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Article II.—THE PENNSYLVANIAN TETRAPODS OF LINTON, OHIO

By Alfred S. Romer

26 Text Figures

CONTENTS

INTRODUCTION

For the early history of land vertebrates the material from the Coal Measures is of paramount importance. Permo-Carboniferous forms are numerous, but they show us a stage in which many early amphibian groups were highly specialized, and some were apparently already extinct, while the deployment of the reptiles was well under way. On the other hand, pre-Pennsylvanian remains are extremely rare, although tetrapod development must have begun in the Devonian.

In Europe, a true Coal Measures fauna was early described by Huxley from Kilkenny, while Atthey, Huxley and others gave accounts of the forms (mainly labyrinthodonts) from English and Scotch localities, especially Newcastle. Watson has, in various papers, reinterpreted much of this material (pointing out especially the importance of the Embolomeri), while the work of Fritsch, Credner and others on forms from central Europe has shed considerable light on Coal Measures fossils, although much of their material dates from a somewhat higher series of horizons, comparable with the Permo-Carboniferous of North America.

In America a superficial survey of the state of our knowledge of true Pennsylvanian forms (in which category late Pennsylvanian deposits containing the "Red Beds" fauna are to be excluded) seems to show that it is in a satisfactory condition. More than 80 species of tetrapods have been described from deposits of Westphalian age, mainly from three localities, the Linton cannel discussed below, the erect trees of the Joggins, Nova Scotia, and the nodule beds of Mazon Creek, Ill. The Linton material was described mainly by Cope, that from the Joggins by Dawson, while Moodie has described additional forms, mainly from

Mazon Creek and Linton. The latter has summarized our knowledge of the American Pennsylvanian amphibians in his useful "Coal Measures Amphibia of North America" (1916).

The prospect is at first pleasing. From this wealth of species it would at first sight seem possible to obtain an adequate conception of the life of the Pennsylvanian of North America. Closer inspection, however, is disappointing in its results. In almost no instance is there sufficient material for us to either be able to assign a form to its proper position in the classification, or to obtain an idea of its general morphology. One species is known only from an element of the shoulder girdle; a second from a jaw fragment; a third from the top of the skull; and so on. This in itself gives rise to the suspicion that if these various elements could be correlated, the number of supposed forms might be considerably reduced.

Stronger support for the idea that this is really the case is suggested by a consideration of the Linton fauna. From this single locality have come about two-thirds of described American forms. Nearly 60 species from this locality are remains of tetrapods or have been thought to be such. And yet all these specimens have come from an area not much more than 100 yards in diameter, in a layer of cannel coal four to six inches in thickness, the formation of which can have taken but a very short time, geologically speaking (Newberry, 1878, pp. 736–737). Is it reasonable to assume that more than half a hundred species of amphibians inhabited this pool almost simultaneously?

The present paper is an attempt to restudy the Linton tetrapods. A few forms from Cannelton, about 15 miles to the northeast, and somewhat lower in the section, have been included.

I have attempted to effect a systematic revision of the fauna, with the frank purpose of obtaining a reduction in the number of species, so that some idea of the morphology and appearance and habits of these forms may be obtained. It is quite probable that in this "lumping" of species I may have proceeded too far, and that further material may prove that in several instances forms regarded here as synonyms may really be separate species. However, the results are, perhaps, somewhat nearer the truth than the present situation.

Since many of these amphibians undoubtedly passed their entire lives in this type of habitat, immature forms are to be expected among the finds, and size can thus not be used as a criterion of specific or generic difference.

The specimens are all preserved, in a crushed condition, as a car-

bonaceous material in slabs of cannel coal. Usually the blocks are split through skulls and other elements, leaving half of the "bones" on one side, half on the other. Such specimens often show little or nothing of surface structure. In such cases, as pointed out to me by Professor D. M. S. Watson, the "organic" material can be removed by the use of hydrochloric acid, enabling both surfaces of the bone to be recovered in squeezes. Unfortunately, many of the specimens are represented by one side only, and since many are types this method of treatment could not always obtain.

This material is normally difficult of interpretation. In addition, pyritization and consequent decay have usually occurred to some extent, rendering what were probably good specimens when first collected very poor at the present time. I have not hesitated to criticise former interpretations of structures and sutures, and I need not add that my own are likewise open to criticism.

Many of the specimens discussed were figured by Cope in 1875, and by Moodie in 1916; the illustrations in these two works should, in most cases, be consulted in connection with the descriptions given below.

The largest collection, containing most of the types, is that in the American Museum of Natural History, New York. This includes most of the specimens collected by Newberry, while a few of his finds are to be found at Columbia University. A considerable number of slabs from the Lacoe Collection are in the U. S. National Museum, Washington, and a few specimens are in Walker Museum, University of Chicago.

These specimens were obtained while the Linton "Diamond" Mine was in active operation, roughly from about 1855 to 1880. In 1920, the mine was reopened for a short time, and Dr. J. E. Hyde of Western Reserve University obtained a small but interesting collection. The roof of the mine has now fallen in, and it is improbable that additional material will ever be obtained from this locality.

For rendering the above material available to me for study, I wish to thank Curators Barnum Brown, Walter Granger, W. K. Gregory, and G. G. Simpson of the American Museum, Curator C. W. Gilmore of the National Museum, and Professor J. E. Hyde of Western Reserve University.

Specimens mentioned below without further designation are those in the American Museum of Natural History; those prefixed by NM are in the National Museum; those with WR in Western Reserve University; with WM in Walker Museum, University of Chicago.

Abroad, there are a number of specimens from Linton in the

British Museum, others in Berlin (some of which have been described by Jaekel and Schwarz), and it is not impossible that there are a few specimens in other institutions.

As this study was approaching completion, Professor Watson informed me that the British Museum specimens were being prepared and studied by him and Miss M. Steen at University College, London. A comparison of our results shows that we are in essential agreement in most respects. Certain of the forms are not represented, or poorly shown in the British Museum material, but in several cases the material is better, and two forms represented by single specimens in this collection are, as far as I know, not found in the American material.

LYSOROPHIA

Lysorophus is a well-known form from the Lower Permian of North America, with characteristic vertebræ, an elongate body with very small limbs, and, especially, a very peculiar type of skull and branchial arch structure, which has most recently been investigated by Sollas (1920). Its position has long been a matter of debate; Broili believed it to be an ancestor of the reptiles, but the more general opinion has been that it is a very "advanced" amphibian, and Williston and others have suggested its possible relationship to the urodeles. There are no pre-Permian forms which have been assigned to this group previously. However, a member of this group (although without such great specialization of the cranial roof) is present in the Lower Carboniferous of Scotland, and is described in a paper by Watson now in press (*Palæontographica Hungarica*). It appears probable that the form from Linton generally known as *Cocytinus gyrinoides* is a close relative of *Lysorophus*, a conclusion which Professor Watson informs me he has also reached.

Cocytinus gyrinoides Cope

C. gyrinoides Cope, 1871*a*, p. 177; 1874, p. 278; 1875, pp. 360–365, Fig. 5, Pl. xxxix, fig. 4; Moodie, 1916, pp. 67–69, Figs. 16, 16*a*.

Molgophis wheatleyi Cope, 1874, p. 263; 1875, pp. 369–370, Pl. xlv, fig. 1; Moodie, 1916, pp. 149–150.

? = *Brachydectes newberryi* Cope, 1868, p. 214; 1869, pp. 14–15; 1875, p. 388, Pl. xxvii, fig. 2; Moodie, 1916, pp. 175–176.

Types.—*C. gyrinoides*, 6925; *M. wheatleyi*, 6897; *B. newberryi*, 6941.

This form is best represented by the type, figured and described by Cope. The specimen shows the under side of a skull, well developed branchial arches, and the anterior portion of the vertebral column. I have figured the cranial region in comparison with a modification of

Sollas' ventral view of *Lysorophus*. The comparison is quite close. The width of the skull of the present form appears to be somewhat greater, but much of this may be due to crushing. The slight ridge visible behind the left jaw may be an indication of the squamosal region leading up from the quadrate. Extending far back of the jaws there is seen what appears to be a broad plate representing the parasphenoid region, behind which appears the first vertebra. The configuration here is remarkably similar to that of *Lysorophus*.

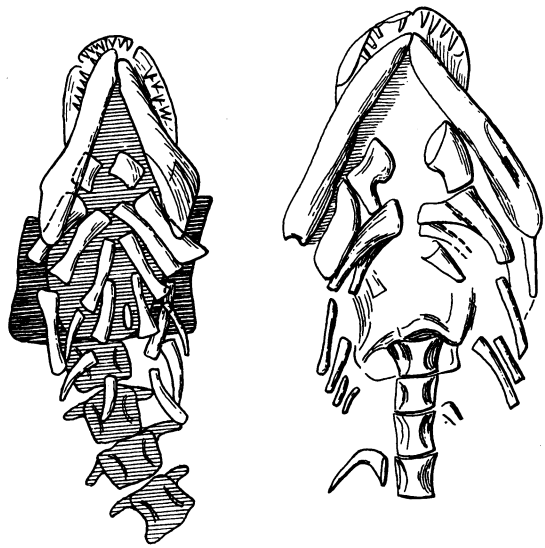

Fig. 1. Right, *Cocytinus gyrinoides*, ventral view of type, × 1½. Left, *Lysorophus*, modified from Sollas, for comparison.

The branchial arches are quite well preserved and are similar to those of *Lysorophus*. The hypohyals and ceratohyals are large. On the left side I cannot distinguish without some doubt the first ceratobranchial from the adjacent ceratohyal. On the right side, a fourth branchial appears to be present.

The type of *M. wheatleyi* is undoubtedly a specimen of this form, although the displacement of the ribs gives it a somewhat different appearance at first sight. The skull is not now visible. The description of it by Cope, however, is almost word for word that of an imperfectly preserved cranium of *Lysorophus*.

Cope has described a pair of small lower jaws as *Brachydectes newberryi*. The teeth are rather large, few in number and confined to the

anterior half of the jaw, which is short, rather shallow in front and very deep posteriorly. There is no Linton form other than *Cocytinus* with which these jaws can be correlated (unless, quite improbably, *Ctenerpeton*, in which the skull is unknown). The short tooth row rules out all others except the diceratosaurids, and the teeth are much too large for that genus.

The lower jaws of the type of *Cocytinus* are seen only in ventral view, and a direct comparison is thus out of the question. But a comparison with the jaw of *Lysorophus* (as seen, for example, in the figures of Sollas, 1920) shows that there is close agreement in the proportions, tooth row, etc., and it is highly probable that the "*Brachydectes*" jaw is that of *Cocytinus*.

Moodie assigns *Cocytinus* to the urodeles on account of its well developed branchial arches. This is hardly an adequate reason. It is quite possible that the lysorophids are related to the modern caudates; but for the present it seems advisable to separate these forms from the modern ones and from other Palæozoic types not closely related as well. The great specialization already attained by this Pennsylvanian form suggests that the lysorophids were a very early offshoot of the primitive amphibian stock and are perhaps best regarded as constituting a separate order.

AISTOPODA

This group was erected by Miall for *Ophiderpeton* and *Dolichosoma*. The characters then listed were the possession of elongate vertebral centra and the absence of limbs. The body is elongate. The ribs are short and straight, sometimes with an "uncinate process" projecting from them.

The aistopods are already highly specialized in the Pennsylvanian and apparently had become extinct by Permian times. It seems certain that they had had a long history as an independent group.

Two American forms, corresponding closely to the genera named above, are to be placed here.

OPHIDERPETONTIDÆ

The less "degenerate" members of the group, with well developed (although short) ribs of a complicated structure, and a good ventral armor.

Ophiderpeton amphiuminis (Cope)

Oestocephalus amphiuminis COPE, 1868, pp. 218–220; 1871, p. 41.
Oestocephalus remex (partim) COPE, 1869, pp. 17–19; 1871, p. 46; 1871*b*, p. 53;

1875, pp. 380–386, Pls. XXVII, fig. 5; Pl. XXXI, fig. 1, Pl. XXXIII, fig. 2; Pl. XXXV, fig. 5; Pl. XLIV, fig. 3; MOODIE, 1909*a*, p. 27; 1916, pp. 143–145.

Thyrsidium fasciculare COPE, 1875, pp. 365–366, Pl. XXXI, fig. 2; Pl. XLII, fig. 3; SCHWARZ, 1908, pp. 70–73, Figs. 5–9; MOODIE, 1909*a*, p. 27; 1916, pp. 145–146, Fig. 8.

Ichthyerpeton squamosum MOODIE, 1909, pp. 69–72; 1909*a*, p. 24; 1916, pp. 135–137.

TYPES.—*O. amphiuminis*, 6857 (a cotype) (Cope's Pl. XXXIII, fig. 2) and probably *T. fasciculare*, 6900 (Cope's Pl. XXXI, fig. 2), *I. squamosum*, NM 4459, 4476.

Our knowledge of the genus has hitherto been obtained mainly from the material from Kilkenny and Nyřan, described by Huxley and Fritsch. Huxley (1867, pp. 364–366, Pl. XXII) figured an extremely elongate amphibian, with upwards of sixty holospondylous vertebræ present in his complete specimen. On the abdominal surface is a ventral armor of thin and much elongated scales; no traces of limbs or girdles are to be seen. The skull, unfortunately, is not well preserved, but apparently was not of great length. The Nyřan material has added considerably to our information, as described by Fritsch (1883, pp. 119–124, Pls. XVII, XIX, XXI, XXIV) and Schwarz (1908). The structure of the vertebræ, including the complicated transverse processes, is well illustrated by these authors, as well as the peculiar ribs. Unfortunately the head has not been well preserved in this material.

Fig. 2. *Ophiderpeton amphiuminis*, vertebræ and ribs, × 2. From a specimen in Walker Museum.

Remains of this type have been recognized previously in American material only by Schwarz, in *Thyrsidium*. However, it is not uncommon at Linton, but its identification had been prevented by a mistake on the part of Cope. Cope described *Oestocephalus amphiuminis* from two skulls and anterior portions of the body. The skulls were elongated, the teeth small, in a single series, and somewhat recurved. The body showed, as may be seen from his figures, an abdominal armor of long needle-shaped scutes, very similar to those of *Ophiderpeton*. Cope later, in error, associated these specimens with the *Urocordylus*-like tails which he had described as *Sauropleura remex*, and this hybrid animal has since been known as *Oestocephalus remex*. However, a check

of the material available shows that there is no evidence for such an association, whereas, as noted elsewhere, the *O. remex* caudals are very definitely to be associated with another type of body.

Meanwhile, *Thyrsidium fasciculare* had been described by him from specimens similar to those of *O. amphiuminis*, but showing complicated transverse processes. Schwarz (1908) described vertebræ and ribs of a specimen which he identified as *Thyrsidium*, and noted its resemblance to *Ophiderpeton*. I have developed specimens of *O. amphiuminis*, some so identified by Cope, revealing structures comparable to those of Schwarz's figure, and so similar to those of *Urocordylus* that generic identity seems highly probable. There are minor differences in the shape of the ribs and transverse processes, but these may well be regional in their nature. Even the notch in the prezygapophyses noted by Fritsch (1883, p. 120, Fig. 65) in *Ophiderpeton* is repeated in this material, It seems certain that *O. amphiuminis* and *T. fasciculare* are synonymous, and that the form is a member of the genus *Ophiderpeton*.

While the ventral squamation consists of thin elongate elements, the more lateral scutes are shorter and rounded in shape. Such scutes appear to have been well up the sides of the body, if not forming a complete covering. This is in agreement with Fritsch's findings.

Moodie has described (1909*b*) two specimens in the National Museum as representing a new species, *I. squamosum*, belonging to the genus *Ichthyerpeton*, found by Huxley (1867, pp. 367–368, Pl. XXIII) in the Jarrow material. Moodie characterized it as a completely scaled amphibian, with elongate scutes ventrally and rounded ones dorsally. Upon examination these specimens clearly pertain to the present species, whereas Huxley's *Ichthyerpeton* is an embolomerous labyrinthodont and, incidentally, is stated by him not to be completely scaled.

Of the forms included in the above synonymy, two are associated by Moodie in a common family with the elongate nectridian types, and a third placed in a family of labyrinthodonts, both of which associations are obviously incorrect.

PHLEGETHONTIDÆ

This is best known from *Dolichosoma* from Jarrow (Huxley, 1867, pp. 366–367, Pl. XXXI, fig. 3) and Nyřan. It is an extremely elongate form, with vertebræ essentially similar to those of *Ophiderpeton*, but with reduced ribs, as described especially by Fritsch (1883, pp. 108–109, Pls. XVII, XVIII, XXII, XXIII) and Schwarz (1908, pp. 76–79, Figs. 14–16). The skull is elongate; a general idea of its superficial features may be had from Fritsch's description.

Phlegethontia linearis Cope

Molgophis macrurus (partim, in errore) Cope, 1868, pp. 220–221.

P. linearis Cope, 1871*a*, p. 177; 1874, p. 262; 1875, pp. 366–367, Pl. xliii, figs. 1, 2; Schwarz, 1908, pp. 74–76, Figs. 12, 13; Moodie, 1916, p. 154, Fig. 8.

