palatal teeth suggests that some irregularly placed denticles were once present there.

Oedaleops, so far as can be seen, possesses all the ophiacodont qualities of *Eothyris*. The only typically ophiacodont structure known to be lacking in *Oedaleops* is the supracanine buttress on the median side of the maxilla. This region is not visible in *Eothyris*. The existence of some sort of maxillary brace is suggested in *Baldwinonus trux* and *Stereophallodon* (Romer and Price, 1940). It is present in *B. dunkardensis* (Romer, 1952). These eothyridids are larger than *Eothyris* and *Oedaleops*, their maxillary tusks are relatively heavier. Perhaps supracanine support was not required by eothyridids with smaller teeth.

Although most available morphological evidence favors inclusion of the Eothyrididae in the suborder Ophiacodontia, it is worth noting that the posterior skull table in *Oedaleops* and the occipital structure in *Eothyris*, although poorly known, seem to resemble the caseids more than typical and contemporary ophiacodontids. *Colobomycter*, were it not for its resemblances to *Eothyris*, might not have been assigned to the Ophiacodontia. Since the eothyridid lineage is probably at least as ancient as that of the Ophiacodontidae (see below), it may eventually be necessary to place the Eothyrididae elsewhere, perhaps in a group with the caseids.

[30]

Phylogeny within the Eothyrididae.—The stratigraphic distribution of the eothyridid species may be tabulated as follows:

Lower Permian	*Bayloria morei*	Arroyo Formation
	Colobomycter pholeter *Delorhynchus priscus*	Arroyo correlative?
	Eothyris parkeyi	Belle Plains Formation
	Baldwinonus trux *Oedaleops campi*	New Mexico Cutler Formation
	Baldwinonus dunkardensis	Mount Morris limestone (Washington Gp.)
Pennsylvanian	*Stereophallodon ciscoensis*	Pueblo Formation
	Stereorhachis dominans	"Uppermost Stephanian"

Eothyris and *Oedaleops* comprise the central "core" of the family Eothyrididae, if only because they are currently the best known representatives. The major differences between them are largely related to the higher degree of specialization in the dentition of the geologically younger *Eothyris.* The conclusion that *Oedaleops* is close to if not actually in the line of descent leading to *Eothyris* is inescapable.

Of the other members of the family only *Colobomycter* is well enough understood to be considered in much detail. It is thought to occur later in time than *Oedaleops* or *Eothyris,* and it has advanced beyond them in the direction of the Caseidae (Vaughn, 1958). *Colobomycter's* dentition represents an advancement over the *Oedaleops* grade perhaps parallel to but not equalling the development in *Eothyris.* It shows no tendency toward the highly specialized and thoroughly "uneothyridid" dentitions of *Casea* and its close relatives. Vaughn inferred a phyletic series of *Eothyris-Colobomycter-Casea* in which *Eothyris* and *Colobomycter* represent distinct side branches of the main *Casea* stem, with the *Eothyris* phylum diverging earlier than that leading to *Colobomycter.* The foregoing comparisons between *Oedaleops* and *Colobomycter* suggest that the latter represents an offshoot from an *Oedaleops-Eothyris* line at a pre-*Oedaleops* level. This suggestion suffers as much (if not more) from a lack of connecting forms as does Vaughn's interpretation, but it is supported by stratigraphic position no less than his.

Delorynchus was perhaps related to *Oedaleops* in about the same degree as *Colobomycter.* The narial construction and sculpture pattern suggest a closer approach to the caseids than is seen in *Oedaleops* or suspected in *Colobomycter.* The subisodont dentition inferred from the anterior four

maxillary teeth may be a relict of a more primitive condition. It might as well represent a trend away from the presumably strictly carnivorous dentition of the other eothyridids toward a form more suited to an omnivorous diet. If a relict, however, this would imply an earlier derivation of a *Delorhynchus* branch than any leading to *Colobomycter, Oedaleops,* or *Eothyris.*

Bayloria morei was recognized as an eothyridid by Olson in 1941, but subsequent writers have not considered it further. Presumably a contemporary of *Colobomycter,* from the Arroyo Formation in Texas, this tiny creature (skull length, 28.5 mm.) has fewer and less specialized teeth in the maxilla. It seems primitive in the same ways that *Eothyris* and *Oedaleops* do. The naris is large for so small a skull, but the broadly rounded rostrum does not project far beyond the tooth row. A relatively huge septomaxilla appears on the side of the face, a feature not seen in other eothyridids. The postorbital bar is very broad, suggesting a relationship to *Colobomycter.* The posterior part of the cranium is said to be poorly preserved, but the hinder part of the parietal plate appears to be depressed, suggesting a trend toward the *Oedaleops* condition, or even advancement beyond this. Unique among pelycosaurs is the position of the pineal foramen which opens *below* the level of the skull table and behind the apex of the broadly V-shaped transverse occipital crest. The broad postparietal is reminiscent of *Oedaleops.* Elongate posterolateral parietal extensions on either side of the parietal depression are analogous to the supratemporal construction in *Oedaleops,* but the supratemporal bones which are large are difficult to interpret. The lateral plate of the squamosal is exceptionally small for a pelycosaur and unlike the broad plates seen in *Eothyris* and *Oedaleops.*

