

The vertebrae mentioned by Case (1907, p. 81, pl. 1, figs. 9-13) as possibly pertaining to "a large species of *Poliosaurus*" are presumably those of the present species.

Ophiacodon major sp. nov.

Holotype, AM 4109; Loc. VIc; Clyde formation, Clear Fork group.

The last and largest species of the genus, with an estimated weight of about 230 kg. Known only from fragmentary remains from the Clyde formation of Texas and Oklahoma.

The presence in the Texas beds of exceptionally large animals of the "*Theropleura*" type was recognized by Case (1907, p. 28), and the species *Theropleura grandis* created for their reception. Unfortunately, as explained later (see *Dimetrodon grandis*), he chose as the type certain vertebrae which prove to belong to the large Clear Fork *Dimetrodon*, and a new name is necessary. We have taken as the holotype a specimen which includes a series of 10 vertebrae running from the lumbar to the proximal caudals; this was used by Case in the description of "*Theropleura*" *grandis*, and it would appear that he had considered using it as the type. These vertebrae are definitely ophiacodont in structure and, except that they are one-third larger, they are not distinguishable from the corresponding elements in *O. retroversus*.

This specimen is from the Clyde formation of Texas. From the same horizon and region was obtained an ilium of appropriate size and from a locality rather lower, at about the boundary between Belle Plains and Clyde formations, comes a specimen of *Ophiacodon*, again of exceptionally large size, which includes a pelvis, femur, and a number of vertebrae. A pair of enormous femora was found in an Oklahoma deposit presumed to be equivalent to the Clyde.

This material, taken as a whole, indicates the existence of a very large form of *Ophiacodon*. Were these remains contemporaneous with *O. retroversus* it might well be argued that we have merely sorted out exceptionally large specimens of that species; but this is not the case. *O. retroversus* flourished in the Admiral and Belle Plains formations; from the Clyde we know only a single specimen from the lower part of the formation. Undoubtedly the specimens noted here represent a large end form of the phylum to which *O. retroversus* belongs and have descended from that species. The increased size and later geologic occurrence seem to merit specific separation.

Materials:

AM 4109, VIc. The type, 10 vertebrae, described by Case (1907, p. 88-89 and fig. 26, labelled 4130-34 in error).

AM unnumbered. Military Trail, Baylor County, Texas (= Clyde formation, Loc. VIc.). Ilium.

AM 4083, Ve. Femur, pelvis, several vertebrae.

AM 1814. Deep Red Run, Oklahoma, ? Clyde formation. Heads of two femora, distal end of one.

AM 4056 (part). "Elm Creek" (? Clyde formation). Mixed bones, including large *Ophiacodon* ilium and vertebrae.

Family EOTHYRIDIDAE

Ophiacodont pelycosaurs, primitive in most known regards but paralleling the higher sphenacodonts in the development of much enlarged canines

and showing a tendency toward elongation. Possibly a composite assemblage but perhaps group of highly predaceous reptiles which were dentists in the Autunian. Included are the genera *Stereophallodon*, and *Baldwinonius*.

It has been generally assumed that the presence in the maxillary canines was indicative of a position in the sphenacodontid series. Theoretical considerations and actual findings indicate this is not universally true. Canines appear to have been differentially enlarged, in the primitive pelycosaurs and, indeed, in the primitive amphibians. It would thus not be improbable, a priori, that the size of these teeth had occurred in pelycosaurs other than the ophiacodonts. This has proved to have been the case. Forms are now known which cannot be regarded as members of that group or as at all closely related to that group. Of the forms of the Stephanian was discovered half a century ago; the present study. None is at all adequately known. The presence of powerful maxillary canines with other primitive nature which show close similarities to the dental specializations are so marked that, for the present, it is advisable to consider them as constituting a separate subfamily. It must be emphasized that our knowledge of the forms is so limited that there is no guarantee that they form a single homology. It is to be regarded as a provisional assemblage.

Of *Stereophallodon* and *Baldwinonius* we possess only a few specimens; of *Stereorhachis* we have in addition a few specimens. There is thus little basis for an attempt to give an account of the face as in *Eothyris*.