P. serpens Cope, 1874, p. 263; 1875, p. 367, Pl. xxxii, fig. 1; Moodie, 1916, p. 154.

Types.—*P. linearis*, 6886; *P. serpens*, 6899.

The general characters of this form may be made out from Cope's figures; it appears to be very similar to *Dolichosoma*. *Phlegethontia* possessed a very elongate body (with more than 100 vertebræ in one specimen) and an elongate head. Cope states that ribs are absent, but in the larger specimen very thin rib-like structures are seen. There is no trace of them in the smaller specimens described as *P. linearis*, but as Fritsch (1883, p. 107) recognized, this seems due to the fact that these are immature forms in which ossification of these slender structures would obviously not yet have taken place. The vertebræ have been described by Schwarz (1908).

Hay and Moodie both place the genus in the Molgophidæ. There does not appear to be any reason for this association other than the supposed limbless condition in both cases. The structure of the vertebræ seems to be quite different. The vertebræ are somewhat similar to those of *Dolichosoma;* the differences are perhaps sufficient to retain the generic separation, but there can be no doubt of the close relationship of the two forms.

NECTRIDIA

This group was established by Miall to include especially *Ceraterpeton* and *Urocordylus*, described by Huxley (1867) from Jarrow. While these appear to differ widely in their skulls, they have a common type of vertebral structure, the caudals being quite unlike those found in any other described forms. The chevrons attach to the under side of the single centrum and expand into a fan-shaped structure which is usually pectinated distally; the neural spine is similar in general appearance. It seems probable, because of the chevron attachment, that the "centrum" is really the intercentrum, with which the hæmal arches usually articulate in land forms. The dorsals likewise have anteroposteriorly elongated neural arches, often with a pectination present. Zygosphene-zyantrum articulations are present. Watson (1913) has pointed out that in *Batrachiderpeton* the skull structure may be interpreted as a modification of the embolomerous plan, and that even in forms with a peculiarly modified skull pattern, the palatal structure is still quite primitive.

Two main types may be distinguished, both of which are represented at Linton; one with an elongate body with a well developed ventral armor, and with a skull which perhaps is rather "normal" except for elongation; the other with little or no ventral armor, but with the tabular region of the skull produced into long horn-like structures. Both groups are common in the Pennsylvanian, and both are represented in the American Permo-Carboniferous by end forms. In addition, there are a number of forms of rather uncertain position, such as *Scincosaurus* of Bohemia, with *Ctenerpeton*-like armor, *Sauravus* of the French Carboniferous, ?*Lepterpeton* from Jarrow and probably others.

UROCORDYLIDÆ

This family includes several carboniferous genera. It is represented by *Urocordylus* of Huxley (1867) from Ireland and Bohemia, and several American forms. All have elongate bodies, with the vertebræ characteristic of the Nectridia, an elongate tail, limbs of moderate to small size, a somewhat elongate head, and a well-developed ventral armor. The family is typically Pennsylvanian, although there is no doubt that *Crossotelos*, of the Wichita, was a late survivor of the group.

There appear to be three members of this family in the Linton material: (1) a form best represented by *Ctenerpeton alveolatum* (most of the remains of which are usually incorrectly placed in *Oestocephalus*); (2) and (3) two smaller forms with shorter neurals and hæmals commonly described as *Ptyonius*, more correctly as *Sauropleura*.

Ctenerpeton remex (Cope)

Sauropleura remex COPE, 1868, pp. 217–218; 1871, p. 53.

Oestocephalus remex (partim) COPE, 1869, p. 17, Fig. 2; 1871, p. 41; 1871*b*, p. 53; 1875, pp. 381–386, Figs. 9 ("3"), Pls. XXXII, Fig. 2, XXXIV, Fig. 4; SCHWARZ, 1908, pp. 86–87, Figs. 29–30.; MOODIE, 1909*a*, p. 27; 1916, pp. 143–145, Figs. 3, 8.

Ctenerpeton alveolatum COPE, 1897, pp. 83–84, Pl. III, fig. 1; MOODIE, 1909*a*, p. 24, Pl. X; 1916, pp. 166–167, Pls. XIX, XXIII, fig. 2.

TYPES.—*S. remex*, 6903 (Cope, 1875, Fig. 3), *C. alveolatum*, NM 4475.

Urocordylus was first described by Huxley (1867, pp. 359–362, Pl. XX) from Kilkenny; a good idea of much of its general appearance may be gained from his plate. Girdles and both anterior and posterior limbs are present; the ventral armor consisted of rather broad thin scales arranged in chevron. The caudals are especially characteristic, with very tall and fluted hæmals and neurals. An American form which is very closely related is that included in the above synonymy. Its general characteristics, as far as known, may be seen in Moodie's plate of

Ctenerpeton. I have no certain knowledge of its skull, and the limbs are also incompletely known. The belly was covered by a series of broad dermal scutes well illustrated in Moodie's figure. They are punctate along their posterior edges, much as in Fritsch's *Scincosaurus*. The lateral members of each series are robust, and the series terminates laterally with a comb-shaped edge. As far as can be seen from Huxley's figures the ventral armor of *Urocordylus wandesfordii* was comparable. The tail vertebræ are remarkably similar to those of that type.

This form is usually called *Oestocephalus*. *Sauropleura remex* was first described by Cope from caudal vertebræ of the urocordylid type; *Oestocephalus amphiuminis* from remains which included the head and anterior portion of the body. Cope later associated the two as *Oestocephalus remex*, but a check of his material shows that there is not the slightest evidence for this combination. As noted previously, the cranial and thoracic material is that of an aistopod. On the other hand, the association of "*Sauropleura*" *remex* and *Ctenerpeton* is shown in the type of the last-named genus, in a specimen figured by Cope (1875, Pl. XXXIV, fig. 4; No. 6909) and in an excellent specimen (5453) in Western Reserve University. The name *Oestocephalus* is not available for this form, since the type of that genus is an aistopod.

O. rectidens is probably a synonym of *Erpetosaurus radiatus*.

Sauropleura pectinata Cope

S. pectinata COPE, 1868, pp. 216–217.

Oestocephalus pectinatus COPE, 1869, p. 20; 1874, p. 266.

Ptyonius pectinatus COPE, 1875, pp. 377–378, Pls. XXVIII, figs. 2 (pt.), 4, 6; XXIX, fig. 2; XXX, fig. 3; XXXV, figs. 1, 3, 4?; XLIV, fig. 3?; SCHWARZ, 1908, pp. 82–86, figs. 23, 24, 26; MOODIE, 1909*a*, pp. 24–25, Pl. VIII, fig. 3; 1916, pp. 142–143, Figs. 8, 30, Pl. XX, fig. 2.

Oestocephalus serrulus COPE, 1871*a*, p. 177.

Ptyonius serrulus COPE, 1875, pp. 379–380, Pls. XXVIII, fig. 5, XXX, fig. 1; MOODIE, 1916, pp. 142–143.

Oestocephalus vinchellianus COPE, 1871*a*, p. 177.

Ptyonius vinchellianus COPE, 1874, p. 266; 1875, pp. 376–377, Pl. XXVIII, fig. 1; SCHWARZ, 1908, Fig. 27; MOODIE, 1916, p. 141.

TYPES.—*S. pectinata*, 6876, 6882, 6896, *S. serrula*, 6895, *O. vinchellianus*, 6872.

This and the following species include the amphibians commonly known as *Ptyonius*. The general characters of the body are well seen in Cope's figures. The form is elongate, with a very long tail, with short, pectinated fan-shaped neurals and hæmals, in contrast with the more slender elements of *Ctenerpeton*. The dorsal surface of the skull has been figured by Jaekel (1909). There are large clavicles and inteclavicle, and

the ventral armor is well developed. The limb material is poor; I have not studied the evidence with care, but while some of the specimens which, in Cope's figures, appear to show limbs are doubtful, and others are now imperfect, it seems certain that small limbs were present.

This is perhaps the most abundant form in the Linton cannel. A considerable number of species of "*Ptyonius*" have been described, but I have been able to distinguish only two with any assurance. *S. pectinata* seems to be characterised by ventral scales much more slender than those of *S. marshii* (the contrast is well seen in Cope, 1875, Pl. XXVIII, fig. 2), and a more elongate head. (Compare his Pl. XXXV, fig. 1, and Pl. XLI, fig. 2.)

The only character given to distinguish *vinchellianus* from *pectinatus* by Cope is the shape of the interclavicle, and the difference here, as Moodie notes, is slight. *S. serrulus* was founded on a small specimen, which as Moodie states cannot be differentiated from *S. pectinatus*. (The contrast appears marked if comparison be made with the form shown on the same plate of Cope's 1875 paper. This specimen, however, appears to belong to the following species.)

Cope proposed the name *Ptyonius* for the forms here called *Sauropleura*, and stated (1897, p. 86) that *S. digitata* was the type of this last genus. However, he himself had previously designated *S. pectinata* as the type of *Sauropleura* (1868, p. 217); *S. pectinata* has been designated by Moodie (1916) as the type of *Ptyonius*; hence this last name must unfortunately be relegated to the synonymy.

In Europe this genus has been recognized only at Nyřan by Fritsch.

Sauropleura marshii Cope

Colosteus marshii COPE, 1869, p. 24.

Oestocephalus marshii COPE, 1871*a*, p. 177.

Ptyonius marshii COPE, 1875, pp. 375–376, Pls. XXVII, figs. 6, 7; XXVIII, figs. 2, 3; MOODIE, 1916, pp. 141–142.

Ptyonius nummifer COPE, 1875, pp. 374–375, Pl. XLI, figs. 2, 3; MOODIE, 1909*b*, p. 356, Pl. LXIII, fig. 3,; 1916, p. 142.

Hyphasma lævis COPE, 1875*a*, p. 16; 1875, pp. 387–388, Pl. XXXVII, fig. 4; MOODIE, 1909*b*, pp. 356–357, Pl. LXIII, fig. 3; 1916, p. 71.

TYPES.—*S. marshii*, 6862, *S. nummifer*, 6891, *H. lævis*, 6877.

The form discussed here has been differentiated above from *S. pectinata*, as far as our present knowledge of it goes. Specimens which are definitely assigned to it are few, but in default of certain distinctions in the caudals there are a number of specimens which may pertain to this form rather than *S. pectinata*. The best example is the type of *nummifer*, as illustrated by Cope. *S. marshii* is differentiated from this by Cope

because of the more elongate interclavicle of the former; but it seems probable that the anterior end of this element has been obscured in the type of *nummifer*. *Hyphasma lævis* was characterised by Cope as possessing both thin and thick scutellæ, in a double layer. It seems, however, that this specimen is one of *S. marshii* with the ventral armor in a crumpled condition, and the thin scutes are the normal ones of the species turned somewhat sideways.

CERATERPETONTIDÆ

This family is represented by a number of Coal Measures forms, of which *Ceraterpeton* of Huxley (1867) is the oldest and in some respects the best known (Watson, 1913, has pointed out that the material may represent two allied genera). The elongate tail is of nectridian type, with characteristic arches; the body is elongate, the limbs fairly well developed. There is some evidence of the presence of five toes in the manus, as suggested by Smith Woodward's figure (1897) of this genus, and confirmatory evidence in *Diceratosaurus* (Jaekel, 1903) and *Diplocaulus* (Douthitt, 1917).

The most remarkable feature, however, is the presence of the peculiar horn-like projections from the tabular region.

Batrachiderpeton, from Newsham, the skull of which has been well described by Watson (1913), is obviously a relative. *Scincosaurus* of Nyřan may belong here, despite some apparent discrepancies, in Fritsch's description. *Diceratosaurus*, discussed below, is the only known American representative, this form having appeared under several names in the existing literature.

The structure of the vertebræ and skull in these amphibians is such that they cannot be regarded as related to the ancestral reptiles. But there are several curious points of similarity in other parts of the skeleton: (1) *Diplocaulus*, as described by Douthitt (1917) possesses a separate coracoid, a structure not known in other Palæozoic Amphibia; (2) this same form has an entepicondylar foramen in the humerus, not found in any other known amphibian; (3) as noted above, it is possible that these forms may have had 5 digits in the hand. The third may be an error, the other two may be due either to parallel development, or, more probably, to the retention of primitive characters lost by most amphibians. But it is not impossible that the group of presumable Embolomeri from which these forms are derived may have been close to the ancestors of the reptiles.

Diplocaulus is obviously derived from the *Ceraterpeton* group; but

not merely its greater emphasis of the peculiar "horns" but also, as Watson has noted, its palatal modifications, seem to render it necessary to place it in a separate family.

Diceratosaurus brevirostris (Cope)

Tuditanus brevirostris Cope, 1874, p. 272; 1875, pp. 393–394, Pl. xxvi, fig. 3; Moodie, 1909*b*, Pl. lxiv; 1916, pp. 88–89.

Ceraterpeton punctolineatum Cope, 1875*a*, p. 16; 1875, p. 372, Pl. xlii, fig. 4.

Diceratosaurus punctolineatus Jaekel, 1903, pp. 109–134, Pls. ii-v; Moodie, 1909*b*, p. 356. Pl. lxv; 1916, pp. 115–119, Pls. xv, xvi, fig. 5, Pl. xiv, fig. 4.

Ceraterpeton tenuicorne Cope, 1875, p. 372, Pl. xlii, fig. 2; 1897, pp. 85–88, Pl. iii, fig. 2.

Eoserpeton tenuicorne Moodie, 1909, pp. 76–79, Fig. 20; 1909*a*, p. 355, Pl. lxiii, fig. 1; 1916, pp. 123–125, Figs. 11, 25; 1875, p. 388, Pl. xxvii, fig. 2; Moodie, 1916, pp. 175–176.

Types.—*T. brevirostris* 6933, *D. punctolineatum* 6866, *E. tenuicorne* 6836.

The American horned forms are all apparently to be included in one species, *Diceratosaurus brevirostris*. Jaekel has given figures of much of the skeleton, showing the upper surface of the skull, palate, vertebræ, shoulder girdle and anterior limb in great part. On the dorsal surface

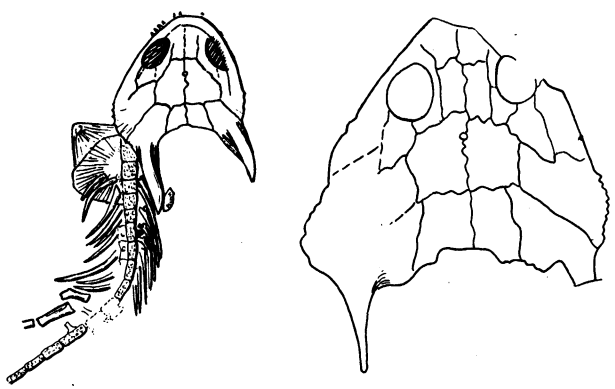

Fig. 3. *Diceratosaurus brevirostris*. Left, type of "*Tuditanus*" *brevirostris*, × 1. Right, type of "*Eoserpeton tenuicorne*," × 1¼.

of the skull, as described by him, the "perisquamosal," occupying the usual position of tabular, squamosal and supratemporal, is a unique feature. The palate has moderate interpterygoid vacuities, intermediate in size between those of *Batrachiderpeton* and *Diplocaulus* but with the pterygoids structurally united with the parasphenoid; the marginal teeth are confined to the anterior end. The sculpturing which Jaekel

shows to have been present on the dorsal surface of the neural arches is a feature not reported in other genera. The dermal shoulder girdle has expanded clavicles and interclavicle and, according to Jaekel, small sculptured cleithra. Five fingers are reported in the manus.

With his description the American material may be easily brought into line in many regards. The type skull of *D. punctolineatus* has been figured by both Cope and Moodie. This shows a portion of the anterior part of the body. The characteristic "horn" is well exhibited, and the sculpturing is identical with that described by Jaekel. To this is attached a portion of the skull, covering approximately the "perisquamosal" region. Clavicle and interclavicle resemble those described by Jaekel. Moodie says there is no cleithrum, but as Cope's figure shows, there is a small element just behind the "horn" which corresponds well with the bone described by Jaekel. To the left of the column is a peculiar element variously called by Moodie coracoid or scapula. It is obviously the same element as that described by Smith Woodward (1897) as a scapula, and would appear to be the element described by Watson (1913) as a cleithrum in *Batrachiderpeton*. The surface exhibited does not show sculpturing. It is possible that it is the internal surface of the left cleithrum, but it is also possible that it is a peculiar scapula.

Jaekel says there are 12 presacrals, a sacral and over 100 caudals. This may be questioned, as the type appears to show 13 without a sacral.

Tuditanus brevirostris was described by Cope from an individual which exhibits a skull and the anterior portion of the body. The specimen, as may be seen from his figure, was covered by matrix at the right posterior corner. Excavation here reveals the fact that a typical "horn" is present, and traces of the other can be made out lying close in to the backbone. The skull bones are represented mainly by impressions of the inner surface of the roof. Such sutures as I can determine are shown in the figure. They agree with those shown by Jaekel in *Diceratosaurus* in general, but there appears to be a suture separating the "perisquamosal" into tabular and squamosal (see below).

The contour of the horns is somewhat different from that given by Jaekel in *Diceratosaurus*. In his figure there is no constriction posteriorly, the curve of the side of the skull passing smoothly into the horn, while there is a marked constriction in this specimen. This apparent difference appears to be due to the varied effects of crushing.