The animal seems to possess sufficient eothyridid qualities to fall within the scope of the family, but it is difficult to imagine its origin from any of the other known members. Nor could any of these be descended from *Bayloria* since it is among the latest known members. The small size of *B. morei* raises the question: might the unique specimen be an immature member of some other species known (if at all) only from adult individuals?[8]

Baldwinonus, Stereophallodon, and *Stereorhachis* are known mainly from the very incomplete postcranial skeletons. So little is known of their cranial features that inferences about their place in the Eothyrididae are largely speculative. They may not be eothyridids at all; the main reason for placing them here is the existence of large anterior canine tusks which in the case of *Stereorhachis* and *Stereophallodon* had attained an advanced stage of development at a comparatively early time. It can be argued that the synapsid

---

[8] The oft-repeated statement that juvenile reptiles are but "carbon copies" of the adults is not precisely true, especially at very young stages. In crocodilians, for example, hatchlings have markedly different cranial proportions and teeth from their parents.

dentition appears always to have been highly sensitive to adaptive pressures. Hence dental characters may not be very reliable paleotelic factors where, as between *Stereorhachis* and *Eothyris*, considerable temporal gaps exist. If these genera are eothyridids they are the giants of the family, bulking as large as medium to large species of *Ophiacodon*. Nothing is known about cranial proportions in *Baldwinonus* except that the jaw was probably longer than in the short-faced eothyridids. *Stereorhachis* and *Stereophallodon* seem to have had long high snouts. Perhaps these two genera represent an early radiation of eothyridids which paralleled *Ophiacodon* in rostral development and sphenacodonts in dental adaptations. *Baldwinonus* could be a late survivor of such a radiation.

The position of *Tetraceratops* is the least certain of any of the forms so far considered despite the existence of a large part of the skull. A large and complex septomaxilla may indicate some relationship to *Bayloria* where, as in *Tetraceratops*, the bone is perforated by a large foramen on one side of the face at least. This, however, does not seem to be an eothyridid character. If *Tetraceratops* is an eothyridid it can only be very peripheral to the other genera.

The antiquity and derivation of the Eothyrididae.—Oedaleops, in the early Permian, is the oldest eothyridid for which we have even a meager knowledge of the cranial anatomy. Its relatively archaic skull shows few similarities to skulls of the contemporary ophiacodonts *Ophiacodon* and *Varanosaurus*. The oldest ophiacodontid, *Clepsydrops*, seems fairly similar in postcranial structure to the later *Ophiacodon* (see Romer and Price, 1940; Romer, 1961a). Although Romer and Price suggest that the canine-bearing face was shorter in *Clepsydrops* than in later ophiacodontids, it would be surprising if the *Clepsydrops* skull as a whole was much more like *Oedaleops* than is that of *Ophiacodon*. There is nothing to suggest that *Clepsydrops* in the late Pennsylvanian stands much closer to eothyridid origins than does *Ophiacodon*.

In searching for ancestors it is to be expected that adaptive (specialized) features will disappear as phyla are traced back to more generalized levels of organization. Few paleotelic characters should be expected to survive through long evolutionary intervals. Thus the single morphological feature that unites eothyridids structurally with later caseids and earlier edaphosaurs (essential agreement between Pennsylvanian and Permian *Edaphosaurus* skulls is assumed), and at the same time distinguishes all these from the Ophiacodontidae and Sphenacodontia, is the large supratemporal bone and various details involved with its accommodation in the skull roof. On the assumption that the slender delicate supratemporals of sphenacodonts and noneothyridid ophiacodonts are more likely to have been derived from broad

[33]

anthracosaurlike bones than *vice versa*, it may be supposed that ancestors of *Eothyris* and *Oedaleops* had large supratemporals inserted diagonally into the posterolateral corners of the parietal plate.

Romer (1946), Watson (1954), and others, necessarily resorting to the philosophy of the structurally ancestral type, have noted significant resemblances between *Eothyris* and the captorhinomorphs *Limnoscelis* and *Paracaptorhinus*. Both these cotylosaurs have broad supratemporal bones inserted behind the parietal lappets, oriented much as in *Eothyris* and *Oedaleops*, but lacking the long contact between supratemporal and postorbital. But *Limnoscelis* is a contemporary of *Oedaleops*, and *Paracaptorhinus*, though its precise age is unknown, is almost certainly a lower Permian genus. Whatever resemblances they show to the eothyridids are certainly owing either to inheritance of primitive reptilian qualities (parallel evolution) or to convergence.