The skull of *Eothyris* is described in the account of its proportions and remarkable primitive features. However, the presence of a number of maxillary canines shows that in that genus, at least, the type of the face as in *Eothyris*. Both *Eothyris* and *Stereorhachis* are of the dentist type of platelike supraoccipital. The quadrate bone is typically ophiacodont, and the angular bone and *Stereophallodon* is again ophiacodont, lacking the dentist type. The jaw in *Eothyris* and *Stereorhachis* is similar to that in *Ophiacodon* but not so powerful as in the Sphenacodontidae.

The teeth are in all cases conical and sharp tip, pressed or with the sharp anterior and posterior canines. The maxillary canines are greatly enlarged and advanced sphenacodontid conditions. The posterior canines are markedly smaller than the canines, the contrast being immediately succeeding them being especially marked. The number of maxillary teeth as a whole varies from 10 to 12. The number of precanines, *Baldwinonius* and *Eothyris* show a tendency for the development of a step in the maxillary series.

Part of the column is present in three of the genera. The column is comparable to those of the ophiacodontids, but with a little tendency for the development of a ventral keel.

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Family EOTHYRIDIDAE

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Possibly a composite assemblage but perhaps representative of an early
group of highly predaceous reptiles which were replaced by the sphenaco-
dents in the Autunian. Included are the genera *Eothyris*, *Stereorhachis*,
Stereophallodon, and *Baldwinonus*.

It has been generally assumed that the presence in a pelycosaur of much enlarged
maxillary canines was indicative of a position in the sphenacodontid group; but both
theoretical considerations and actual findings indicate that this need not be uni-
versally true. Canines appear to have been differentiated, although in general little
enlarged, in the primitive pelycosaur and, indeed, in many stem reptiles and even
amphibians. It would thus not be improbable, *a priori*, to find that exaggeration in
size of these teeth had occurred in pelycosaur other than the familiar sphenaco-
dents. This has proved to have been the case. Four genera of predaceous pelyco-
saur are now known which cannot be regarded as members of the Sphenacodontidae
or as at all closely related to that group. Of the four, *Stereorhachis* of the French
Stephanian was discovered half a century ago; the other three were found during
the present study. None is at all adequately known as yet, but all combine the
presence of powerful maxillary canines with other cranial or postcranial features of
primitive nature which show close similarities to those of the Ophiacodontidae.
The dental specializations are so marked that, for the present at least, we think it
advisable to consider them as constituting a separate ophiacodont family, the Eothy-
rididae. It must be emphasized that our knowledge of these forms is so inadequate
that there is no guarantee that they form a single homogeneous group, and the family
is to be regarded as a provisional assemblage.

Of *Stereophallodon* and *Baldwinonus* we possess only a few fragments of the skull
and column; of *Stereorhachis* we have in addition a few limb and girdle bones. *Eothy-*
ris is represented by a complete skull, but the postcranial skeleton is unknown.
There is thus little basis for an attempt to give an extended family diagnosis.

The skull of *Eothyris* is described in the account of that form. Whether many of
its proportions and remarkable primitive features were repeated in other genera is
unknown. However, the presence of a number of precanine maxillary teeth in
Baldwinonus shows that in that genus, at least, there was no such marked shortening
of the face as in *Eothyris*. Both *Eothyris* and *Stereophallodon* exhibit an ophiaco-
dodontid type of platelike supraoccipital. The quadrate, as seen in all except *Stereo-*
rhachis, is typically ophiacodont, and the angular and articular region in *Eothyris*
and *Stereophallodon* is again ophiacodont, lacking the angular notch seen in sphenaco-
dodontids. The jaw in *Eothyris* and *Stereorhachis* is somewhat more stoutly built than
in *Ophiacodon* but not so powerful as in the Sphenacodontidae.

The teeth are in all cases conical and sharp tipped but never to any degree com-
pressed or with the sharp anterior and posterior cutting edges seen in the sphenaco-
dodonts. The maxillary canines are greatly enlarged—the sole feature comparable to
advanced sphenacodontid conditions. The postcanine maxillary teeth tend to be
markedly smaller than the canines, the contrast between the canines and the teeth
immediately succeeding them being especially marked in *Stereophallodon* and *Eothy-*
ris. The number of maxillary teeth as a whole varies greatly, however, as does the
number of precanines, *Baldwinonus* and *Eothyris* being two extremes. There is no
tendency for the development of a step in the maxilla.