Posterior to the skull, Cope noted that there seemed to be some sort of continuous notochordal sheath enveloping the region of the vertebral column. This appearance, upon examination, seems to be due to the

fact that the vertebræ are preserved with their original articulation, and since the neural arches extend the full length of the spine, they form a continuous mass in which it is difficult to detect breaks. The sculpturing covering the arches can be seen in the specimen. Some of the ribs appear to be distinctly double-headed, despite Jaekel's statement that the apparent tuberculum is not such a structure. A well developed transverse process is visible is some cases. Generally, however, details are not clear in the specimen.

The type skull of *Eoserpeton tenuicorne* has been restudied, and I can find no grounds for a separation from the present species. My interpretation of the elements of the roof differs in a number of respects from that of Moodie, certain of his sutures being, apparently, cracks in the ventral aspect of the then unprepared roofing elements. His attempted subdivision of the "perisquamosal" is certainly incorrect, and I was at first inclined to believe in the unity of this element. However, there is, apparently, a line of demarcation running back on either side from the parietal to the outer side of the "horn," quite obviously separating the tabular from the squamosal (but with no trace of a distinct supratemporal). The sculpture patterns of the two elements have adjacent centers near this suture, and consequently the superficial appearance is that of a single element. Further, it is not improbable that the suture might be obliterated during life, as appears to have been the case in Jaekel's individual.

"*Diceratosaurus*" *robustus* and "*Diceratosaurus*" *lævis* are not members of this genus, but belong to quite another group, as does "*Tuditanus*" *mordax*.

PHYLLOSPONDYLI

Branchiosaurs have not been previously reported in the Linton fauna; the typical members of the group are of Permo-Carboniferous age.[1] Moodie, however, has assigned several forms from the Pennsylvanian of Mazon Creek to this group, and other forms from this locality (including *Amphibamus*) are also branchiosaurs; while Watson (1921) has described a primitive branchiosaur (*Eogyrinus*) from the English Coal Measures.

Two forms (Family Peliontidæ) from the Linton deposit are certainly primitive branchiosaurs, morphologically close to the ancestry of the Permian forms. Two others (Family Colosteidæ) are aberrant in the shape and roofing elements of their skulls, but possess palates suggesting the branchiosaurs and are perhaps to be associated with vertebral

[1]Bulman and Whittard (1926) have recently given excellent redescriptions of many of these forms

material apparently of a primitive branchiosaur type. Still another branchiosaur group is that represented by the specialized *Stegops* and its allies.

PELIONTIDÆ

This family may be retained for the inclusion of primitive branchiosaurs, differing from the more typical forms in the presence of an intertemporal. The palate is primitive, including such features as a movable articulation of the pterygoid with the basipterygoid process, the retention of the ectopterygoid, etc. The postcranial skeleton, as far as known in the forms discussed below, is essentially branchiosaurian in character.

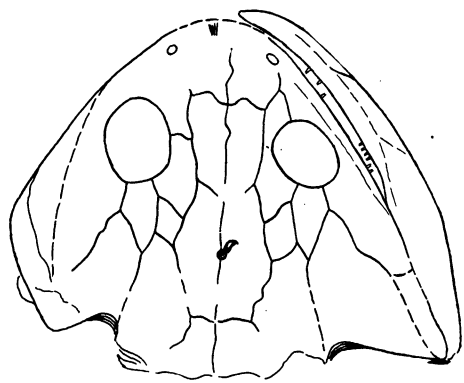

Fig. 4. *Pelion lyelli.* Type of "*Saurerpeton latithorax*," × ¾.

Pelion lyelli Wyman

Raniceps lyelli WYMAN, 1858, p. 160; COPE, 1869, p. 9.

Pelion lyelli WYMAN, in Cope, 1875, pp. 380–391, Pl. XXVI, fig. 1; MOODIE, 1916, pp. 72–74, Fig. 17; Pl. XXIV, fig. 1.

Dendrerpeton obtusum COPE, 1868, p. 213; 1869, pp. 12–13, Fig. 1.

Tuditanus obtusus COPE, 1875, pp. 396–397, Fig. 11; 1885, p. 407.

Erpetosaurus obtusus MOODIE, 1909*b*, Pl. LX, fig. 2; 1916, pp. 98–100.

Sauropleura latithorax COPE, 1897, pp. 86–88, Pl. III, fig. 4.

Saurerpeton latithorax MOODIE, 1909, p. 80, Fig. 23; 1909*a*, pp. 23–24; Pl. IX, 1916, pp. 162–165; Pl. XVII; Figure 35.

TYPES.—*P. lyelli*, 6841, *D. obtusum*, 6928, *S. latithorax*, NM4471.

This form is known mainly from the types of the three species named above. Except for the labyrinthodonts and *Colosteus scutellatus*, the presumably adult specimens are the largest amphibians in the Linton fauna.

The type of *S. latithorax* gives the best idea of the general appearance of the form, well shown in Moodie's plate. The specimen includes a

nearly complete skull seen in dorsal view and considerable postcranial material. The type of *D. obtusum* is a somewhat imperfect skull, originally showing mainly the impression of the inner surface of the roofing bones. This has been prepared to show the palate.

As may be seen from the figures, the two specimens are nearly identical in size and in the arrangement of the cranial elements, orbits, etc. That they are cospecific is also evidenced by the fact that a small bit of sculptured bone originally present on *D. obtusum* corresponded exactly with the sculpturing on the better preserved specimen.

The type of *P. lyelli* is a somewhat smaller individual, of which the ventral aspect of the skull and jaws and anterior portion of the body is shown. As noted below, there can be little doubt that it is identical with the skulls just mentioned, despite the differences in size.

The dorsal surface of the skull is well shown in the *S. latithorax* skull; much of the pattern can be confirmed by the findings on the other specimen. Moodie has attempted an interpretation of the cranial elements; I find myself in disagreement with his results in a number of respects.

In neither specimen are the sutures in the internarial region visible, and in both the posterior end of the table is incomplete.

The skull is broad in general contour, with a height, on a somewhat unreliable estimate, of not more than one-third the width. The orbits are placed far forward. The table of the skull was broad, the otic notches shallow.

In general appearance and in the disposition of many of the elements the cranial roof is similar to that of *Leptorophus* of the Permian. One feature of interest, however, is the presence of an intertemporal. This is roughly diamond-shaped, and has the apparently primitive relations with neighboring bones. The sutures bounding this element may be clearly seen on the left side in Moodie's figure of *S. latithorax*, where the ventral impression of the bone is visible. On the right side, bone is present on the anterior portion of the intertemporal; although the surface is not perfect, it seems certain that the ridges and enclosed pits radiate from the supposed center of this element. The presence of the intertemporal appears to be confirmed on one side of the *T. obtusus* specimen; the sutures can be seen in Moodie's figure (1909*b*).

The type of *D. obtusum* has been developed so as to exhibit the palate. The marginal teeth are small and numerous; almost universally there is a regular alternation of tooth and vacant pit. The maxillary extends back past the posterior boundary of the ectopterygoid. The premaxilla appears to have been excluded from the internal naris by the prevomer; medially, the two premaxillæ appear to extend back-

ward in a narrow process (on which one or two teeth are present on each side) to effect a contact with the anteromedial extremities of the prevomers. Lateral to this process are circular palatal vacuities, surrounded by these two elements and presumably for the accommodation of large mandibular teeth. The prevomer is a bone of complicated shape. The two prevomers have little or no contact with each other; their medial boundaries overlap the parasphenoid ventrally, and a process extends back a short distance over the lateral margin of that element. There is a long contact with the premaxillæ lateral to the palatal vacuity, just internal to which lie a large thenar tooth and pit. There is a short contact with the palatine between the internal naris and the interpterygoid vacuity. A foramen, presumably for a blood vessel, is present internal to the narial margin. The internal nares are rather large and subcircular in outline, and are almost entirely surrounded by the prevomers and palatines, although the maxilla enters into the lateral boundary.

The palatine is a Y-shaped element, the longer anterior arm extending inwardly as a narrow bar between internal naris and interpterygoid vacuity to the vomerine

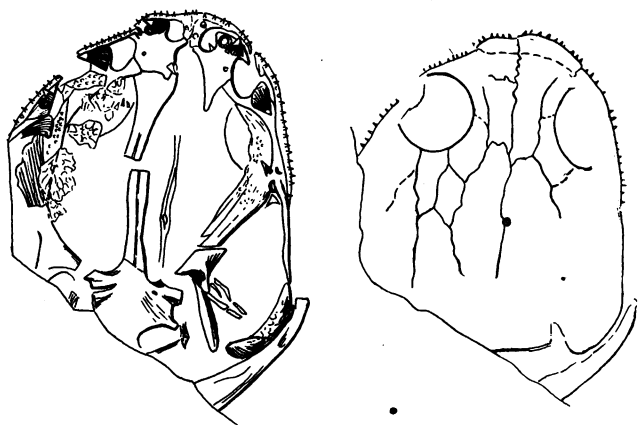

Fig. 5. *Pelion lyelli.* Ventral and dorsal views of the type of "*Dendrerpeton obtusum,*" × ¾.

contact, the lateral arm extending a short distance along the outer side of the internal naris, and bearing a very large tooth. On neither side is there any evidence of a pit accompanying this tooth. The structure of the posterior portion of the element is not altogether certain, partially owing to the fact that on the right side of the skull the lateral roofing elements are broken and buckled under the palate, breaking the bones in this region and obscuring their relations. It appears, however, that the posterior branch is thin and elongate, has long lateral contacts with the maxilla laterally and the pterygoid medially, and is in contact with the ectopterygoid posteriorly. This last element is a small bone, bearing a thenar tooth and pit much smaller than those of the more anterior elements. It has a long contact laterally with the maxilla and medially with the palatine; there is little if any contact with the pterygoid. Posteriorly the jugal appears to send a strong inward extension directed somewhat ventrally for the support of the pterygoid.

The pterygoid has a long palatal ramus, which nearly reaches the prevomer anteriorly, and posteriorly appears to bear a flange (although not a strong one) for the lower jaw. That portion of the ramus which lies external to the palatine and ectopterygoid is thickly studded with small teeth. The pterygoid is freely movable on the braincase, having a strong V-shaped inwardly directed process the posterior edge of which articulates with the anterior edge of the basipterygoid process. The quadrate ramus is short, and, although crushed in the specimen, appears to have been moderately deep. In the angle between the articular process and the quadrate ramus, a paraotic process, imperfectly preserved on either side, extends dorsally, inwardly, and somewhat posteriorly.

The parasphenoid extends forward as a broad bar, slightly ridged in the midline, between the two interpterygoid vacuities. It expands anteriorly, and appears to continue far forward, being covered laterally in ventral view by the prevomers. The basicranium is imperfect posteriorly. There are well-developed thickened basipterygoid processes. The braincase is broad, partially due to crushing.

The postcranial skeleton of "*Saurerpeton*" shows the squamation to have been somewhat "cycloid" in character, as in typical branchiosaurs. The vertebræ are not well preserved. The ribs are moderately short and but slightly curved. The clavicles and interclavicle are broadly ex-

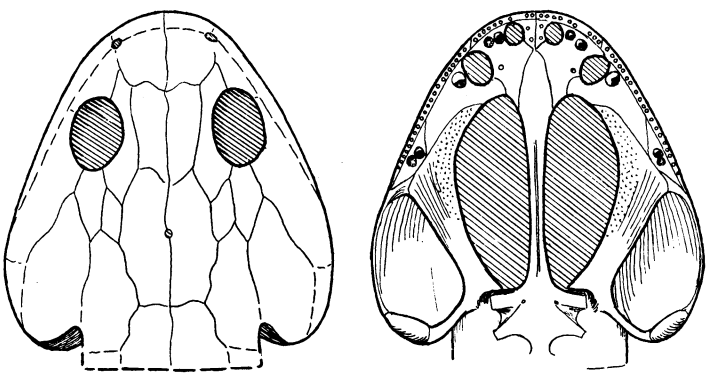

Fig. 6. *Pelion lyelli.* Restoration of skull, dorsal and ventral views, ×¾, the size of presumably adult specimens.

panded on the ventral surface, much as in typical branchiosaurs, and suggesting a bottomliving habit. The interclavicle is ornamented with small pits in the central portion, and light radiating lines towards the margins. Most of the elements of the anterior limbs are present; there appear to have been four toes in the manus.

Pelion lyelli, one of the earliest amphibians described from the Linton deposit, shows (covered with an obscuring film) the ventral surface of a rather small skull, with jaws in place, rather large anterior limbs and part of the vertebral column. Ribs, and dermal scutes, are

absent, presumably due to post mortem separation. The skull is short and wide, and obviously of the general type found in this species and the following one. It is of the size of *P. tabulatus,* and I believed at one time that it represented that form. However, the limbs in that species are much smaller in proportion to the skull than in the *P. lyelli* type, while the more robust limbs of the *Saurerpeton* specimen are of the same proportions.

That this form is a primitive branchiosaur is certain. The dorsal surface of the skull, as noted above, is very similar to that of certain of the Permian forms, except for the presence of the intertemporal, a primitive feature. The postcranial skeleton, as far as preserved, is in agreement with this conclusion.

The palate is in most respects that which might have been expected in an ancestor of the branchiosaurs. The absence of the anterior palatal vacuities in typical branchiosaurs is undoubtedly related to the reduction of the larger internal mandibular teeth normally present in the Embolomeri. The thenar teeth of the present form are essentially on the embolomerous plan; they are reduced or absent in later branchiosaurs. The shape of the palatine is essentially that of this element in the Permian forms. The presence of an ectopterygoid is a very primitive feature, not found in forms of any later stage. This element is here of comparatively small size, with the thenar teeth somewhat reduced. Its loss would convert the lateral region of the palate into the type found in typical members of this group. The pterygoid is of the primitive type noted by Watson in *Eogyrinus.* The articulation of this element is with the anterior margin of the basisphenoid region, much as in the Embolomeri, whereas in later branchiosaurs it attached more posteriorly and dorsally, and was presumably fixed.

The palate of *Pelion* tends strongly to confirm Watson's thesis that the branchiosaurs are descended from primitive labyrinthodonts, or, at least, from forms with a skull structure of the type found in primitive members of that group.

Branchiosauravus tabulatus (Cope)

Tuditanus tabulatus Cope, 1877, p. 577.

Erpetosaurus tabulatus Moodie, 1909, pp. 52–56, Figs. 8, 9; 1909*b*, pp. 347–351, Pl. lix, fig. 2, Pl. lxii, fig. 2; 1916, pp. 100–104, Fig. 22, Pl. xxv, fig. 2.

Tuditanus sculptilis Moodie, 1909, pp. 61–63, Figs. 11, 12; 1909*a*, pp. 23–23; 1916, pp. 105–107, Pl. xviii, fig. 1.

Tuditanus walcotti Moodie, 1909*a*, pp. 16–19, Pl. vi, fig. 1; Pl. vii, fig. 1.

Erpetosaurus walcotti Moodie, 1916, pp. 93–96, Fig. 21.

Erpetosaurus minutus MOODIE, 1909*a*, pp. 21–23, Pl. VIII, fig. 1; 1916, pp. 104–105, Fig. 22, Pl. XX, fig. 1.

TYPES.—*T. tabulatus*, 6837, *T. sculptilis*, WM 12315, *T. walcotti*, NM 4474, *E. minutus*, NM 4545.

This small and primitive branchiosaur is best represented by the type skull and by the greater part of the skeleton in a specimen in Western Reserve University (No. 5446).

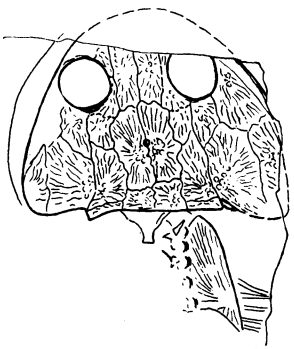

Fig. 7. *Branchiosauravus tabulatus*. Dorsal surface of skull of type, × 1.

The skull is of small size, short and broad (especially the table), and with large orbits situated somewhat anteriorly; the otic notches are shallow, and the general appearance is suggestive of branchiosaur relationships. The sculpturing consists essentially of a system of radiating and somewhat branching ridges, with some pitting near the center of the elements.

The anterior end of the skull is missing; the outlines of the elements preserved are for the most part very similar to those described by Watson in *Eogyrinus* from the English Coal Measures. In the English form the postfrontal is described as an elongated element reaching far back to a broad contact with the supratemporal. In the present specimen, I first believed this to be the case. Reexamination, however, seems to show that the supposed posterior portion of the postfrontal has a separate center from which the ridges of the sculpturing radiate (this is well shown on the right side in Moodie's photograph), and there appears to be considerable evidence for a suture separating this area, the intertemporal, from the small postfrontal.

I have not attempted to develop the palate of this specimen. The impression of the anterior portion of the ventral surface suggests that, in the anterior region, at least, the palate was similar to that of *Pelion*.

The type shows a clavicle, parts of several limb bones, and rather obscure traces of a few vertebræ and ribs. This is admirably supplemented by the Western Reserve specimen, in which most of the skeleton from the shoulder girdle to the pelvic region is preserved, although not all of the details are clear. The ribs are rather short and nearly straight, but longer than in typical branchiosaurs. There are about 20 presacrals shown between the shoulder girdle and the pelvis, and the total of the presacrals was probably about 25. The postcranial skeleton

appears to have been similar to that of *Amphibamus*, from Mazon Creek, which is a rather primitive branchiosaur.