Recent additions to our knowledge of older reptiles make it possible to consider some of these in relation to eothyridid origins although we still must reason within the context of structural ancestry. *Protoclepsydrops haplous* Carroll is of great interest here. This tiny creature, known only from an incomplete skeleton and some scraps from the erect trees at Joggins, Nova Scotia, is one of the oldest known reptiles (Westphalian B), and is thought to be ". . . either a forerunner of the pelycosaurs in general or a very primitive ophiacodont." (Carroll, 1964, p. 82). The parietal plate, which is the only part comparable with *Oedaleops*, is wide and has broad lappets whose notched posterior margins imply the former existence of wide supratemporals in the skull table. A large centrally-located pineal foramen can be seen in the illustration (Carroll, 1964, Fig. 13), and there appears to have been a strong posterolaterally directed process reminiscent of the slender finger of parietal that separates the supratemporal and tabular bones in *Oedaleops*. Emargination (or depression) of the posterior edge of the parietal plate shown in the illustration would produce parietals with essentially the outlines seen in *Oedaleops*. Although the morphological evidence for an eothyridid-*Protoclepsydrops* relationship is tenuous and the assumption is highly speculative, from a temporal standpoint at least *Protoclepsydrops* is surely closer to the origin of eothyridids than the Permian cotylosaurs. Since the Ophiacondontidae were well differentiated by about late Pennsylvanian times (Romer, 1961), any dichotomy that also produced the Eothyrididae probably occurred no later than middle Pennsylvanian time.

Reptiles of approximately middle Pennsylvanian age from which useful cranial material has been described include, besides *Protoclepsydrops*, the cotylosaurs *Hylonomus* and *Archerpeton*, from the Westphalian (B) at Joggins, Nova Scotia, *Tuditanus* from the Westphalian at Linton, Ohio, and *Cephalerpeton*, from Westphalian (C) beds at Mazon Creek, Illinois.

[34]

Hylonomus lyelli Dawson, recently restudied by Carroll (1964), seems to be a primitive romeriid captorhinomorph in which paired postparietals and tabulars evidently entered into the skull roof. These and other bones of the skull table are visible only from below, and no trace of a supratemporal is seen in this aspect. It is assumed therefore that this bone occupied a superficial position in the skull roof. Carroll (1964, Fig. 2) reconstructs it as a small sliver of bone between tabular and squamosal after the fashion of other romeriids (see Watson, 1957, Figs. 7–9). The posterior edge of the skull table is almost straight tranversely, and no distinct parietal lappets are present.

This is a far different structure than the broadly emarginated and depressed posterior skull roof seen in *Oedaleops*. It is theoretically possible to derive the latter type of skull margin from the *Hylonomus* condition by increasing the surface for insertion of the superficial extensor musculature on the back of the skull. This may have happened in pelycosaurs and their immediate ancestors as these adopted a less sprawling, more active form of locomotion. Then lengthening of the neck would have demanded stronger support for the head. Such changes would not account for a great increase in size of a small supratemporal bone, however. Continuing emargination of the occipital border seems to have had an opposite effect on the supratemporals of later romeriid captorhinomorphs, sphenacodonts, and non-eothyridid ophiacodonts. *Hylonomus* was evidently not close to the eothyridid ancestry.

Of the skull of *Archerpeton anthracos* Carroll (1964) only a maxilla and parasphenoid are known. The material is inadequate for any sort of phyletic assumptions, but as far as preserved the maxilla figured by Carroll (1964, Fig. 11) is shaped generally as in *Oedaleops*. The teeth become larger anteriorly, but it is unknown whether canines developed. The teeth are more numerous than in the eothyridids, but such comparisons are virtually meaningless in view of the difference in time between the occurrences of the fossils.

Tuditanus punctulatus Cope is assigned to the family Tuditanidae most recently by Baird (1958), who states that it is the most generalized captorhinomorph known. Carroll (1963) implies that *Tuditanus* is again being regarded as a microsaur. Among its primitive features, coincidentally or not resembling eothyridid conditions, are a large supratemporal, and postparietals and tubulars that are said to be occipital in position. A vestigial otic notch is recognizable. The supratemporal has a postorbital contact, but unlike eothyridids (or any other pelycosaurs) there is also a broad contact between the supratemporal and the postfrontal. The animal is obviously aberrant in its great body elongation and would seem unsuited for a structural or actual ancestor of any known later reptiles.

[35]

Cephalerpeton ventriarmatum Moodie as described by Gregory (1948; 1950) seems at first glance to be very unlike *Oedaleops* or *Eothyris*. Nares are small, the rostrum is acuminate, and the postorbital bone is small in relation to the postfrontal. Most unusual is the short but very broad parietal plate which apparently lacks lateral lappets. Supratemporal bones are unreported.

On the other hand the dentition is not unlike what might be anticipated in an ancestor of eothyridids. As in *Oedaleops* and most other pelycosaurs there are three fairly long slender teeth in the premaxilla. These are followed in the maxilla by three relatively small and slender teeth, then by two larger "canines," and several somewhat smaller teeth. Near the posterior third of the maxillary series a secondary dental peak occurs. There are only 17 teeth in the upper jaw, a surprisingly small number for a primitive reptile, but a figure that is approached by *Oedaleops* and *Eothyris*. The teeth seem heavy for the size of the skull and there are no evident replacement gaps, another feature reminiscent of eothyridids. The teeth are said to show labyrinthodont-like fluting. No suggestion of fluting is seen in *Oedaleops*, but there is perhaps a faint trace of something of the sort near the bases of some teeth in *Eothyris parkeyi* (possibly also due to damage). In the Museum of Paleontology at Berkeley, however, there is a fragment of a reptile jaw from the Lawton fissures that may belong to either *Colobomycter* or *Delorhynchus*. This bears heavily fluted teeth. Repeated cautions about the reliability of dental characters in early reptiles notwithstanding, the dentition of *C. ventriarmatum* is suggestive of some eothyridid relationship. The extremely large orbits, so often correlated with small skulls in vertebrates, are not particularly significant by themselves, nor is the possibility of sculpture on the skull bones (inferred from the rugose character of some jaw and pectoral elements). In spite of some "un-reptilian" features of the palatal bones, however, the pterygoid displays a reptilian flange which bears a transverse row of small teeth.