Part of the column is present in three of the genera. The vertebrae are in general
comparable to those of the ophiacodontids, particularly *Clepsydrops*. There is
little tendency for the development of a ventral keel, except to a slight extent in the

never a prominent ventral lip on the ends of characterized by an essentially flat ventral sur- marked by a double longitudinal ridge. The ngated than in ophiacodontids, and those of age sphenacodont. The zygapophyses appear at the neural arches are transversely narrow ont fashion. In *Stereophalloodon* the nature of xpanded ilium.

pendicular skeletal material preserved. The e similar to those of the ophiacodontids. Un- erial makes it impossible to discover whether ontidae was present here and whether the hind tionately large.

ializations seen in these genera are associated otated that while one form—*Eothyris*—is small, r in its fauna, and the other two rank among rly the eothyrids tended to be dominant types. *Eothyris*, which may be regarded as a diminutive o be Stephanian in age and come from horizons r are small and rare. Since the sphenacodonts ers of the entire Autunian tetrapod assemblage, der eothyrids were their functional predecessors r forms among the amphibians, cotylosaurs, and rboniferous. Faunas of that date are as yet knowledge may well reveal a considerable array ps as varied as their sphenacodont successors. ion of the family from the primitive pelycosaur

l features paralleling the sphenacodontids, it is y genetic connection between the two families ition; since, as will be seen, large canines evolve s of the Sphenacodontidae, they cannot have been r.

us *Eothyris* Romer
pe, *E. parkeyi* Romer.

Eothyris parkeyi Romer
(Figures 3, 53)

Holotype, MCZ 1161, Loc. Vd. Belle Plains for-

archaic in skull structure but specialized in ace and complete absence of maxillary teeth ed canines. Known from a single skull from

during the course of the present study, is known was figured in its present condition in the original g sketches a restoration is attempted in which are slight crushing to which the specimen had been

subjected. The superficial dermal elements are for the most part adequately preserved, and much of the occiput is visible. Little is seen of the palate, and the internal structure is unknown.

The skull measures but 65 mm. in length, and *Eothyris* is thus an exceedingly small form for a pelycosaur. In skull size only *Casea*, *Glaucosaurus*, *Tetraceratops*, and

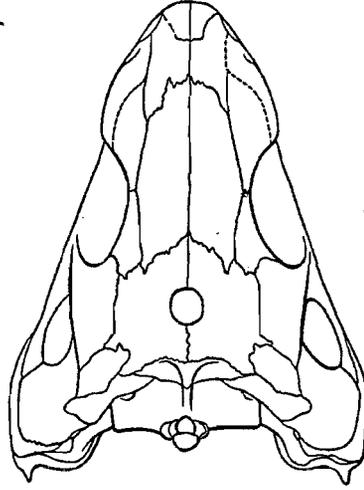


FIGURE 53.—*Eothyris parkeyi*, type skull in dorsal view
× 1.

Mycterosaurus are at all comparable among American forms, and *Elliotsmithia*, *Mesenosaurus*, and the immature "*Palaeohatteria*" material of old-world pelycosaurs.

The skull shows an interesting combination of exceedingly primitive characters and a high degree of specialization of the face and dentition. In its proportions it is obviously low, very broad, and short, the shortness being due to a remarkable decrease in the length of the facial region associated with the type of dentition. The absence of postcranial material renders it impossible to give dimensions in linear units. If, however, we arbitrarily assume that the orbit is, as is frequently the case, about 10 units in antero-posterior length, we obtain the following measurements: total length 34 units, facial region 10 units, height at orbit 7 units, width at quadrate 25 units. These figures, when compared with those for other pelycosaurs, are in agreement with first impressions. The postorbital and orbital regions are of normal length; the face is shorter by far than in any other pelycosaur except edaphosaurs. The lack of height is presumably a primitive feature; here comparable figures are found in *Varanosaurus* as well as a number of edaphosaurs. The posterior breadth is unusual and exceeded only by large and advanced sphenacodonts. Except for the facial shortening the proportions appear to be quite archaic and suggestive of cotylosaurians.

In correlation with the changed proportions of the snout the premaxillae and nasals are short. The frontals are of moderate length. Alone among pelycosaurs *Eothyris* shows the primitive condition of pre- and postfrontals meeting above the orbit; this situation is particularly remarkable as being found in a small animal, for such forms tend to have relatively large eyes which may cause considerable excision

of the skull roof above them. The broad skull table, with a relatively large pineal opening, is almost amphibian in appearance; this, however, must be discounted to some extent in considering the fact that the underlying braincase must be relatively broad in such a small form. The lateral margins of the table are not so abruptly marked off from the side walls of the skull as is usually the case in pelycosaurs; there is merely a gradual rounding downward of the postorbital. This last bone is unusually broad posteriorly, and the supratemporal is much more highly developed than in any other pelycosaur. The bone is wedged into the postero-lateral corner of the parietal, just as in other members of the group. Broom (1938a, fig. 1) labels this element tabular. The tabular is, however, quite distinct, and the element in question is exactly comparable in position to the supratemporal of other pelycosaurs.