E. sculptilis has for its type a small skull in Walker Museum, from the Cannelton locality. It is quite imperfect, and the sculpturing is poorly preserved, and most of the sutures are doubtful. I cannot confirm Moodie's interpretation of the cranial elements. As far as I can make them out, they appear to agree with those of *P. tabulatus*. The type of *T. walcotti* appears to be an immature specimen of the present species, apparently identical in the sculpturing of the interclavicle, and in the ribs and limb elements as far as preserved. The skull has been crushed, making it appear narrower than was really the case. *E. minutus* appears to be the skull of an immature individual of this type; the sutures are difficult to determine, but are seemingly similar to those of *P. tabulatus*.

It is unfortunate that among the many generic names included in the synonymy of the Linton material, there is none which may be applied to the present form. It is possible that it is generically identical with some of the branchiosaurs from other Pennsylvanian localities, but provisionally it may be called *Branchiosauravus tabulatus*.

COLOSTEIDÆ

The two forms placed in this family are probably to be regarded as branchiosaurs, but branchiosaurs of a peculiar type, and with many primitive characters reminiscent of the labyrinthodonts. Especially characteristic is the anterior position of the orbit and the consequent elongation of the elements posterior to it.

Colosteus scutellatus (Newberry)

Pygopterus scutellatus NEWBERRY, 1856, p. 98.

Colosteus scutellatus COPE, 1869, pp. 22–24; 1873, p. 418; 1874, p. 275; 1875, pp. 407–408, Pl. XXIX, fig. 3, Pl. XXXIII, fig. 1; 1877, p. 578.

Sauropleura scutellata COPE, 1897, p. 88; MOODIE, 1916, pp. 156–157, Pl. XXI, fig. 5.

Rhizodus angustus NEWBERRY, 1856, p. 99; 1868, p. 145; 1873, p. 342, Pl. XXXIX, fig. 6; SMITH WOODWARD, 1891, p. 348.

Colosteus crassiscutatus COPE, 1869, pp. 22–23.

Sauropleura newberryi COPE, 1875, pp. 404–405, Pl. XXXVII, Fig. 2(?), Pl. XLI, fig. 5; MOODIE, 1916, p. 158.

Anisodexis enchodus COPE, 1885, p. 406; 1897, p. 88.

Sauropleura enchodus MOODIE, 1916, p. 162, Pl. XVI, fig. 4.

Leptophractus lineolatus COPE, 1877, p. 576; MOODIE, 1916, pp. 169–170, Pl. XXII, fig. 1.

Sauropleura longidentata MOODIE, 1909, pp. 74–76, Figs. 18, 19; 1916, pp. 160–161, Pl. XVI, figs. 2, 3.

Macrerpeton deani MOODIE, 1916, pp. 184–185, Fig. 40, Pl. XXI, figs. 1, 2.

Diceratosaurus robustus MOODIE, 1909, p. 67, Fig. 15; 1909*b*, p. 355, Pl. LXIII, fig. 2; 1916, pp. 122–123, Fig. 24*b*.

=?*Molgophis macrurus* COPE, 1868, p. 220; 1869, p. 20; 1874, p. 263; 1875, p. 368, Pl. XLIII, fig. 1; MOODIE, 1916, pp. 147–148.

Molgophis brevicostatus COPE, 1875, p. 369, Pl. XLIV, fig. 1; SCHWARZ, 1908, pp. 73–74, Figs. 10, 11; MOODIE, 1909*a*, p. 27; 1916, pp. 148–149, Fig. 32.

Pleuroptyx clavatus COPE, 1875, pp. 370–371, Pl. XLII, fig. 1; Pl. XLIV, fig. 2; 1875*a*, p. 16; MOODIE, 1909*a*, p. 27; 1916, pp. 151–153, Fig. 33.

TYPES.—*Pygopterus scutellatus* 6916, *R. angustus*, unknown, *C. crassiscutatus*, ?6916, *S. newberryi*, 6932, *L. lineolatus*, 6828, *S. longidentata*, 6945, and reverse in British Museum, *S. enchodus*, 2558, *M. deani*, 2934, *D. robustus*, 6929, *M. macrurus*, specimen in Columbia University, *M. brevicostatus*, 6840, *P. clavatus*, 6838.

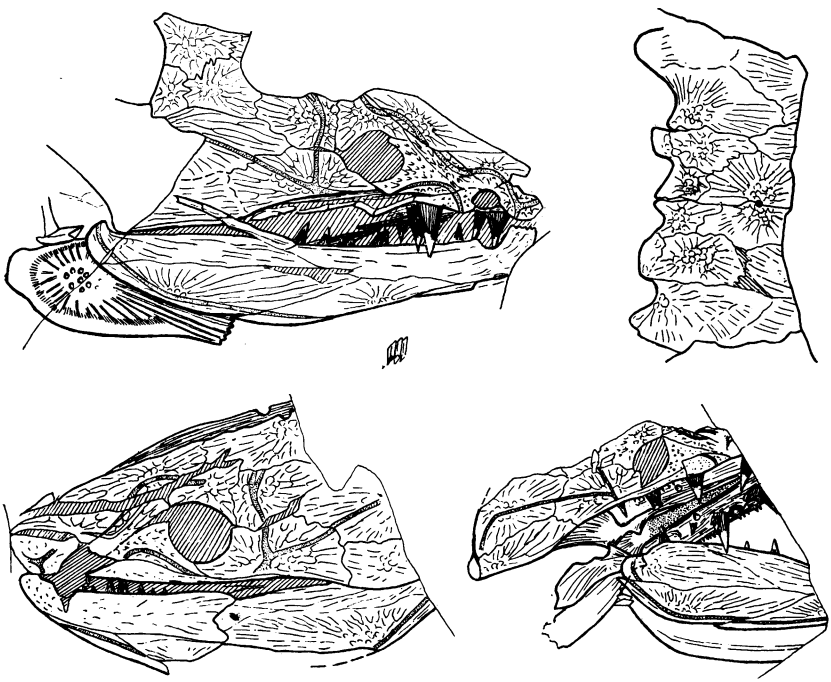

Fig. 8. *Colosteus scutellatus*. Left, right and left sides of type skull, × ¾. Right, above, table of skull of No. 6918, × ½, below, type of "*Sauropleura newberryi*," × ¾.

The species described below is one of the larger Linton forms, rivaling the labyrinthodonts in size and having many labyrinthodont characters; in all probability, however, it is an aberrant although

primitive branchiosaur. It is known from numerous specimens showing the remains of the skull, while several individuals exhibit the dermal armor of the body and the dermal shoulder girdle. In addition, it is probable that considerable postcranial material of the *Molgophis-Pleuroptyx* type is to be associated with this form.

It is certainly related to *Erpetosaurus radiatus* (next to be described) in many features, including the anterior position of the orbits and the consequent peculiar character of the postorbital, but differs from it in the well-defined lateral line canals, the smaller orbits, and in other features mentioned below.

It is necessary to discuss briefly the somewhat checkered history of the type species. It was first described by Newberry as a fish, *Pygopterus scutellatus*. Cope later described an amphibian, *Colosteus crassiscutatus*, and apparently used the type specimen of Newberry's species as his own. Later he recognized the identity, but since the form was obviously amphibian, the new generic name was retained (*Pygopterus* being a good fish genus). In 1897, however, he suggested its relationship to the form known as *Sauropleura digitata*, transferred the present species to that genus, and abandoned *Colosteus*. But in this he was doubly in error, for

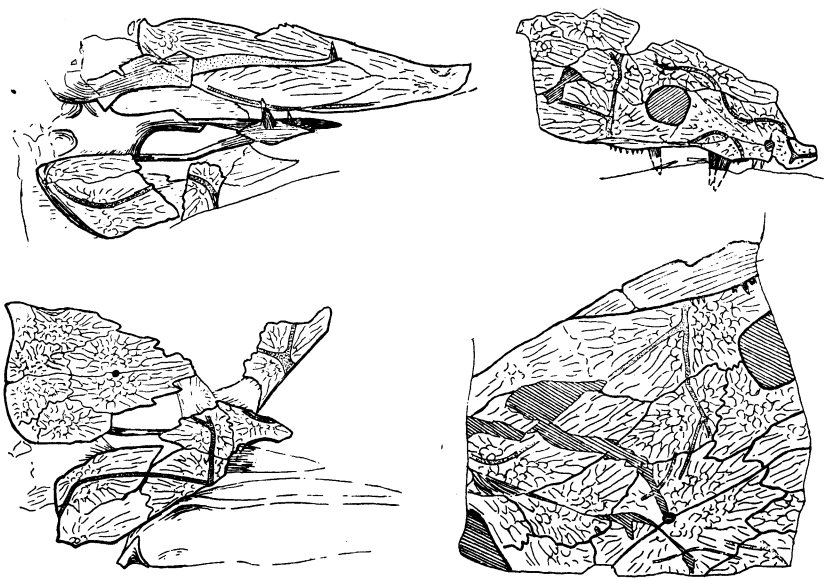

Fig. 9. *Colosteus scutellatus*. Left, No. 6915, × ¾. Right, above, type of "*Sauropleura longidentata*," × ½, below, part of type of "*Macrerpeton deani*," × ⅜.

not only is it improbable that *Colosteus* is related to "*Sauropleura*" *digitata* (discussed later), but also the type of the genus *Sauropleura*, as has been seen, is a nectridian amphibian quite unrelated to either of these forms. *Colosteus scutellatus* is hence the proper name of this animal.

Our knowledge of the skull is derived from a considerable number of specimens, between which practically every detail of the dorsal surface can be determined. These include, among others:

No. 6916, the type of the genus and species, a skull (poorly figured by Cope) showing the external surface of both sides, the lower jaws, the interclavicle and a considerable portion of the dermal armor.

No. 6932, the type of *S. newberryi*, much of the right side of a skull and jaw.

No. 2826, the type of *M. deani*, part of the skull top and jaw of a large specimen.

No. 6945, the type of *S. dentatus*, the right side of a skull and anterior half of a jaw.

No. 6918, the posterior portion of a skull and a large part of the ventral armor, described by Cope in 1877.

No. 6915, a "macerated" skull showing part of the palate as well as roofing elements.

There is considerable variation in size in these specimens, ranging from an estimated skull length of 59 mm. in No. 6932, to about 215 mm. in No. 2826, the last specimen rivaling the contemporary labyrinthodonts in size.

The skull is of the shape found in the more "normal" labyrinthodonts, except that the orbits are situated somewhat in front of the middle of the length. While it is impossible to be sure of the exact proportions, the fact that a majority of the skulls have been crushed sideways suggests that the skull was, in life, comparatively high and narrow. The otic notch is shallow.

The sculpture of the roofing elements consists of a number of pits in the center of each element, from which ridges, bifurcating, radiate toward the periphery. The enclosed valleys deepen centrally, where a pore is present. The pattern is similar to that of the next species. Lateral line canals are evident in a number of places. The lyræ are well developed on the postfrontals, frontals, prefrontals, nasals and premaxillæ. A postorbital canal extends down across the postorbital and jugal. Near the ventral edge of the latter element it meets a canal which extends posteriorly and upward onto the squamosal and then turns down over the posterior edge of the quadratojugal to continue forward along the ventral edge of the lower jaw. The anterior prolongation on the upper jaw of these canals presumably passes forward along the maxilla, curves upward onto the lacrymal, and recurves abruptly downward to the edge of the jaw a short distance behind the nares.

The tabulars are small, not extending nearly as far forward as the dermal supraoccipitals. The table of the skull has a curved posterior border, and there are no tabular horns. The supratemporals are elongate, their anterior ends pushing forward between parietal and postorbital. The last element is very elongate, but narrows

anteriorly, and appears not to reach the orbit, being crowded out by the postfrontal and jugal, a feature undoubtedly related to the forward position of that opening. The frontals are long and narrow. The prefrontals are narrow, but extend forward nearly to the nares lateral to the nasals, which elements have a posterior wedge-shaped extension along the outer sides of the frontals. The premaxillæ carry an anterior prolongation of the supraorbital lateral line canals. The lacrymals were wedged in between maxilla and prefrontals, and I cannot be certain whether they reach the nares. Posteriorly they effect a contact with the elongate jugal below the orbits. The maxillæ are very long, reaching back to about the anterior end of the quadrate-jugals. The marginal teeth are rather thinly spaced.

Curiously enough, I have been unable to obtain a satisfactory view of the palate in any one of the rather numerous specimens. Our knowledge of it is gained mainly from specimens laterally crushed which exhibit portions of the palate between the jaw margins. Such evidence as we have tends to show that it was similar, in most respects, to that of *Erpetosaurus radiatus*.

The details of the braincase are not known. The parasphenoid was toothed for much of its extent. The pterygoids articulated movably with the basisphenoid region; they extended far forward, to about the level of the palatine, with interpterygoid vacuities probably of moderate size. There is some evidence that the palatal ramus bore a series of large teeth—a very unusual circumstance—as well as a series of smaller "denticles." Three large sets of palatal teeth are present, presumably on the ectopterygoid, palatine and prevomer. Those on the ectopterygoid

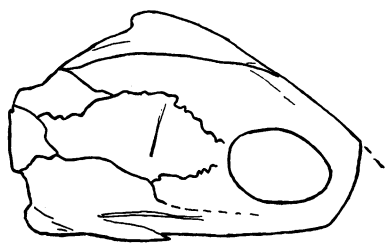

Fig. 10: *Colosteus scutellatus*. Type of "*Diceratosaurus robustus*," × ¾.

are the smallest; the others, in several instances, show both teeth of a pair functioning at the same time. The contacts between the palatine and ectopterygoid, seen in one instance, seem to be comparable to those in *Erpetosaurus*.

The lower jaw is present in several cases but only its outer surface is seen in its entirety. The dentary extends back nearly to the posterior end, in agreement with the posterior reach of the maxillary above. It bears a series of rather stout but thinly spaced marginal teeth, and a

larger internal series, one near the anterior end being especially large and predicting an opening in the prevomerine region of the palate for its reception. There is a large notch on the outer side of the jaw which allows the passage of the prevomerine thenars, which must have been situated very close to the maxilla. Apparently both splenials were present, as well as the angular and a rather large surangular.

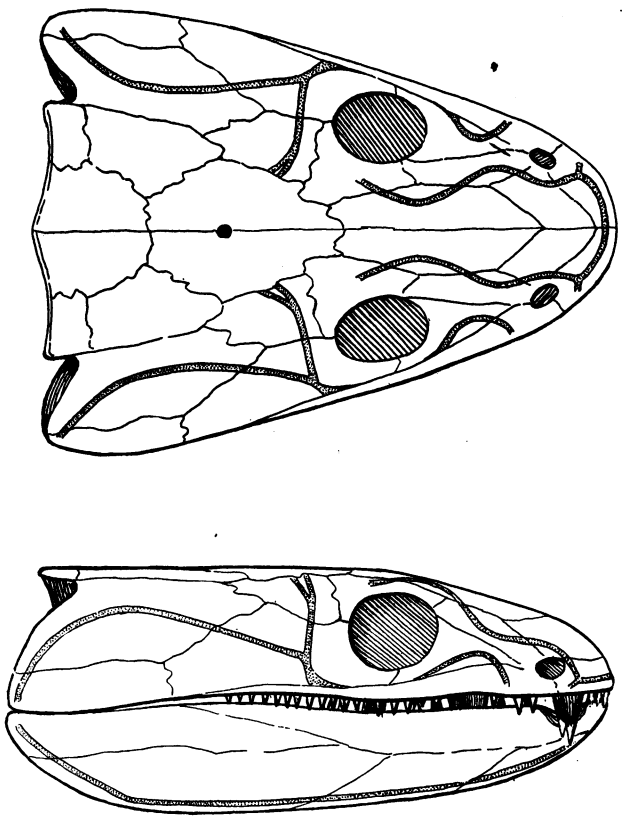

Fig. 11. *Colosteus scutellatus.* Restoration of skull in dorsal and lateral views About 1/6 the size of the largest known skull.

Some postcranial skeletal material is associated not only with the type but also with several other specimens. The clavicles and interclavicle are considerably expanded ventrally, with a more subdued sculpture than that found on the head. The ventral surface of the body was covered by a regularly arranged series of rhombic scutes of the type usually associated with the labyrinthodonts. These have obscured most

of the remains of the axial skeleton. I have found no describable remains of the vertebræ in these specimens. A few anterior ribs were probably nearly straight, the more posterior ones had about the length and curvature found in those of "*Molgophis*" (see below).

With regard to the positon of the forms represented by cranial material and regarded as synonyms, it is at once obvious from the figures that the types of *S. newberryi*, *S. longidentata*, and *M. deani* are the same as the type of the present species. The jaw fragment which is the type of *Anisodexis enchodus* appears to be quite comparable to that of *S. longidentata*. The fragment of jaw which Newberry described as *Rhizodus angustus* would appear from his figure to be of this type as well. "*Leptophractus*" *lineolatus* is a portion of the jaws of a large specimen. *Diceratosaurus robustus* of Moodie is a fragment which shows the characteristic postorbital of this form (it is not a diceratosaurid).