Baird (1958) states that *Cephalerpeton?* [*"Tuditanus"*] *longipes* is a lizard-like romeriid cotylosaur with a sculptured supratemporal bone notched into the parietal plate behind a large lappet. If this species had a dentition like that described in *C. ventriarmatum* or, conversely, if that *Cephalerpeton* had the posterior skull table architecture described in *C. longipes*, *Cephalerpeton* would deserve further examination as a possible eothyridid ancestral structural type among anapsid reptiles.

Thus several of the earliest known reptiles show possible morphological links with the eothyridids. It is not yet possible to place them in a phylogenetic scheme because it is not known whether their resemblances to *Oedaloeps* and *Eothyris* resulted from inheritance by these pelycosaurs of common archaic reptilian structures later modified by convergence, or is due to

a closer, sanguine relationship. But the foregoing comparisons suggest that the eothyridid line may have appeared closer to the time of origin of the Edaphosauria and Ophiacondontia than the known fossil record demonstrates.

Eothyridids and the Nitosauridae.—Romer and Price (1940) have noted postcranial features that seem to establish a relationship between the presumably edaphosaurian family Nitosauridae and the later caseids, also thought by them to have been edaphosaurs. Vaughn (1958) postulates a main caseid phyletic trunk from which branched *Eothyris*, and later, *Colobomycter*. Nitosaurs are supposed to have sprouted from the same trunk at a much earlier time, not specified by Vaughn. The place of *Oedaleops* in this scheme must be examined.

As nitosaurids Romer (1958) included *Mycterosaurus* (the best known genus), *Nitosaurus* (the oldest representative), and perhaps the poorly known *Glaucosaurus* and *Puercosaurus*.

It is virtually certain that *Puercosaurus obtusidens* Williston, from the same general area and horizon as *Oedaleops*, is a tiny cotylosaur. *Nitosaurus greenleeorum* Romer is known from El Cobre Canyon and hence was an approximate contemporary of *Oedaleops* in New Mexico (Vaughn, 1963). Its skull is poorly known, but the animal had longer jaws, a more slender dentary, considerably more teeth (sub-isodont in form), and a higher maxillary bone than *Oedaleops* or *Eothyris*, even though large tusks are not developed.

Glaucosaurus megalops Williston, a contemporary of *Mycterosaurus* in Texas, is known only from a tiny skull whose sutures are mostly indistinct. It is thought to be related to the caseids (Romer and Price, 1940), but so far as comparisons are possible *Glaucosaurus* seems to differ from *Oedaleops*, *Eothyris* (and the caseids) about as much and in the same ways as it differs from *Colobomycter* (see Vaughn, 1958).

Vaughn (1958), basing his considerations mainly on the skull of *Mycterosaurus longiceps* Williston, concludes that, ". . . *Colobomycter* is in some way related to *Mycterosaurus* . . .", and hence by definition to the nitosaurids. He infers an early branching of the Nitosauridae from a main trunk of eothyridid-caseid evolution.

Oedaleops differs from *Mycterosaurus* in most of the ways that *Colobomycter* does: the face is elongate, the skull roof is arched above the orbits, roofing bones are unsculptured, and of course the dentition is different, lacking anterior canines. Possibly of minor importance is the failure of the lacrimal and jugal to meet below the orbit. *Oedaleops* differs from *Mycterosaurus* (and *Colobomycter*) also in the absence of the dorsalward expansion of the maxilla, and in its more "conventional" lacrimal. In the relative breadth and

[37]

height of the skull *Mycterosaurus* and *Oedaleops* stand at opposite ends of a grade with *Colobomycter* in between.

Mycterosaurus resembles *Oedaleops* more than *Colobomycter* in its more usual pelycosaurian postorbital bar. In primitive fashion the jaw articulation is not depressed. The quadratojugal is similarly large in *Mycterosaurus* and *Oedaleops*, but is presumed in both to have been largely hidden in lateral aspect by other bones. The last two features are presently indeterminate in *Colobomycter*. A primitive condition shared by *Oedaleops* and *Mycterosaurus* is the similarly larger number of teeth than occurs in *Colobomycter*. The dentition of *Mycterosaurus* (and *Nitosaurus*) shows little differentiation, but a graded sequence of larger teeth is present in the maxilla. It is interesting that the apex of this series occurs in the anterior third of the maxilla at about the same location as the secondary peak in the *Oedaleops* and *Eothyris* dentitions.