The lacrimal traverses the short snout from orbit to naris. The maxilla swells outward about the base of the canines and is somewhat convex in outline above them; unfortunately, nothing is known of the internal surface in the canine region. Obviously correlated with the lowness of the skull and the relatively large orbits associated with small size, the maxillae occupy much of the lower margins of the orbits; the jugal does not extend far forward and has no contact with the lacrimal. Prefrontal, lacrimal, and maxilla form a broad shelf in the anterior margin of the orbit. There is little development of the internal expansion seen in the posterior margin of the orbit in the Ophiacodontidae. The temporal opening is small and of oval shape; in consequence of its small size the squamosal and postorbital are widely in contact. The cheek slants outward to a much greater degree than is usual in pelycosaurs, so that the temporal opening is exposed in dorsal view to a considerable extent. Related to the lowness of the skull, the slope from skull table to quadrate is gentle. The jaw articulation is in line with the tooth row, and the quadratojugal is very long, apparently still touching the maxilla. There is a distinct indication of the former position of the otic notch in a projection of the lower ends of the tabular and supratemporal.

Due to the presence of the lower jaws and to a refractory matrix, little is seen of the palate. Typical pterygoid flanges, apparently slender and with a row of small teeth, are present well back in the skull, below the anterior part of the temporal opening. The quadrate is present on the right side and is fortunately exposed dorsally. It is, in primitive fashion, broad in a horizontal plane and has a large platelike pterygoid ramus. Its general build is, as far as can be seen, similar to that found in ophiacodontids. The pterygoid ramus is rather laterally placed, and hence it seems certain that there was, as in ophiacodonts and *Varanops*, a middle ear channel medial to it, floored by the quadrate ramus of the pterygoid.

The dorsal rim of the occipital surface is occupied by the interparietal and tabulars. The former is an unpaired element; it bears a longitudinal ridge extended downward on the supraoccipital nearly to the foramen magnum. The tabular is preserved only on the left side and may be somewhat imperfect postero-medially. The occipital aspect of the braincase is visible as a broad subquadrate plate of bone, most of which, if not all, is supraoccipital. Ventro-medially the plate is notched for the upper border of the foramen magnum; poorly preserved exoccipitals are attached here. The bone is further notched at each dorso-lateral corner. If these notches be interpreted as posttemporal fenestrae, then the broad lateral margin of the bone must be considered as an unusually broad paroccipital process. However, the plate resembles closely the supraoccipital as found isolated in *Ophiacodon*. So interpreted, the notches mark merely the division between dorsal and lateral expansions of that element, and the lateral margin of the bone would include the area of lateral attachment to the tabular and the surface to which the opisthotic attached. The construction would thus have been like that of *Ophiacodon*, the posttemporal

fenestra situated far ventrally, and the opisthotic bone. The pretable remains of the opisthotics are present, and of the braincase cannot be made out.

Due to the short face, the lower jaw does not have the anterior part of the ophiacodontid mandible. Dentes are readily visible on the outer surface, and in ventral view the splenial is visible. The angular has a well-developed articular face comparable with that of *Ophiacodon* and without any dentid structure. The articular face for the quadrate is ventrally, and the construction is, as far as can be seen, similar to that of *Ophiacodon*. Except for the most posterior portion the medial surface of the teeth are pointed and tend to be very slightly compressed. The premaxilla carried on the anterior part of the snout is enlarged. In correlation with the shortening of the face, the premaxilla have disappeared completely; in this feature *Eothyris* almost any known example of a sphenacodont. The area of the maxilla is notched in a fashion slightly suggestive of *Varanosaurus*, downward in a plane lateral to that in which lie the teeth. These teeth number about a dozen. Those immediately anterior have but a third or so the length of the tusks. It is what farther back are the largest of the postcanine series. The dentary teeth are imperfectly seen in the anterior series. The dentary teeth are imperfectly seen in the anterior series.