This species grew to a size which would normally warrant us in assigning it to the Labyrinthodontia, and there are many characters suggestive of that group. But the palate, as far as known, appears to differ radically from that of the early members of this order (as discussed under *Erpetosaurus*). Also there are other features such as (for example) the long dentaries, the absence of tabular horns, the small size of the tabulars, the absence of an intertemporal, etc., which suggest a relationship with the branchiosaurs. Except for the characteristic postorbital, the general features of the skull are not dissimilar to those of *Leptorophus*.

The vertebræ and ribs variously known as *Molgophis* and *Pleuroptyx* are perhaps to be assigned to this form. *M. macrurus* was described from a specimen showing a dorsal view of vertebræ and ribs, *M. brevicostatus*, a lateral view; *Pleuroptyx clavatus* from a lateral view showing similar vertebræ, but with expanded ribs.[1] As Cope, Schwarz and Moodie have all suggested, it is highly probable that these forms are the same, the vertebræ being quite similar, and the difference in the ribs is probably a regional one (although I have seen as many as twenty vertebræ without much indication of such a shift). There is considerable difference in size, varying from forms considerably smaller than the types figured by Cope up to one specimen in which the height to the top of the arch is 25 mm. It is not improbable that two or more species may be concealed in the fairly abundant material to which these names are given; the types, however, are all among the larger specimens.

There is a single notochordal centrum, with a ventral flattened ridge, as figured by Schwarz. At about the middle of the height there is a well marked ridge extending

[1]As noted elsewhere, *Molgophis wheatleyi* does not belong here.

horizontally the entire length of the centrum. The neural arch is broad, with a comparatively narrow anterior-posterior attachment to the centrum. There is a large transverse process on the side of the arch somewhat back of the middle; I cannot determine its exact shape as seen in lateral view. There is no neural spine, properly speaking, the dorsal margin of the arch merely rising slightly anterior to the posterior zygapophyses and then curving smoothly downward and forward to the anterior zygaphophyses. The ribs are not elongate, and are comparatively little curved. In some specimens they are simple, in others the "*Pleuroptyx*" type of expansion is visible.

These types are usually placed in the aistopoda, solely on the grounds that they are limbless. In at least one specimen, however (NM4477), there are a number of elements which appear to belong to a rather large limb. There are at present, as far as I can see, no grounds for placing these vertebræ in the aistopods.

On the other hand, the vertebræ resemble considerably those of *Amphibamus*, a small and primitive branchiosaur from Mazon Creek, especially in the construction of the neural arches. This suggests that they pertain to primitive branchiosaurs of some type. The ribs, it is true, are somewhat too long and curved for those of a typical branchiosaur (although *Branchiosauravus tabulatus* approaches their condition), but obviously the primitive branchiosaurs must have passed through a stage comparable to that found here.

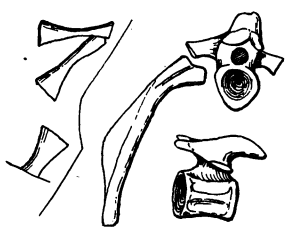

Fig. 12. "*Pleuroptyx*." At right, vertebræ and ribs, from NM 4471. Left, limb bones, from the same specimen, × 1.

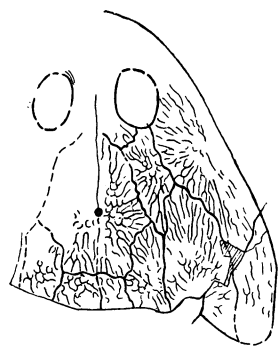

Fig. 13. *Erpetosaurus radiatus*, type, × ½.

This suggests a possible connection with *Colosteus*. In that form we have an animal of comparatively large size represented by numerous specimens showing the skull, but with the vertebral column and ribs practically unknown. In the *Molgophis-Pleuroptyx* group we have vertebræ of a form of similar size, represented by numerous specimens

showing the backbone and ribs, but without any cranial material. Except for the *Molgophis-Pleuroptyx* forms, there is no type in the Linton material whose vertebræ could be associated with the *Colosteus* skulls; except for *Colosteus*, there is no type in the material whose skull could be associated with the *Molgophis* vertebræ. It is highly probable that these specimens represent the postcranial axial skeleton of *Colosteus*.

If these vertebræ are really branchiosaurian, they afford support to the suggestion that the Salientia are derived from the branchiosaur stock. The origin of the transverse process from the side of the arch in the frogs is in agreement with the condition in these vertebræ, although in contrast to Credner's diagrammatic figure of the branchiosaur vertebra.

Erpetosaurus radiatus (Cope)

Tuditanus radiatus Cope, 1874, p. 273; 1875, pp. 394–395, Pl. xxvii, fig. 1, Pl. xxxiv, fig. 3, text fig. 10.

Erpetosaurus radiatus Moodie, 1909*b*, p. 384, Pl. lxii, fig. 1; 1916, pp. 97–98, Fig. 22*f*, Pl. xxv, fig. 1.

Oestocephalus rectidens Cope, 1874, p. 268; 1875, pp. 386–387, Pl. xxvii, fig. 3; Moodie, 1916, p. 145.

E. acutirostris Moodie, 1909*b*, pp. 349–351, Pl. lxi, fig. 1; 1916, pp. 107–109, Pl. xxv, fig. 1, fig. 22*d*.

Diceratosaurus lævis Moodie, 1909, p. 63, Figs. 13, 14; 1916, pp. 120–122, Fig. 24a.

Odonterpeton triangularis Moodie, 1990*a*, p. 19, Pl. vi, fig. 3; 1916, pp. 110–111, Fig. 22*e*.

Tuditanus minimus Moodie, 1909, p. 56, Fig. 10; 1909*a*, p. 23, Pl. viii, Fig. 2; 1916, pp. 91–93.

? = *Colosteus foveata* Cope, 1869, p. 24.

Sauropleura foveata Cope, 1875, p. 406, Pl. xxxvi, fig. 1; Moodie, 1916, p. 161.

Types.—*T. radiatus*, 6922, *O. rectidens*, not identified, *E. acutirostris*. 6924, *D. lævis*, 6923, *O. triangularis*, NM 4465, *T. minimus*, NM 4555, *C. foveata*, 6919.

This form appears to be a close relative of the last, as is suggested by the great similarity in the general shape of the skull and the arrangement of the roofing elements. It differs in its considerably smaller size, its larger and still more anteriorly placed orbits, the almost entire absence of indications of lateral line canals, and the comparatively smaller size and closer crowding of the marginal teeth.

The cranium is known chiefly from the following specimens:

No. 6922, the type of *E. radiatus*, a skull seen in dorsal view. Despite the incomplete nature of the specimen, most of the postorbital sutures can be made out. The orbits appear to be somewhat smaller than in other specimens assigned to this form, an effect probably due to the crushing of the muzzle.

No. 6923, the type of Moodie's *Diceratosaurus lævis*. Developed to show both dorsal and ventral surfaces, both nearly completely. Moodie's interpretation of the sutures is partially incorrect, and the animal is not a diceratosaurid, the "horns" being the normal quadrate region. It was correctly identified by Cope as belonging to *T. radiatus*.

No. 6927, a specimen showing most of the dorsal surface and part of the palate and lower jaw. This was figured by Moodie as a "palate of *Erpetosaurus* sp." but the figure given by him represents a ventral view of the roofing bones of the skull.

No. 6924, the type of *Moodie's E. acutirostris*, showing the dorsal surface of a nearly complete skull. This was identified by Cope as pertaining to the present species. I cannot agree with Moodie's interpretation of the skull elements.

WR, 5440, the anterior portion of a palate and lower jaw.

There is considerable variation in size in these specimens, ranging from an estimated skull length of 82 mm. in the type, down to 39 mm. in No. 6927, while two partial skeletons probably to be assigned here, are apparently larval forms with skulls of much smaller size.

The general appearance of the skull, in dorsal view, presents a number of features of similarity to *Colosteus*, which render it highly probable that the two are closely related. In both, the orbits are situated well forward, although they are considerably

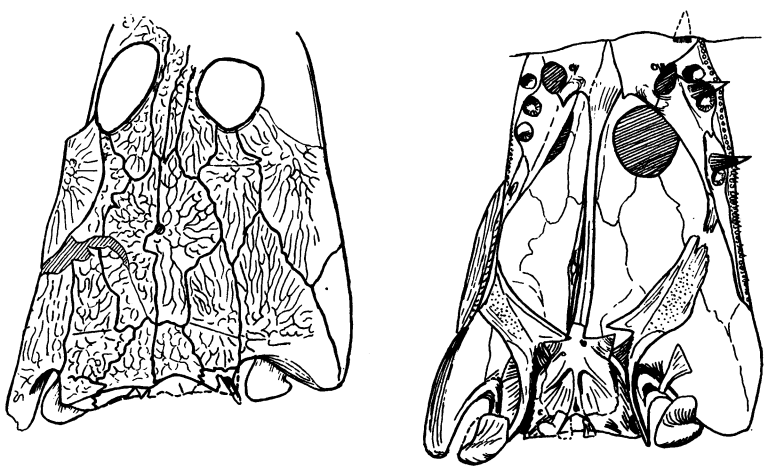

Fig. 14. *Erpetosaurus radiatus*. Type of "*Diceratosaurus lævis*," dorsal and ventral views, × 1.

larger and more anteriorly placed in the present form. In both cases the skulls appear to have been high in proportion to their width. The relations of the elements in the region of the table are similar in the two species. In both the postorbitals are very elongate and nearly entirely excluded from the margin of the orbit, this being apparently due to the forward movement of that opening. The prefrontals, postfrontals and frontals are much narrower in this form than in *Colosteus*, obviously in relation to the increase in size of the orbits, while the more anterior position of these openings has resulted in a shortening of the elements in the region of the muzzle.

Only two specimens give us any information concerning the preorbital region, and while there has been considerable crushing and dislocation, the apparent conditions in the two seem to corroborate each other. The maxilla, narrow posteriorly, increases in depth about opposite the anterior end of the orbit, the jugal meeting the lacrymal here in a rather narrow suture. The lacrymal is a short, broad bone, apparently reaching the external naris anteriorly. The prefrontal is small, the short but broad nasal extending down in front of it to border the lacrymal for some distance.

The sculpturing consists of subcircular pits in the center of the elements, bounded by sharp ridges which laterally bifurcate to enclose deep valleys; each valley contains a small pore at its inner end. There are practically no traces of the lateral line system; in a few instances there are faint indications of a canal on the jugals and postorbitals.

The marginal teeth of both upper and lower jaws are, in contrast with those of *Colosteus*, very small, numerous and closely spaced. The specimen made the type of *Oestocephalus rectidens* by Cope bears teeth appropriate to the present species.

Portions of the palate are shown in three specimens, from which it has been possible to make the reconstruction figured, although there are possibilities of error in several respects. The description given below is mainly from the type of "*D. lævis*." The interpterygoid vacuities are large, the degree of development being about that of the more advanced Rachitomi. In one example much of the space between the pterygoids is seen to have been filled by a large number of small thin bones, bearing small teeth similar to those found on the pterygoids. The cultriform process of the parasphenoid extends far forward, its expanded anterior end lying beneath and between the prevomers. Most of the braincase is preserved, although it is crushed dorso-ventrally, thus accentuating its breadth (which may have been considerable originally). Lying somewhat dorsal to the plane of the bottom of the braincase are large basipterygoid processes with which the pterygoids were movably articulated. Carotid foramina are present, one example showing a well developed groove leading to the opening. A pair of V-shaped depressions, bounded anteriorly and internally by ridges, represent the tubera basisphenoidales. Lateral to the parasphenoid region there are remains of the otic elements, which, however, are crushed and partially obscured by the pterygoids. Near the posterior margin a transverse suture appears to mark the termination of the thin lamina of the parasphenoid which covers much of the ventral surface of the braincase. Posteriorly across this suture runs a ridge which forms a continuation of the medial boundaries of the tubera. This, apparently at about the anterior edge of the basioccipital, bears a deep pit (or foramen?) lying in the mid-line of the skull. The basisphenoid appears to have formed the greater portion of the single occipital condyle, which apparently was deeply concave. On the right side of the type of "*D. lævis*," a small fragment of bone lying on the upper surface of the condyle appears to be part of the exoccipital.

The quadrates are preserved on both sides of this specimen. The non-articular portion appears to have been fairly large and to have extended some distance upward and inward between pterygoid and squamosal. The last element has a well developed flange extending ventrally to meet the quadrate ramus of the pterygoid, which is very deep and appears to have extended ventrally much beyond the ventral surface of the braincase. Just behind the basipterygoid processes it extends far dorsally and inwardly in a pronounced paraotic process. A fan-shaped bone, complete on the left

side of "*D. lævis*" and partially visible on the left, appears to be the disarticulated epipterygoid. At about the division between quadrate and palatal rami the pterygoid is excavated ventrally in a semicircular area. The articular process commences near the lateral margin of the palate and extends inward on the anterior edge of the palatal ramus at a somewhat higher level than the main body of this structure. The palatal ramus (much of which is studded with small teeth) appears to have run forward along the inner side of the ectopterygoid to the posterior end of the palatine.

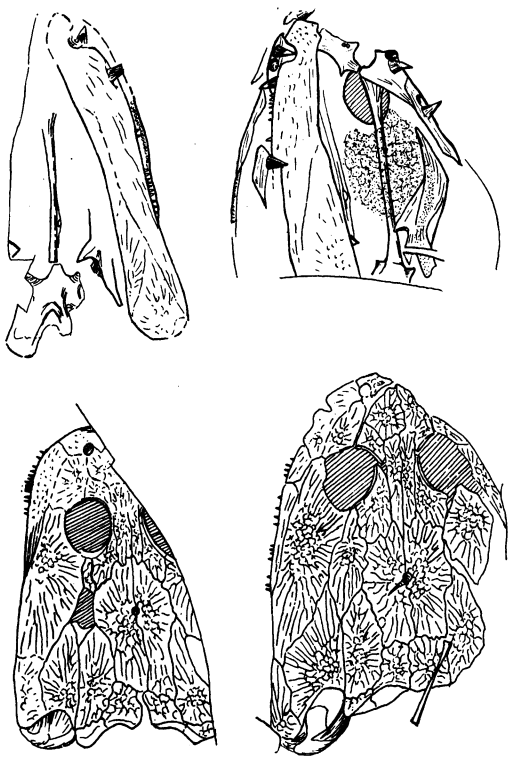

Fig. 15. *Erpetosaurus radiatus.* Above No. 6927, × 1. Below, left, type of "*Erpetosaurus acutirostris,*" × ¾, right WR 5440, × 1.

The ectopterygoid is an elongate element, probably sending a slender extension posteriorly internal to the maxilla; it bears a tooth and pit near its anterior termination. The palatine is considerably larger, and of irregular shape, bearing a tooth and pit near its short external contact with the maxilla. Just anterior to this is a deep pit for the accommodation of a long tooth in the lower jaw; this pit is apparently entirely in the palatine process of the maxilla, the anterior border of the palatine passing inward posterior to it and forming most of the posterior and lateral boundaries of the internal naris. Behind this opening the bone has a short contact with the prevomer, and sends a long process back internal to the ectopterygoid, articulating with the pterygoid.

The prevomer is of irregular shape, articulating with the palatine by a lateral process behind the naris, and forming much of the medial margin of that opening. Its anterior portion is not preserved, but it appears to have borne a large tooth, while a smaller tooth and pit lie internal to the naris. The two prevomers appear not to have had much contact with each other, the parasphenoid lying between them, and also extending dorsal to them as well.

The lower jaw is not well preserved. All the primitive elements of the outer surface appear to have been present, but the dentary was remarkably large and reached far back, while the surangular, beneath its posterior end, extended much farther ventrally at the expense of the angular than was usually the case. A notch near the anterior end, as in *Colosteus*, allowed the passage of the prevomerine thenar. At least one large internal tooth was present in the lower jaw (not far back of the notch) and presumably others were present.

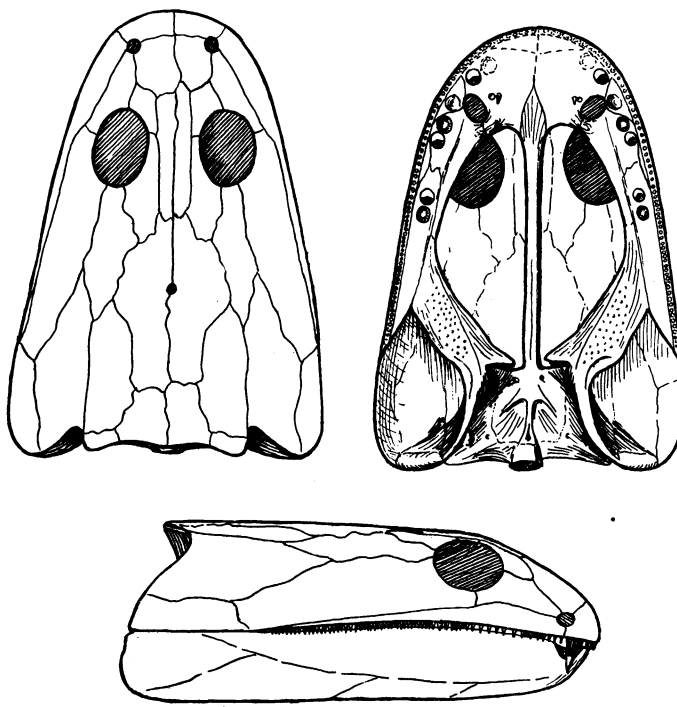

Fig. 16. *Erpetosaurus radiatus.* Restoration of skull, about ⅔ the size of the type.