In none of these features does *Mycterosaurus* resemble *Eothyris* more than *Oedaleops*. Thus *Mycterosaurus* and *Oedaleops* seem about as closely related in cranial structure as *Mycterosaurus* and *Colobomycter*. It is significant that the resemblances to the former are of a primitive nature, those to the latter seem related to specializations.

Mycterosaurus, it should be noted, has an expanded ilium reminiscent of but less extreme than that in *Casea*. This may be especially significant in view of the considerable difference in the proportions of the skeletons as a whole (see Romer and Price, 1940, Fig. 71). If *Mycterosaurus* is properly placed in the Nitosauridae (*Nitosaurus* itself shows some iliac expansion) this ilium seems to support the idea that nitosaurids and caseids had a common ancestry in the way suggested by Vaughn.

Under this interpretation the Nitosauridae could be classed with edaphosaurs only if the phylum leading to the Caseidae was generally bradytelic, with origins considerably more ancient than the existing fossil record shows. The archaic appearance of *Oedaleops* and *Eothyris* occurring at a relatively late time suggests that this may in fact have been the case. Presently known nitosaurs may attest to survival of a conservative branch of the Edaphosauria paralleling the similarly conservative eothyridids among the Ophiacodontia. Resemblances in the postcranial skeletons of nitosaurids and caseids (see Romer and Price, 1940) might then be attributed to parallel evolution and not necessarily interpreted as evidence of closer than subordinal relationship. Whether the Nitosauridae represent the "basal stock" of the Edaphosauria early derived from some eothyridid ancestor, and whether this ancestor was technically an edaphosaur or ophiacodont remain moot questions awaiting discovery of connecting forms. In neither case, however, would polyphyly

have to be invoked to explain the similarities between some edaphosaurs, ophiacodonts, and caseids.

Eothyridids and the Caseidae.—The Caseidae have long puzzled students of Permian reptile systematics. It has even been suggested that they should rank equally with all other pelycosaurs, but to my knowledge no one in recent years has seriously objected to its inclusion in the Pelycosauria. Williston and later Case placed the Caseidae in its own suborder whereas Romer has long included it in the Edaphosauria. As recently as 1957 Watson still seemed to regard edaphosaurian disposition as improbable, and Olson (1962) appears to favor recognition of a caseoid group equivalent to the Edaphosauria.

Caseia[9] itself is so unusual that its sudden appearance in the fossil record seems to have surprised some systematists (though not paleobiologists—see Olson, 1962). Until recently the relationships of this genus and its giant relative *Cotylorhynchus* could only be viewed in an horizontal perspective, but now Olson has shown the caseoids to be a varied group with a long history of radiation subsequent to the appearance of *Casea broilii* in the early Permian. Watson (1957) tentatively suggested *Eothyris* as a possible caseid ancestor, but the discovery of *Colobomycter* provided the first concrete evidence that the caseids may indeed have descended from the eothyridids (see Vaughn, 1958).

Among the most striking features of *Casea* and its close relatives is the high obtuse rostrum that projects forward beyond the tooth row and surrounds the huge narial chamber (for illustrations of *Casea* and its giant relative *Cotylorhynchus*, see Romer and Price, 1940, Pls. 19–20). The reconstructed rostrum of *Oedaleops* (Fig. 5) is exactly what would be expected as an antecedent of the *Casea* construction. In primitive fashion it does not project as far forward as in *Casea*, and it is much lower. The nares are smaller and the inner narial wall and shelf construction which are unique properties of *Casea* and *Cotylorhynchus* are only incipient in *Oedaleops*. They are nevertheless better developed there than in any other noncaseid pelycosaur, except *Delorhynchus*, whatever that may be.

Resemblances go much further than this. The skulls of *Oedaleops* and *Eothyris* have more the proportions of the *Casea* skull than any non-eothyridid pelycosaur; the skulls were low, the occipital region depressed. The orbits, though large, do not cause the skull roof to bulge upward above them. The parietal shows some tendency to become subdermal behind the pineal foramen and a transverse occipital crest is relatively undeveloped or