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There are no remains of the postcranial skeleton mentioned earlier with regard to skull dimensions seen that they imply a linear unit of about 1.8 mm. *Mycterosaurus*.

From the above description it is seen that *Eothyris* is similar to the ophiacodontids in a great many respects, but still more primitive than the ophiacodontids in the shape of the skull table, and the temporal region. It is in many respects more primitive than any of the known pelycosaurs. On the other hand, the skull structures show an extreme type of development of the kind that is characteristic of ophiacodontids. It suggests that *Eothyris* is a sphenacodontid. However, it is more advanced than those of even most of the more primitive sphenacodonts, while, on the other hand, the general skull build is a great deal more primitive than those of even most of the more primitive sphenacodonts. In *Haptodus* in which the canines are little developed, the relationship that the Tasmanian wolf bears to the Tasmanian devil applies with more force to the suggestive resemblance of *Eothyris* and the theriodonts.

The *Eothyris* type is from an Upper Wichita deposit, and the other genera here associated with it. Presumably it is its "cousin" *Varanosaurus* in the Clear Fork.

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fenestra situated far ventrally, and the opisthotic bones small elements. No inter-
pretable remains of the opisthotics are present, and the condition of the remainder
of the braincase cannot be made out.

Due to the short face, the lower jaw does not have the slender build seen in the
anterior part of the ophiacodontid mandible. Dentary, angular, and surangular
are readily visible on the outer surface, and in ventral view the lower edge of the
splenial is visible. The angular has a well-developed ventral flange which is exactly
comparable with that of *Ophiacodon* and without any trace of the peculiar sphenaco-
odontid structure. The articular face for the quadrate extends inward almost hori-
zontally, and the construction is, as far as can be seen, similar to that of *Ophiacodon*.
Except for the most posterior portion the medial surface of the jaw is not visible.

The teeth are pointed and tend to be very slightly recurved but are round in
section, never compressed. The premaxilla carried three teeth, none very greatly
enlarged. In correlation with the shortening of the face precanine maxillary teeth
have disappeared completely; in this feature *Eothyris* is more specialized than
almost any known example of a sphenacodont. There is, however, not the slightest
indication of a maxillary step. The canines are, for the size of the animal, remark-
ably large and powerful. The area of the maxilla on which they are carried swells
out in a fashion slightly suggestive of *Varanosaurus*, so that the canine pair projects
downward in a plane lateral to that in which lie the more posterior maxillary teeth.
These teeth number about a dozen. Those immediately posterior to the canines
have but a third or so the length of the tusks. It is of interest that the teeth some-
what farther back are the largest of the postcanine series; there is, as it were, a sec-
ondary focus of maxillary tooth development, also seen in several other pelycosaur
genera. The dentary teeth are imperfectly seen but appear to have been rather
uniform in size; there was no appreciable enlargement of the anterior members of the
series.

There are no remains of the postcranial skeleton definitely known. If the infer-
ences mentioned earlier with regard to skull dimensions are at all correct, it will be
seen that they imply a linear unit of about 1.8 mm., and hence a bulk about that of
Mycetosaurus.

From the above description it is seen that apart from the face and dentition
Eothyris is similar to the ophiacodontids in a great array of features. Further, it is
still more primitive than the ophiacodontids in the build of the supraorbital area,
the skull table, and the temporal region. It is in many regards the most primitive
of known pelycosaurs. On the other hand, the short face and associated dental
structures show an extreme type of development of predaceous habits far removed
from those expected in a pelycosaur ancestor and quite different in direction from the
milder dental differentiations of ophiacodontids. The dentition would at first sight
suggest that *Eothyris* is a sphenacodontid. However, its dental peculiarities are
more advanced than those of even most of the most specialized sphenacodontids,
while, on the other hand, the general skull build is archaic; there are no traces what-
ever of the characteristic family features seen even in sphenacodontids such as
Haptodus in which the canines are little developed. It is thus obvious that *Eothyris*
is not at all closely related to the sphenacodontids; it bears to them much the same
relationship that the Tasmanian wolf bears to the Canidae. The same argument
applies with more force to the suggestive resemblance of the canine region in *Eothyris*
and the theriodonts.

The *Eothyris* type is from an Upper Wichita deposit. It is thus later in time than
the other genera here associated with it. Presumably it is here a relict type, just as
is its "cousin" *Varanosaurus* in the Clear Fork.