No postcranial material is associated with any of the specimens used in the above description. However, at least two small skeletons which were made the types of new species by Moodie are probably larval forms of this species. The type of *T. minimus* is a small skull and partial

skeleton, which has been figured by Moodie. Such sutures as can be observed on the skull (mainly in the region of the table) are in agreement with those in the present species. It will be noted that the remains suggest a body of about the proportions of the Permian branchiosaurs, for example, with the length of the trunk about two and one-half times that of the skull, and rather well developed limbs.[1] The dermal shoulder girdle shows a considerable ventral expansion of clavicles and interclavicle.

The type of *Odonterpeton* is a still smaller skull and partial skeleton. Little can be made of the cranial sutures, but the general characters of the skull suggest that it is a larva of *E. radiatus*.

The interclavicle, which is the type of *Colosteus foveata*, is possibly to be assigned to this form. If compared with the interclavicle of *Colosteus*, it will be found to differ from it mainly in the somewhat greater emphasis of the pits and ridges of the sculpture, a difference which is also true, to some extent, as regards the sculpture of the cranial elements.

The problem of the *Molgophis-Pleuroptyx* material has been previously discussed.

Under *Colosteus* the relationships of these two forms have been discussed in general. The palate, not well known in that type, remains for consideration here.

That it possesses a large number of primitive features, in which it resembles the Embolomeri, is obvious without detailed consideration.

The palate is comparable to the palate of the Rachitomi in certain respects. But that *Erpetosaurus* can be considered as a form ancestral to that group is highly improbable. For example, while the interpterygoid vacuities are much larger than those of *Eryops*, the free articulation of the pterygoids with the braincase, ordinarily lost in the Rachitomi, is still preserved in this type.

A comparison is suggested with the palate of a primitive branchiosaur, such as *Pelion* of the same locality. There is a considerable difference in skull proportions which may be responsible for the lack of a long contact between pterygoid and palatine in the present form, *Pelion* here being more primitive. The two are similar in the development of large interpterygoid vacuities but with the retention of freely articulated pterygoids; in the great anterior prolongation of the interpterygoid vacuities, which leaves but a small bar between these openings and the nares; in the consequent narrow articulation of palatine and prevomer; in the Y-shaped palatines; in the general structure of the prevomers

[1]Five metatarsals are present.

(as far as known in the present form); in the broad anterior end of the parasphenoid, which has a large ventral exposure between the prevomers and lies above much of the prevomers in both cases. Many of these resemblances in the anterior portion of the palate are features which are carried over into such a Permian branchiosaur as *Leptorophus*, and suggest that *Colosteus* and *Erpetosaurus* are related to the branchiosaurs, and are to be considered members of that group in a broad sense.

STEGOPIDÆ

This family has been erected primarily for the reception of *Stegops*, a peculiar "horned" type, which, as noted below, is probably a branchiosaur. In it may also be included other forms which resemble *Stegops* in the general construction of the palate, etc., but differ in degree and type of specialization.

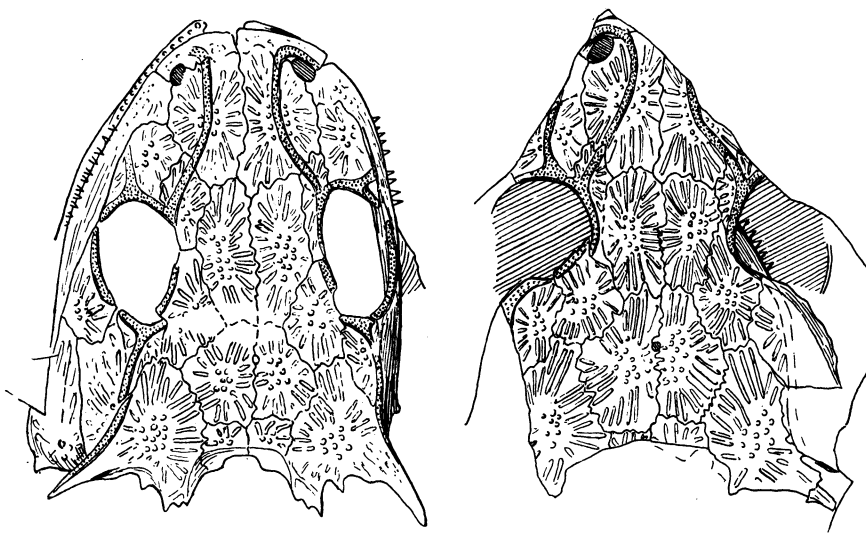

Fig. 17. *Stegops divaricata.* Dorsal views of the type skull and that of "*Erpetosaurus tuberculatus*," × 1.

Stegops divaricata (Cope)

Ceraterpeton divaricatum Cope, 1885, pp. 406–407.

Stegops divaricata Moodie, 1909, p. 79, Figs. 21, 22; 1916, pp. 112–114, Fig. 23, Pl. xxv, fig. 3.

Erpetosaurus tuberculatus Moodie, 1909*b*, pp. 348–349, Pl. lviii; 1916, pp. 109–110, Pl. xxvi, fig. 1.

Types.—*C. divaricatum*, 2559 and WM 12311 (same specimen), *E. tuberculatus*, 6952.

Stegops is known almost entirely from the two skulls which are the types of the species given above. That of *Stegops divaricata* is practically complete, and exhibits a nearly perfect skull roof, together with much of the palate, although the under surface is partially obscured by the jaws which lay along its lateral margins. The type of "*E. tuberculatus*" showed little in its original condition, but upon development reveals the greater part of both surfaces of a similar skull, with some postcranial material.

As seen from above, the skull is comparatively short and broad, with the orbits about in the middle of the length and placed far apart. The most striking feature is the presence of "horns" in the tabular region, while other projections are found more medially. The ornamentation consists of a group of rounded tubercles in the center of each element, and radiating from them a series of nearly straight ridges, the most prominent of which are usually in groups of three or more, running parallel to one another towards the centers of ossification of the adjacent elements.

What appear to be the lateral line canals appear as a set of rounded much raised ridges, which, as far as I have seen them, run forward from the "horns" along the outer side of the tabulars and reach the posterior margin of the orbits on the postorbital. From here they form a ring entirely surrounding the orbits. Anteriorly two ridges extend the system forward, one traversing the prefrontal to pass forward along the length of the nasal and loop backward on the premaxilla anterior to the external naris; the second ridge turns down over the lacrymal and presumably turned forward on the maxilla to join the ridge just described. There are apparently fine pores on the surface of these ridges, while the ventral surface of the bone is also elevated, suggesting the presence of a tubular "canal" beneath the roofing bones.

The elements of the median row of roofing bones are all remarkable for their breadth; especially noticeable is the large size of the nasals, and the shortness of the parietals. The lacrymal is short and is excluded from the naris by a contact between maxilla and nasal. The postfrontal is large, but both the postorbital and jugal are comparatively small, although the former has a long posterior process carrying one of the lateral line ridges. There is but one large element, in which I can detect no suture in the usual position of the tabular and supratemporal.

The sides of the skulls are imperfect in the temporal region, but the squamosal seems to have been rather small, and the quadratojugal comparatively large, with some evidence of spinescence on this last element.

The teeth in both jaws are numerous, and rather stout and bluntly conical.

On the palatal surface, one is immediately struck with the very large size of the interpterygoid vacuities and the large prevomers. A chagreen of small teeth covers practically all the exposed surface of the prevomers, vomers and ectopterygoids and pterygoids and most of the exposed surface of the parasphenoid and the ventral surface of the braincase as well. As in *Erpetosaurus*, there are indications of small ossifications bearing these small teeth which lay in the roof of the mouth in the interpterygoid vacuities. The thenar teeth on the prevomers and pterygoids are in their usual position, but are of very small size (I have not seen those which may have been present on the ectopterygoids). The prevomers, as noted above, are extremely large, have a broad contact anteriorly with the premaxillæ, and form most of the

internal margins of the large internal nares. Medially a process extends back from them some way along the anterior end of the parasphenoid. The palatines are very broad anteriorly, forming the posterior margin of the nares, and have a broad contact with the prevomers medially; posteriorly they appear to send back a long process between the pterygoids and ectopterygoids. These last elements are not well seen, but were apparently small. The palatal ramus of the pterygoid extends well forward, but apparently does not reach the prevomers. More posteriorly, where it turns medially towards the braincase, its surface is very broad. There is a well developed articular process, with an anterior portion turned upward and at a somewhat higher level; this portion of the process extends farther medially than the more posterior portion, which is on the level of the palatal ramus. The quadrate ramus is not well preserved, but appears to have been short; it is covered with small teeth for some distance.

The anterior end of the parasphenoid broadens out and appears to have extended for some distance dorsal to the prevomers, as well as appearing between them for

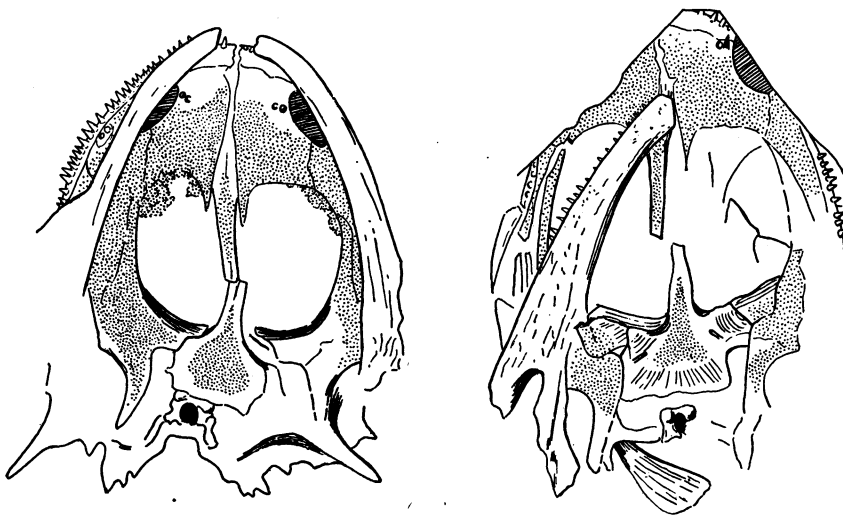

Fig. 18. *Stegops divaricata.* Ventral views of the type skull and that of "*Erpetosaurus tuberculatus,*" × 1.

some distance. The braincase shows few details. It appears to have been very broad, with large basipterygoid processes. The carotid canals and the grooves leading to them are seen in one specimen. Much of the occipital complex is present in both specimens. The condyle appears to have been far advanced towards the double condition; the foramen magnum was small.

The lower jaw was remarkably slender anteriorly. More posteriorly there seems to have been a flange on the ventral surface, the posterior border of which is uncertain; still more posteriorly there is a very long outgrowth from the lower margin. This "spinescence" is in keeping with the similar features of the skull roof.

A small amount of skeletal material is present in the *E. tuberculatus* type. A clavicle preserved is slim, little expanded ventrally, and ornamented with straight lines. The humerus is a fairly large element. There are crumpled masses of rather thin scutes which appear to resemble somewhat those of *Eusauropleura*. There are no traces of vertebræ preserved.

I know of no Pennsylvanian forms (other than those mentioned below as belonging to this family) which are at all closely related, although *Platystegos* of Dawson (1895) may be of this nature. It is obvious, however, that *Stegops* is closely related to several Permian forms, including *Acanthostoma* of the Rothliegende, *Dasyceps* of the English Permian, and *Zatrachys* and *Platyhistrix* of the American Permo-Carboniferous, the skulls of which are best figured by Jaekel (1911), von Huene (1910), Broom (1913) and Williston (1911) respectively.

All these forms differ from *Stegops* in the development of an "internasal vacuity," in the greater development of the "muzzle" as a whole (not so much expanded, however, in *Acanthostoma*) and in the lesser development of the tabular "horns."

The similarities, however, are extremely numerous: the general "spinescence" of the posterior portion of the skull, with the elongation of the tabulars; the similarity in the sculpturing of the roofing elements (that of *Platyhistrix*, the only form available to me, is almost identical with that of *Stegops*); the development of raised ridges for the lateral line (seen, for example, in the preorbital region in *Zatrachys*); the apparent absence of the supratemporal (except perhaps in *Zatrachys*), the tabular extending far forward; the short, broad parietals, frontals and (especially) the nasals; the large prevomers studded with small teeth (*Acanthostoma, Platyhistrix*); the slender lower jaw (*Acanthostoma, Platyhistrix*); the reduced thenar teeth (*Acanthostoma*).

Acanthostoma appears to be intermediate in structure between *Stegops* and the larger Permian forms.

Of these forms, *Zatrachys*, *Dasyceps* and *Platyhistrix* are usually regarded as members of an aberrant family of rachitomous labyrinthodonts; *Acanthostoma* is thought to be an aberrant branchiosaur.

The assignment to the Rachitomi of the three forms named is apparently based upon the assumption that any large Palæozoic amphibian must be a labyrinthodont. There is little association of postcranial skeletal material with these forms, and certainly no sure association with a rachitomous type of column. Aspidosaurid vertebræ have been tentatively associated with *Zatrachys*, but there is no evidence for this, and

these vertebræ are known to belong to a very different type of skull. In *Platyhistrix*, association with elongate neural spines (not at all aspidosaurid in character) is certain. In one instance, Williston (1911) found the greater part of a centrum, which he then stated to be certainly associated with a spine, although crumbling had obscured the actual contact. This centrum is obviously "holospondylous"; it is much too large to be a rachitomous intercentrum. Williston later (1915) figured this spine again but omitted the centrum; he had then associated *Platyhistrix* with the Rachitomi and, presumably, this structure was embarrassing.

In *Acanthostoma* there appear to have been no such elongate neurals. Geinitz and Deichmüller (1882) have figured several vertebral columns associated with skulls. From their figures it would appear that the vertebræ and ribs are unmistakably branchiosaurian in character.

The skulls of these forms show no certain indications of relationship to the Rachitomi. There are many characters reminiscent of the Labyrinthodontia, but these are features which might have been inherited from a common primitive ancestor. On the other hand, the palate, known in *Acanthostoma* and *Stegops*, is quite similar to that of typical branchiosaurs. It is reasonably certain that all these forms are specialized phyllospondyls.

It is quite possible that other large Permian forms, generally considered as Rachitomi, but without positive evidence in the way of postcranial material, may prove to be members of other groups.

"Tuditanus" mordax

T. mordax Cope, 1874, p. 274; 1875, p. 395; Moodie, 1909*b*, Pl. lxiv, fig. 2; 1916, p. 119.

Tuditanus mordax was founded by Cope on a poor specimen exhibiting sculptured elements. He later suggested that it should be assigned to the form now known as *Diceratosaurus*. Moodie has regarded it as a synonym of *D. punctolineatus*, and believed it to represent the dermal shoulder girdle. Unfortunately for this interpretation, the specimen is an imperfect skull, with teeth extending far back along the margins, thus rendering its assignment to *Diceratosaurus* out of the question, although the sculpturing is not dissimilar. The skull is very short and broad, with large orbits. I have been able to make little of it. An excellent specimen, however, is to be described by Professor Watson and Miss Steen. It is a member of this group.

The British Museum collection also contains a single specimen of a form with a palatal construction similar to that found in this group, but

with a very elongate skull. This type, to be described by Professor Watson and Miss Steen, is, as far as I know, entirely new.

LABYRINTHODONTIA

The structure and relationships of the Carboniferous labyrinthodonts[1] were poorly understood until Watson, in 1925, described the skulls of several European genera and attempted a restoration of the postcranial skeleton. He pointed out that these early forms, as far as known, belonged to the Embolomeri, a group which appears to include the ancestors of the later labyrinthodonts and which exhibits many of the characters to be expected in the ancestors of all land vertebrates.

Three members of this group are present at Linton. I have, in addition, discussed briefly below labyrinthodont remains from the Pennsylvanian (proper) of other North American localities.

BAPHETIDÆ

Apparently an early side branch of the labyrinthodont stock, this group is abundant throughout the Carboniferous, and is represented by such forms as *Baphetes*, *Loxomma* and *Orthosaurus*, in all of which are to be found the elongated orbits which are a characteristic feature. This type has not previously been reported from Linton.

Macrerpeton huxleyi (Cope)

Tuditanus huxleyi COPE, 1874, p. 274; 1875, pp. 397–398, Pl. XXXIV, fig. 2.

Macrerpeton huxleyi MOODIE, 1909, pp. 72–73, Fig. 17; 1909*b*, p. 354, Pl. LIX, fig. 1; 1916, pp. 182–184, Pl. XXVI, fig. 2.

Sauropleura pauciradiata COPE, 1874, p. 275; 1875, p. 408, Pl. XL, figs. 1–2; MOODIE, 1916, pp. 158–160, Fig. 34.

Sauropleura newberryi (partim, in errore) COPE, 1875, p. 404, Pl. XXXVII, fig. 3; MOODIE, 1916, p. 158.