[9] For purposes of this discussion *Casea* refers to the best known and geologically oldest species, *C. broilii* Williston, from the lower Vale beds of Baylor County, Texas.
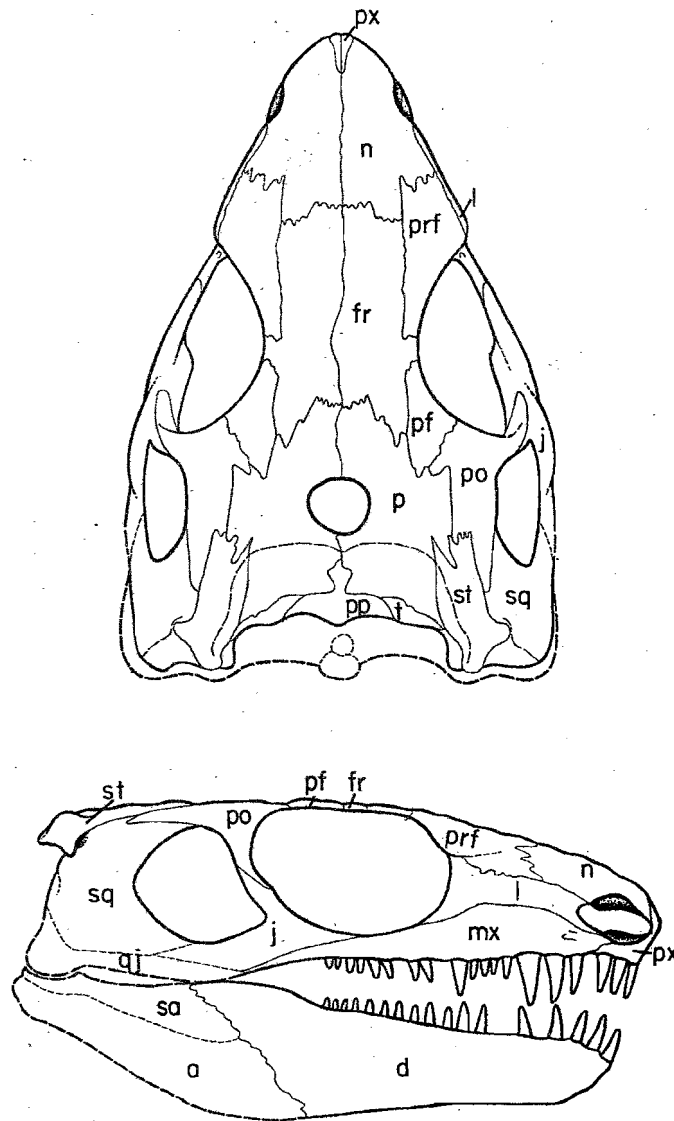
[39]

Fig. 5. *Oedaleops campi* Langston. Reconstructed skull and jaws based mainly on U.C.M.P. Nos. 35758 and 67225. The posterior cheek plate has been shifted backward, the postorbital bar has been straightened, and the depth of the skull as preserved has been increased to compensate for obvious crushing (see Fig. 1). The outline of quadrato-jugal and posterior mandibular elements are conjectural. × 1. a, angular; d, dentary; fr, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pf, postfrontal; po, post-orbital; pp, postparietal; prf, prefrontal; px, premaxilla; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; t, tabular.

[40]

absent. The cranial roof is broad and the prefrontal bones are expanded so that the tooth row was presumably hidden in dorsal aspect. The frontals enter the orbital rim *via* a narrow lateral process. The supratemporal in caseids and eothyridids is similarly large, though somewhat larger in the latter group; the pronounced nuchal swelling at the postparietal is similarly developed. In spite of different proportions, the relationships between lacrimal, jugal, and maxilla are the same (except *Colobomycter*); the arrangement of the facial bones seem more similar between *Oedaleops* and *Casea* than between *Casea* and *Colobomycter*. The pineal foramen of *Casea* is the largest in pelycosaurs, but among them the foramen of *Oedaleops* seems closet in both relative and absolute size. The shape of the deep dentary in *Oedaleops* with its obtuse anterior outline and strong posterior endentulous ascending process is suggestive of conditions in *Casea*.

Features in which *Oedaleops* differs from *Casea* are mostly attributable to a less specialized organization. These include, in addition to the less aberrant development of the rostrum and nares:

1. A longer face in *Oedaleops*
2. Retention of an anisodont carnivorous dentition, specialized in a different direction from that in *Casea*
3. A jaw articulation near the level of the tooth row
4. An occipital plate (presumably as in *Eothyris*) more inclined than in *Casea*
5. A temporal fenestra in more "normal" pelycosaurian position, not far down on the side of the cheek as in *Casea*
6. Cheeks (presumably) less vertical than in *Casea*
7. Squamosal wider in both its lateral and occipital flanges

The regularly corrugated sculpture of *Oedaleops* differs markedly from the pitted, almost crocodilian, rugosity of *Casea* roofing bones. Whatever significance this may have, the other differences are of the sort one might reasonably expect to occur between an ancestor and descendent with the characters of *Oedaleops* and *Casea*.

Resemblances between these genera seem to me more significant than those observed between *Colobomycter* and *Casea*, and *Oedaleops* does not share any of the obvious specializations in cheek architecture and the lacrimal which distinguish *Colobomycter* from *Casea*. *Oedaleops* shows a more primitive cheek architecture than occurs in *Casea*, but one from which the *Casea* arrangement might have been derived.

Eothyris resembles *Casea* in most of the ways that *Oedaleops* does. The specialization of the jaw apparatus has progressed in another direction from that of the caseids, however, and the genus stands farther from them morphologically than does the earlier *Oedaleops*. Cranial resemblances between caseids and the less known eothyridids are not apparent.

[41]

From both a structural and chronological viewpoint *Oedaleops* appears the closest approach to a hypothetical *Casea* ancestor among the eothyridids. Its dental specialization may be too advanced, and the form of the sculpture may be too different to place the genus in the direct lineage leading to the caseids, but I have little doubt that it lies very close to this lineage.

Delorhynchus, were it better known, might show even closer affinities to *Casea* than does *Oedaleops.* The unusual narial structure and sculpture appear much like *Casea,* the nares perhaps, and the sculpture certainly, are closer to *Casea* than to *Oedaleops.* About the only objections to placing *Delorhynchus* in the caseid lineage are the dorsal extension of the maxilla and the still mainly predaceous dental equipment. Romer and Price (1940) suggest that the lacrimal, abbreviated in a protocaseid (they thought nitosaurid), may again have entered the naris in *Casea* as a result of facial abbreviation. If this is correct the first objection disappears. The second objection derives from a too-close adherence to notions about irreversibility; there are examples of more radical shifts from carnivorous to herbivorous dentitions in synapsids than seemingly would be required to produce the isodont *Casea* or *Cotylorhynchus* dentition from that of *Delorhynchus* (see Romer, 1961b). The simple, pointed, slightly recurved subisodont cones with swollen bases and secant coronal ridges described in *Delorhynchus* may evince a reversion to less predaceous habits in the direction of the caseid adaptations.

If these interpretations are correct the Caseidae were probably derived at a comparatively late date from some eothyridid source. Their resemblances to nitosaurs may have been inherited *via* the Eothyrididae from a similarly ancient ancestry among the ophiacodonts, or they may have acquired them independently. The typical edaphosaurs could have been similarly derived and retained primitive occipital architecture resembling that of eothyridids and caseids. If the caseids were derived latterly from an eothyridid ophiacodont they can hardly be regarded as edaphosaurs in a phyletic sense. They may indeed belong in a separate suborder of their own for which Williston's term Caseosauria is still available. Olson, apparently arriving at a similar conclusion, uses the term Caseoidea in his phyletic scheme (1962, Fig. 69).

The phyletic ideas expressed in the foregoing discussion are presented graphically in the accompanying diagram (Fig. 6).
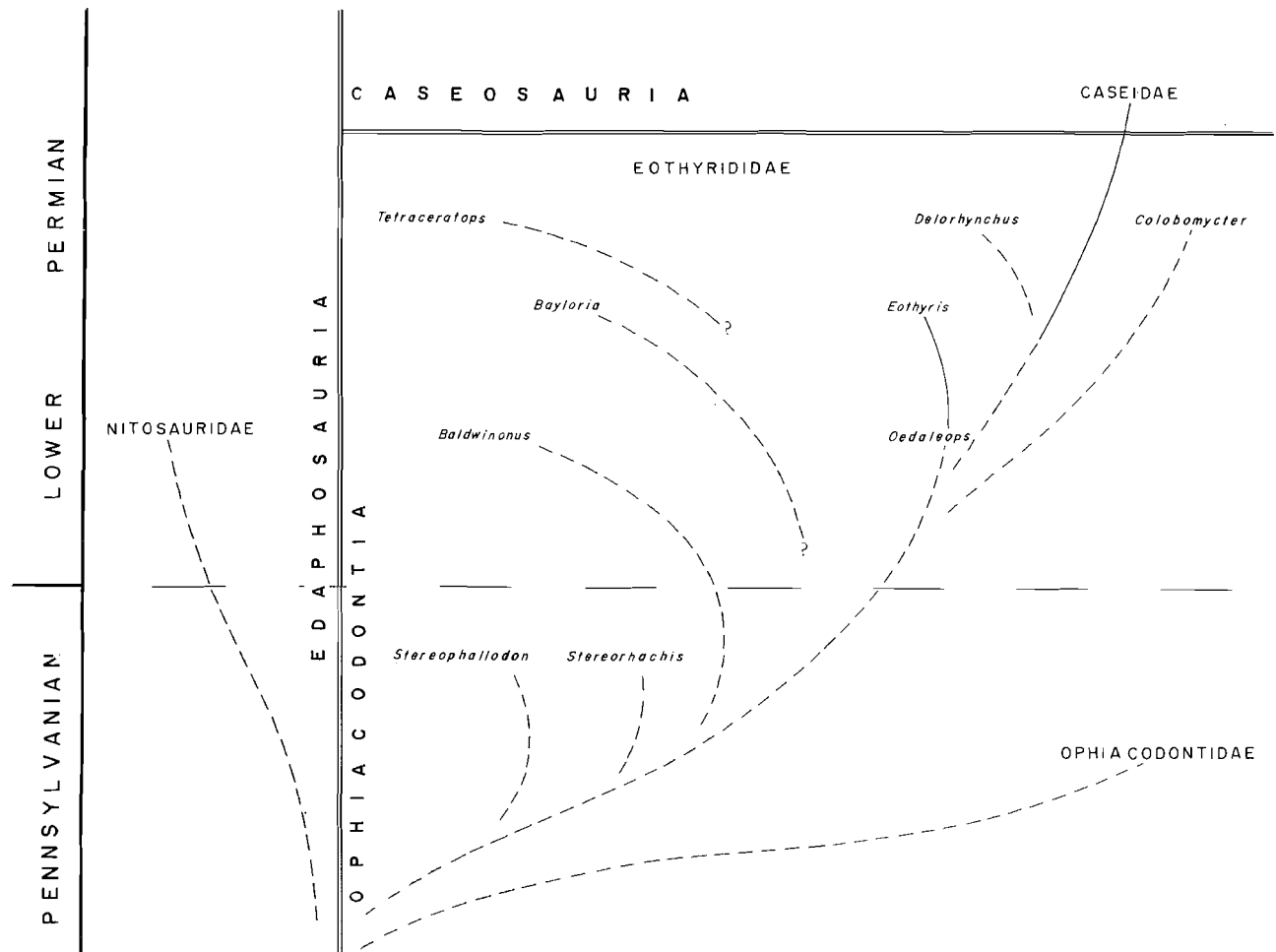
Acknowledgments