Colosteus scutellata (partim, in errore) COPE, 1875, Pl. XXXVI, fig. 2.

Sauropleura scutellata (partim, in errore) MOODIE, 1916, Pl. XIV, fig. 3.

Leptophractus dentatus MOODIE, 1916, p. 169, Fig. 36.

=?*Ichthyacanthus ohioensis* COPE, 1877, pp. 573–574; 1885, p. 9; MOODIE, 1916, pp. 171–172.

TYPES.—*Macrerpeton huxleyi* 6834, *Sauropleura pauciradiata*, 6920, *Leptophractus dentatus*, 6946, *I. ohioensis*, lost.

This baphetid is known from at least two specimens showing the ventral armor and dermal shoulder girdle, several isolated dermal girdle elements, and, more especially, two skulls. Our knowledge of the skull

[1] I use this term in the broad sense, to include Embolomeri and Rachitomi, as well as the Stereospondyli (labyrinthodonts proper).

of this form rests mainly on two specimens. One, a small individual (No. 2933), was incorrectly associated by Cope with the type of *Sauropleura newberryi*. It was figured by Cope, but he was able to make little of it; upon development it proves to consist of a complete skull and jaws. The second is the type of *M. huxleyi*, a partial skull of larger size. This was incorrectly interpreted by Cope and Moodie. The orbit visible in their figures appears to be circular in outline. Upon development,

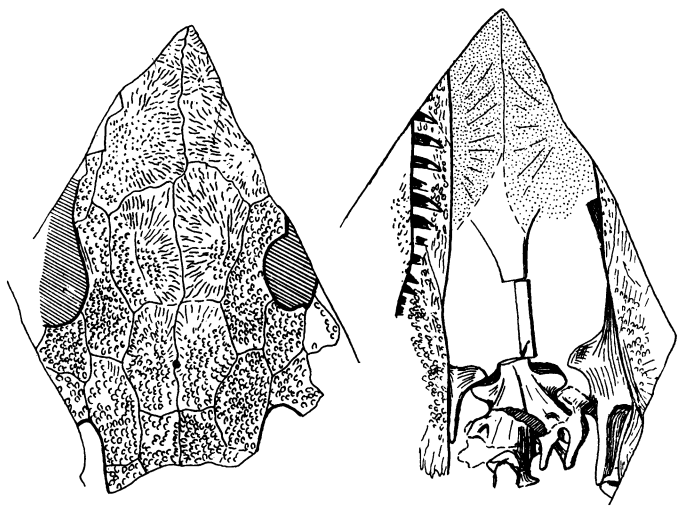

Fig. 19. *Macrerpeton huxleyi*. Dorsal and ventral views of the type specimen, × ½.

however, the other orbit shows a typical loxommid shape. Moodie in 1909 attempted an interpretation of the skull elements which is incorrect, since he has mistaken the lateral for the median side. Much of the palate is shown on the reverse.

The dorsal surface of the skull is best shown in the smaller specimen. The sculpturing consists, in the region of the table, of large pits showing little radial arrangement; elsewhere in the skull a few small pits are to be found in the center of the elements, and from these radiate numerous fine lines. The quadrate region is missing on both sides. The posterior portion of the table is in good condition, showing rather small tabulars and long supratemporals, which run forward to the postfrontals. On both sides of this specimen there is some suggestion that the anterior portion of these elements is to be separated as an intertemporal. This, however, is certainly not the case in the larger specimen, and it is possible that this appearance is merely due to the general broken condition of the median portion of the skull in the orbital region. The dermal-supraoccipitals are moderately long. Only the posterior portions of the parietals are preserved; anterior to this, the dorso-ventral crushing to which

the skull has been subjected has resulted in one of the pterygoids being pushed through the skull roof, with a consequent destruction of elements in this region. Only the anterior portions of the frontals are visible.

The prefrontals are elongate elements bounding the upper anterior margins of the elongate orbits; the nasals are elongate and very broad anteriorly. The premaxillæ are missing. It is possible that internasals may have been present, as in *Orthosaurus* and possibly *Baphetes*, but if so they must have been small, and a premaxillary of rather normal size would have filled this space satisfactorily. A small, T-shaped septomaxilla is visible on the right side in the position of the external naris.

The lacrymal extends the full distance between naris and orbit, and extends some distance back below the "orbit" to a contact with the jugal. This latter element is very elongate. On it are traces of lateral line canals, leading up anteriorly from the maxillary suture and extending onto the postorbital, with the beginning of a branch backward towards the squamosal from a point low down on the jugal. The postorbital is rather small in this specimen, with but a short contact with the prefrontal above. The squamosal appears to extend upward to a line running forward from the lateral margin of the table, somewhat in contrast with *Orthosaurus;* there are traces of a lateral line canal on this element. It and the quadrate-jugal are truncated posteriorly by the margin of the slab, and the quadrate region is absent.

The other specimen, the type of *M. huxleyi*, presents some conspicuous differences from the last one. Both are obviously baphetids, and both have the same type of sculpturing, but in proportions and in sutures they differ in many respects. However, similar very marked differences are found in the various specimens of *Orthosaurus* (Compare Embleton and Atthey's specimen, 1874, and that figured by Watson, 1925), and I have ventured to consider that the differences here are due likewise to a difference in growth stages and individual variations. The most obvious apparent contrast is in the width of the interorbital region. This is real, to some extent; however, it is much exaggerated by the crushing and compression of the smaller specimen. A real difference is to be found in the mutual relations of squamosal, postorbital, postfrontal and supratemporal. In the large specimen, the contact between postorbital and postfrontal is much larger than in the small specimen, and the postorbital-supratemporal contact correspondingly smaller, although the postorbital extends farther posteriorly. The postfrontal extends farther back in the large specimen, and the line of contacts between postfrontal and supratemporal and the elements medial and lateral to them are straighter. These differences are, curiously enough, almost exactly the differences between Watson's restoration and Embleton and Atthey's skull.

The interpretation of the fronto-nasal region in this specimens is perplexing. What appears to be the center of ossification of the frontals

seems clear from the arrangement of the lines of the sculpturing. There is considerable evidence for a suture separating these apparent elements from more anterior ones with perfectly distinct centers which might at first glance be considered as nasals. But if so, these bones extend much farther back than they do in the smaller specimen, meeting the postfrontals. On the left side an apparent suture anteriorly might be considered as separating the nasal from an internasal, while on the opposite

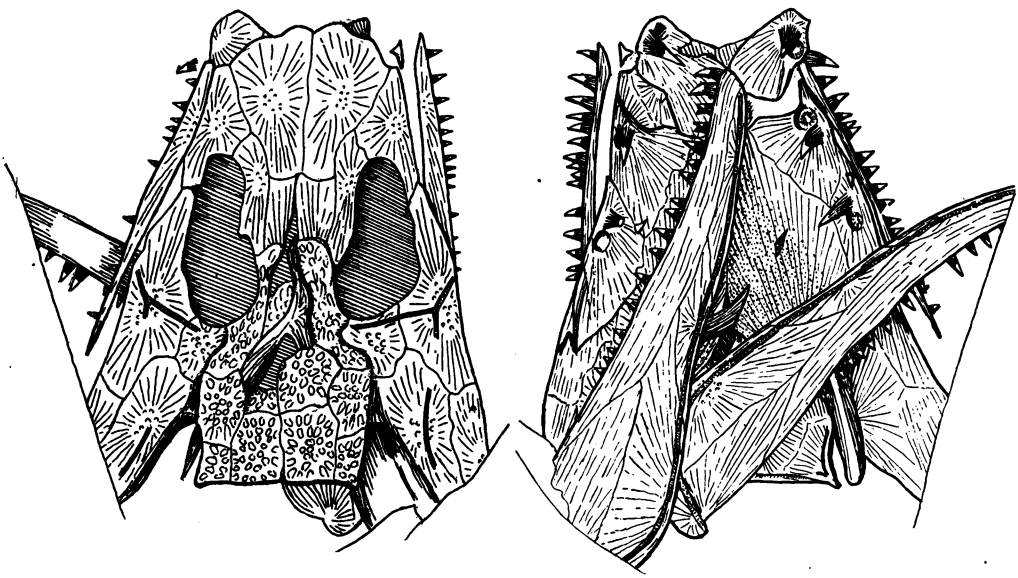

Fig. 20. *Macrerpeton huxleyi.* Dorsal and ventral views of No. 6944, × 1.

side two rather distinct centers are visible here. I have no adequate explanation of this condition to offer, other than to suggest that these seeming elements may be minor secondary centers in the development of the nasal and frontal bones; the internasal in other baphetids may have been a center of the same character.

A portion of the palate is visible in the smaller specimen; the rest is unfortunately obscured by the lower jaws. The prevomers, palatines and ectopterygoids each bear a large thenar tooth and pit in what appears to have been the primitive labyrinthodont arrangement. The prevomers are slightly imperfect anteriorly, so that it is not impossible (although improbable) that a vacuity to receive the large anterior teeth on the dentary was present. Their curved and somewhat elevated postero-lateral margins obviously formed the anterior and medial borders of the internal nares. The palatines are broad bones extending far in on the palate; they have a slim process extending forward laterally external to the nares, the process continuing back as a

ridge curving in medially behind these openings. The ectopterygoid is somewhat narrower, but of considerable length. There is no trace of an extra postectopterygoid element, which Watson has suggested might have been present in *Orthosaurus*. On the left side there appears to be a brace extending inward from the lower margin of the jugal to strengthen the posterior margin of the ectopterygoid and the pterygoid at the edge of the fenestra for the temporal muscles. On this side the pterygoid is disarticulated posteriorly. This last element is very large and broad anteriorly, and, although a median suture between the two sides is seen for only a short distance, the interpterygoid vacuities were obviously very small. The surface of the palatal ramus is thickly studded with fine teeth. Most of the quadrate ramus is seen, somewhat displaced, on the left side. The process articulating with the braincase is not clearly visible in the ventral view, but this may be seen from above in a break through the roof of the skull in the parietal region.

The braincase appears to have been lost before burial, as the under surface of the table, as far as visible, shows no traces of it.

The ventral surface of the larger specimen gives some information which supplements that derived from the smaller. This palate is poorly preserved, much broken and badly pyritized, while the sides of the skull have been doubled under on both sides, rendering only the central portion visible at all. Part of the pterygoids are visible anteriorly, thickly studded with small teeth. Somewhat more posteriorly they appear to have been badly broken, but the region lateral to the braincase is seen on both sides. A comparatively thin articular process extending dorsally and medially may be made out. On the left side there are obscure traces of a very tall paraotic flange passing from the pterygoid dorsally above the braincase.

Anteriorly the cutriform process of the parasphenoid may be seen dorsal to the pterygoids. It is broad in this region (beneath the frontals) and narrows rapidly as it passes backward. Most of the braincase is preserved, although crushed dorsoventrally and not in a very good condition. The basipterygoid process is large and quite thick, facing anteriorly and somewhat ventrally. Behind this there is a lateral expansion into the otic region, the surface rising towards the table of the skull laterally. A depression appears to represent the fenestra ovale. The posterior boundary of the parasphenoid (? or basisphenoid) may be traced across the ventral surface. Curved ridges represent the tubera basisphenoidales. The condyle is of primitive type, a single subcircular cavity, mainly formed by the basioccipital, but with the exoccipitals entering into the dorso-lateral parts. The lower jaw is represented by two nearly complete rami in the small specimen, and fragments of both sides in the larger form. The inner surface is unfortunately not exposed in any case. The outer surface is of the primitive character and needs no comment. A lateral line canal is visible along the entire length of the lower margin.

The teeth are all grooved at their bases, smooth in approximately the upper two-fifths. The basal portions are cylindrical; distally they are somewhat compressed, with some development of a cutting edge anteriorly and posteriorly, much as in Embleton and Atthey's description of "*Loxomma*." However, there is some tendency generally towards a backward curvature of the tips, especially noticeable in the large anterior dentary teeth.

The skull reconstruction, illustrated, is based mainly on the more complete small specimen. It is unfortunate that the posterior portion

of the palate is not better known, as the controlling factor of width in this region is somewhat uncertain.

A specimen (6917) figured by both Cope and Moodie as one of *Sauropleura scutellata* gives some information as to the postcranial structure. (An unnumbered specimen in the National Museum is similar.) That this specimen pertains to *M. huxleyi* is demonstrated by the identity in pattern of the posterior portion of the table of the skull, the only portion of the cranium preserved. The dermal shoulder girdle,

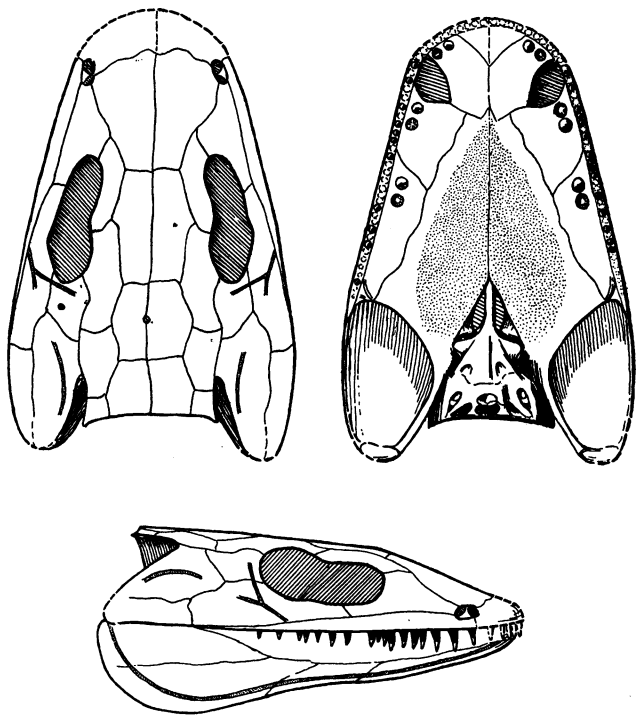

Fig. 21. *Macrerpeton huxleyi.* Restoration of skull.

as may be seen from the figures of Moodie and Cope, includes broad clavicles and interclavicle; there are no cleithra or post-temporals visible. The flattened ventral surface of the dermal elements suggests an early secondary aquatic habitus in this group. The sculpturing consists of radiating lines, which would not be expected from the punctate pattern of the posterior portion of the skull. This radiate arrangement, as may be seen, is identical with that of *Sauropleura pauciradiata,* as figured by Cope and Moodie.

The ventral scales on development are, as usual, rhombic in surface view. The thickened posterior margin, however, has indentations facing posteriorly (usually three in number) in contrast with the smooth margin of the "normal" labyrinthodont scale.

Of the anterior limb elements, the radius and ulna, 10 mm. in length, may be seen in the figures. The humerus is partially obscured by the squamation. It is about 15 mm. long, and of about the proportions of this element in *Trimerorachis*. The vertebræ and ribs are almost completely concealed by the squamation. The ribs were about 30 mm. in length, and, as preserved, had but little curvature. They are spaced approximately 8 mm. apart.

The skull fragment accompanying these remains has a width across the table of about 85 mm. and an estimated skull length of 23 cm.

The figures given above suggest that *Macrerpeton* paralleled secondarily aquatic forms among the Rachitomi and Stereospondyli in many respects. The skull was exceedingly large in proportion to the body. If about 30 presacral vertebræ were present (the primitive number may have been close to this), the trunk would have measured 24 cm. in length in this specimen, only slightly more than the head. The anterior limb, less the manus, was little more than a tenth the length of the skull, making terrestial locomotion out of the question.

Ichthyacanthus ohioensis was described by Cope from a vertebral column, with ribs and hind limb material present. The specimen was never figured, and apparently it never was placed in any permanent collection, for Cope in 1885 stated that the specimen was not then available. Moodie apparently did not see it (since in 1916 he merely quotes Cope's description), and repeated search in the American Museum and Columbia University, where all other early types from Linton are preserved, has failed to uncover it. It is perhaps best to regard the species as a *nomen nudum*, since Cope's usually somewhat hasty and superficial treatment of other Linton specimens prevents placing too much confidence in the details of his descriptions, in the absence of the possibility of verification. However, it is interesting to consider the possibility that this lost specimen was the posterior portion of the skeleton of *Macrerpeton*. His description of the inclined caudal neural and hæmal arches suggests a typical labyrinthodont condition (cf. *Spondylerpeton*, as described below), and his statement that the tarsus was ossified also suggests this group. He states that the dorsal vertebræ average 4.7 mm. in length, making the limbs quite large for the column. It is quite possible, however, that the "ten dorsal vertebræ" mentioned by Cope really consisted of five centra and five intercentra, making the length of a single segment 9.4 mm., or slightly more than in

the specimen described above. The femur measured 25 mm. in length in this specimen as against 15 mm. for the humerus of *Macrerpeton;* the fibula 15 mm. as against 10 mm. for the radius. A posterior rib in this specimen, 29 mm.; and an anterior one of *Macrerpeton* about 30 mm.

There is thus considerable ground for assigning this lost specimen to *Macrerpeton*. The only seemingly valid objection is Cope's mention of rod-like scutellæ; but a disturbed group of rhombic scutes might well have presented such an appearance if covered with a film of matrix.