[42]

Fig. 6. Suggested phyletic relationships of the Eothyrididae. For discussion see text.

to examine the skull of *Eothyris parkeyi*. The plate was provided by Mr. M. O. Woodburne; the line drawings are by Mrs. Augusta Lucas and Mr. Owen Poe. This study was supported in part by a grant from the Geological Society of America.

REFERENCES CITED

BAIRD, D. 1958. The oldest known reptile fauna. Anat. Rec., 132: 407–408.

BROOM, R. 1938. On a new type of primitive fossil reptile from the Upper Permian of South Africa. Proc. Zool. Soc. London (B), 108, pt. 3: 535–542, 4 figs.

CARROLL, R. L. 1963. A microsaur from the Pennsylvanian of Joggins, Nova Scotia. Nat. Hist. Papers, Nat. Mus. Canada 22: 1–13, 7 figs.

————. 1964. The earliest reptiles. Journ. Linn. Soc. (Zool.), 45, No. 304, 61–83, 14 figs.

Fox, R. C. 1962. Two new pelycosaurs from the Lower Permian of Oklahoma. Univ. Kansas Pub., Mus. Nat. Hist., 12, No. 6: 297–307, 6 figs.

GAUDRY, A. 1880. Sur un reptil très perfectionné trouvé dans le terrain permien. Acad. Sci. Paris C. R., 91: 669–671.

GREGORY, J. T. 1948. The structure of *Cephalerpeton* and affinities of the Microsauria. Amer. Journ. Sci., 246: 550–568, 2 figs.

————. 1950. Tetrapods of the Pennsylvanian nodules from Mazon Creek, Illinois. Amer. Journ. Sci. 248: 833–873, 11 figs.

HOTTON, N. 1960. The Chorda tympani and middle ear as guides to origin and divergence of reptiles. Evolution, 14: 194–211, 4 figs.

LANGSTON, W., JR. 1953. Permian amphibians from New Mexico. Univ. Calif. Pub. Geol. Sci., 29: 349–416, 24 figs.

MATTHEW, W. D. 1908. A four-horned pelycosaurian from the Permian of Texas. Bull. Amer. Mus. Nat. Hist., 24: 183–185, 1 fig.

OLSON, E. C. 1941. New species of Permian vertebrates in Walker Museum. Journ. Geol., 49: 753–763, 3 figs.

————. 1962. Late Permian terrestrial vertebrates, U. S. A. and U. S. S. R. Trans. Amer. Phil Soc. (NS) 52, Part 2: 1–224, 69 figs., 21 pls.

ROMER, A. S. 1937. New genera and species of pelycosaurian reptiles. New England Zool. Club. Papers, 16: 89–96, 1 pl.

————. 1946. The primitive reptile *Limnoscelis* restudied. Amer. Journ. Sci., 244: 149–188, 10 figs.

————. 1952. Late Pennsylvanian and early Permian vertebrates of the Pittsburg-West Virginia region. Ann. Carnegie Mus., 33: 47–112, 13 figs., 2 pls.

————. 1956. Osteology of the reptiles. Univ. Chicago Press, Chicago, Ill.: xxi, 1–772, 248 figs.

————. 1961a. A large ophiacodont pelycosaur from the Pennsylvanian of the Pittsburgh region. Breviora No. 144: 1–7, 1 fig.

————. 1961b. Synapsid evolution and dentition. Internat. Colloq. on Evolution of Mammals. Kon. Vlaanse Acad. Wetensch. Lett. Sch. Kunsten België, Brussels, 1961, pt. I: 9–56, 18 figs.

[45]

————, and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Amer. Spec. Papers no. 28: 1–538, 71 figs., 46 pls.

Thévenin, A. 1910. Les plus anciens quadrupèdes de France. Ann. de Paléon., 5: 1–63, 36 figs., 9 pls.

Vaughn, P. P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and on the origin of the family Caseidae. Journ. Paleo., 32: 981–991, 1 fig.

————. 1963. The age and locality of the Late Paleozoic vertebrates from El Cobre Canyon, Rio Arriba County, New Mexico. Journ. Paleo., 37: 283–286.

Watson, D. M. S. 1954. On Bolosaurus and the origin and classification of reptiles. Bull. Mus. Comp. Zool., 111: 299–449, 36 figs., 1 pl.

————. 1957. On Millerosaurus and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc., London (B), 240: 325–400, 23 figs.

PLATE I. *Oedaleops campi*, n. gen. n. sp. Type specimen U.C.M.P. No. 35758, dorsal aspect showing details of sculpture pattern. × 2.