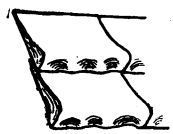

Fig. 22. *Macrerpeton huxleyi*. Ventral scutes presumably to be associated with this form, × 3.

The type of *Leptophractus deani* was described by Moodie as a nearly entire mandible, but is obviously the posterior portion of a dentary. The teeth are apparently similar to those of the present species.

The relationships of *Macrerpeton* with *Baphetes* and *Loxomma* cannot be adequately discussed in the absence of more adequate knowledge of these forms. That it is similar to the *Baphetes* suggested by Watson's figure (1925, Fig. 4*a*) of the palate. *Orthosaurus* is apparently somewhat more specialized.

Orthosaurus sp.

This form, so abundant in the Pennsylvanian of England (cf. Watson, 1925), is not represented in the Linton material available to me. Professor Watson, however, informs me that a single specimen seemingly of this genus is present in the British Museum material.

CRICOTIDÆ

Cricotus of the Permo-Carboniferous (Wichita Group) of Texas appears to be a late survivor of a group of embolomerous amphibians widespread in the Pennsylvanian, and represented at Linton as well as in the European Coal Measures. A characteristic feature is the presence of large fenestræ on the inner surface of the lower jaw.

Leptophractus lancifer (Newberry)

Rhizodus lancifer NEWBERRY, 1856, p. 99; 1873, p. 342, Pl. XXXIX, fig. 9; SMITH WOODWARD, 1891, p. 348.

Rhizodus incurvus NEWBERRY, 1856, p. 99; SMITH WOODWARD, 1891, p. 348.

Leptophractus obsoletus COPE, 1873, pp. 340–341; 1875, pp. 400-401, Pls. XXXVIII, XXXIX, figs. 1-3: MOODIE, 1916, pp. 167–168.

Erpetosuchus kansensis MOODIE, 1911, pp. 489–495; 1910*a*, p. 721.

Eobaphetes kansensis MOODIE, 1916, pp. 189–192, Fig. 42.

? = *Ichthyacanthus playtpus* COPE, 1877, pp. 574–575; 1888, p. 289, Fig. 1; MOODIE, 1915*a*, pp. 34–35; 1915*b*, pp. 509–512, Fig. 2; 1916, pp. 172–174, Pl. XXIII, fig. 1.

TYPES.—*R. lancifer*, *R. incurvus*, unknown; *L. obsoletus*, cotypes[1] 6831 and specimen at Columbia University; *E. kansensis*, NM 6699, *I. platypus*, 7954, Columbia University.

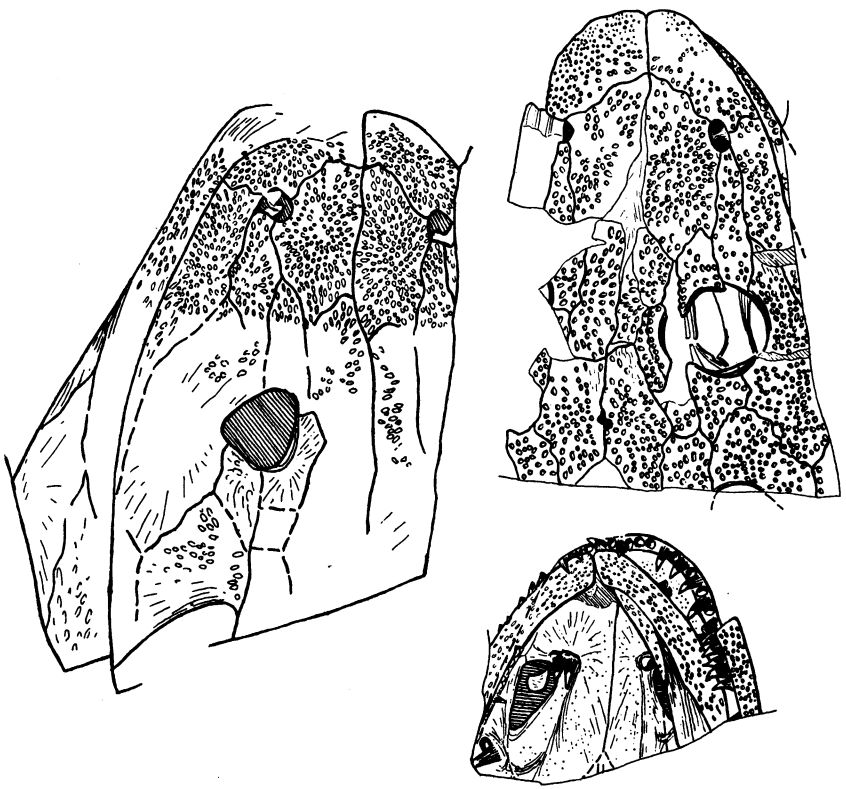

Fig. 23. *Leptophractus lancifer*. Left, No. 2933; right, dorsal surface and part of palate of Nos. 6939–6951, × ½.

Our knowledge of this form is gained mainly from two skulls (both somewhat imperfect) previously assigned to *Macrerpeton*, and never before figured. One (2933) is nearly complete but imperfect posteriorly, with much of the surface ornamentation gone and a number of the sutures doubtful. The negative of the muzzle is present, but the counter-

[1]Moodie states that "455G" (=6830) is the type; but this was not collected until 1874.

part of the posterior part of the skull is missing, and in consequence I have not been able to develop the palate (which is undoubtedly present in the positive block). The second specimen (6939+6951) is slightly smaller in size. Two blocks, upon development, give much of the dorsal surface of the skull; a portion of the palate has been developed in counterpart of the more anterior block.

From these two, taken together, the dorsal surface of the skull can be made out nearly completely. The surface ornamentation consists of deep pits, not very elongate. The orbits are situated slightly posterior to the middle of the skull, and had a somewhat subtriangular shape. Septomaxillæ were present in the nostrils in both specimens. The nasals were large and broad; the frontals considerably smaller. The usual pineal is present, centrally situated between the large parietals. The posterior part of the table of the skull is absent, and I can say nothing of the structure of the tabulars and dermal-supraoccipitals. The supratemporal extends forward to about the level of the pineal; between it and the postfrontal there is interposed an intertemporal, approximately quadrilateral in shape. The post- and prefrontals are of normal construction; the lacrymal is a long element with the primitive reach from orbit to nares, in contrast with such a form as *Eogyrinus*. There is a broad expanse of bone beneath the small orbits, across which the very large jugal extends forward to a broad contact with the lacrymal. The postorbital is roughly triangular in shape, having contacts with the postorbital and intertemporal above, the supratemporal posteriorly, and the jugal and squamosal laterally. The quadrate region is obscure as to detail. The premaxilla is large; its anterior end curves down sharply over the "snout" to the tooth row. The maxilla is broad anteriorly, but narrows rapidly backwards along its contact with the jugal.

The marginal teeth are best seen in the smaller specimen. They are fairly short labyrinthine teeth, somewhat recurved, extraordinarily stout, and set close together. They are suggestive of an intermediate stage between the teeth of more typical labyrinthodonts and the small, closely-set and recurved teeth of *Cricotus*. These teeth are obviously identical with the specimen figured by Cope in 1875 as *Leptophractus obsoletus*, and are of the same nature as the "*Rhizodus*" teeth described by Newberry, which Smith Woodward, in 1891, stated probably were those of labyrinthodonts.

The anterior portion of the palate is partially shown in the smaller specimen. Unfortunately the margins are covered by the lower jaws. The surface is slightly imperfect anteriorly, but it is improbable that a vacuity was present at the anterior end of the palate. (There are no enlarged mandibular teeth on the jaw, which appears to belong to this species.) The prevomers are of very large size, and meet in a large median suture, while medially and anteriorly they bound the large triangular internal nares. This margin of the bone is raised into a ridge, at the anterior end of which is a thenar tooth and pit (both teeth are functioning on the right side). The palatine appears to form much of the external boundary of the naris; close to the posterior border of this opening is an elevation with a tooth and pit.

I cannot be sure of the sutures between the prevomers, palatines and the anterior end of the pterygoids. No specimen shows the posterior portion of the palate; but through the right orbit of the larger specimen part, of the pterygoid and parasphenoid may be seen, indicating that the interpterygoid vacuities were of small size.

The anterior end of the lower jaw is present in the smaller specimen, and nearly the entire left ramus in the larger specimen, but details are obscured. A much better specimen is that from Washington County, Kansas, described by Moodie as *Eobaphetes kansensis*. In the character of the teeth, and in sculpturing, this specimen is obviously identical with the Linton form; and its general proportions are very similar to the ramus present in the larger Linton specimen. The fragment of skull preserved also agrees in dentition and sculpturing with the crania described above. The forms are unquestionably generically identical, and probably specifically as well. The most noticeable features of the jaw (in addition to the dentition and sculpturing) are the great depth posteriorly and the vacuities present on the inner surface. These features are found in two other well-known forms, *Eogyrinus* (Watson, 1912, as "*Pteroplax*") of the Carboniferous of England, and *Cricotus*, of the American "red beds," and the three are apparently closely comparable in most respects. It is much closer to the former because of the presence in both cases of numerous small teeth on the coronoids, absent in *Cricotus*. It is obvious that Moodie has misinterpreted certain of the sutures. They are somewhat obscure, but as far as I can determine them they are similar to those of *Eogyrinus*.

Little postcranial material can be assigned with absolute certainty to this form. It is highly probable, however, that the specimen described by Cope as *Ichthyacanthus platypus* belongs here.[1] This consists of much of the vertebral column of an amphibian of a moderate size, together with part of the pelvis and the hind limbs, one complete. The limb bones are quite similar to those of *Eryops*, the distal end of the femur especially. This specimen obviously belongs to a labyrinthodont (the neural arches are typical), but the film of material covering the specimen has obscured the centra so that it is not perfectly certain that the form is embolomerous rather than rachitomous. But the limbs are much too large in proportion to the vertebræ to belong to *Macrerpeton*, and it is highly probable that the specimen belongs here.

The absence of squamation and ribs, stressed by Cope, is probably due to decomposition and loss before burial. Well developed transverse processes are to be seen on the neural arches. Parts of two ribs were

[1]Moodie's figure shows the essential features.

found with the Kansas specimen, and it is highly probable that large ribs of similar character found in the Linton beds and described by Moodie belong to this form.

Certain large scutes, of the type common in the labyrinthodonts, may belong to this type; but since *Colosteus*, a member of another group which grew to large size, possessed a similar squamation, this cannot be assumed.

The *Ichthyacanthus platypus* specimen would obviously have been associated with a skull of smaller size than those described above; but in the absence of such association, nothing can be said with regard to the bodily proportions in relation to skull size.

The peculiar structure of the lower jaw renders it certain that this form is closely related to *Cricotus* and *Eogyrinus*. From the latter it differs in that the teeth are recurved, shorter and stouter and more closely set; in these features it approaches *Cricotus* more closely. It resembles *Eogyrinus* and differs from *Cricotus* in the presence of numerous small coronoid teeth. The palate is unknown in *Cricotus*. The portion present in *Leptophractus* is quite unlike the anterior region in *Eogyrinus*, as described by Watson (1912, 1925), but it is possible that loss of the anterior portion of the prevomers in his specimen has caused him to misinterpret this region.[1] As far as it is preserved, the *Leptophractus* palate is close to the primitive form from which that of later labyrinthodonts and early reptiles might have been derived.

From *Cricotus* the dorsal surface of the skull differs most obviously in the length of the preorbital region. *Cricotus*, as described by Broom (1913, pp. 664–668, Fig. 1), appears to lack the intertemporal, but this may be due to its inclusion by him in the postorbital. The jugal is extremely large in both cases. The exclusion of the lacrymal from the orbit in *Cricotus* is probably due to the elongation of the region between that structure and the nares. With *Eogyrinus* the comparison is close in most respects, including the similarly shaped orbits, the large jugals and the presence of the intertemporal. In *Eogyrinus*, the lacrymal, however, is excluded from the orbit, and the form is consequently somewhat more specialized than in *Leptophractus*.

These three forms are obviously closely related, *Cricotus* being the last and most specialized, and the other two earlier and more primitive members of the group. All three, as far as the known cranial characters are concerned,[2] might well be placed in a single family, the Cricotidæ.

[1]Cf. the original figure, Atthey, 1876, Pl. IX.

[2]A vertebral column has been associated with *Eogyrinus* by Watson, but as he noted (1925, p. 229) this is perhaps indeterminable.

They obviously form a sterile side branch of the primitive embolomerous stock which ended in *Cricotus* of the American Permo-Carboniferous.

Other American Labyrinthodonts

For the sake of completeness, I have added here a brief discussion of other remains, from the pre-Stephanian deposits of this continent, which appear to be those of labyrinthodonts.

Baphetes planiceps Owen

Baphetes planiceps Owen, 1854, pp. 207–208, Pl. ix; 1855, pp. 9–10; Dawson, 1863, pp. 10–16, Pl. ii (and various other incidental mentions in later papers by Dawson); Moodie, 1916, pp. 168–169, Pl. xxii, fig. 6.

Type.—A specimen in the British Museum.

This, the earliest labyrinthodont described from the American Coal Measures, is represented mainly by a portion of a skull collected by Dawson near Pictou, N. S. As may be seen from the original illustrations,

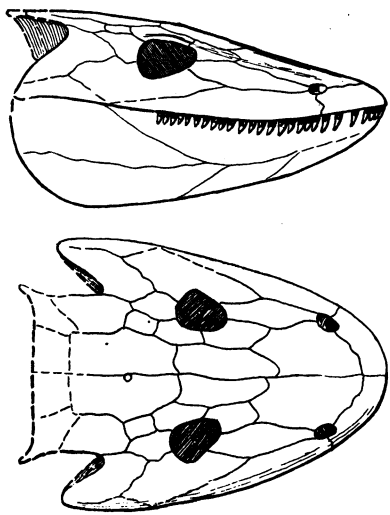

Fig. 24. *Leptophractus lancifer.* Restoration of skull, dorsal and lateral views.

the principal portion preserved is merely the "muzzle," with only the anterior portion of the orbital margins present.[1] The fragment shows that we have to deal with a form related to *Loxomma* and *Orthosaurus* of the English Carboniferous, and to *Macrerpeton*, described above, in all of which the most noticeable peculiarity is the presence of very elongate orbits. The lacrymal is similar to that of *Macrerpeton*, and

[1]Moodie, in his diagnosis of the genus, speaks of the lateral margins below the orbits as "squamosal horns"; but immediately below gives the correct interpretation.

apparently the prefrontals as well. As in that form, the nasals are large and broad. If the lines which appear to bound the nasals anteromedially are sutures and not cracks, internasals were present, although somewhat differently shaped from those of *Orthosaurus*.

A pelvic girdle of embolomerous type from the same locality has been adequately described by Watson (1925, pp. 235–236, Fig. 27). As he points out, however, there is no evidence for assigning the girdle to *Baphetes*.

"**Baphetes**" **minor** Dawson

B. minor DAWSON, 1870, pp. 166–167; MOODIE, 1916, p. 187.

This form is represented only by a fragment of dentary or maxilla, containing a number of blunt labyrinthine teeth. It is obvious that this represents a labyrinthodont of considerable size. But this does not imply a connection with *Baphetes*. The teeth and pitting seem to correspond better, so far as American forms go, with *Leptophractus* of the Linton beds.

Eosaurus acadianus Marsh

E. acadianus MARSH, 1862, pp. 1–16, Pls. I, II; MOODIE, 1916, pp. 187–189, Fig. 41.

This form is known only from two disc-shaped centra described by Marsh from the Joggins, N. S. He regarded them as ichthyosaurian in nature, a reference which the Pennsylvanian date of these deposits renders impossible. It is probable that they pertain to an embolomerous amphibian, the two elements representing the intercentrum and pleurocentrum of a single segment. However, the two bones are too similar in general appearance to render this conclusion any too certain.

Spondylerpeton spinatum Moodie

Spondylerpeton spinatum MOODIE, 1912, pp. 355–357, Pl. VIII, Pl. IX, fig. 1; 1916, pp. 179–180, Fig. 39, Pl. IV, figs. 1, 2.

The type and only known specimen of *Spondylerpeton* is from Mazon Creek, a nodule containing caudal vertebræ of embolomerous type. Moodie's figures of them are somewhat diagrammatic, and I have figured a segment here in somewhat greater detail.

The arch slopes backward, tapering toward the end of the spine. The well-developed zygapophyses are not in contact in the specimen, obviously due to post-mortem dislocation. Arch and intercentrum were firmly united, although the line of suture appears to be visible and placed quite high up. The intercentra and pleurocentra are not dissimilar to those of *Cricotus*. There is a conspicuous longitudinal ridge well down the side, and a smaller ridge above this. The anterior edge of the

pleurocentrum is beveled off at the upper margin, fitting against the lower part of the pedicel of the neural arch. This is formed by the intercentrum, and there is no connection between arch and pleurocentrum. The chevrons (incomplete) are immovably attached to the intercentra, the suture lying well down on the arch itself.

The attachment of the neural arch to the intercentrum is probably the circumstance which led Moodie to call the true intercentra the pleurocentra, for we are accustomed to think of the neural arch as being associated with the latter elements in all amniotes, and in the Rachitomi as well. In the Embolomeri, conditions seem to have been somewhat variable. In *Eogyrinus*, as figured by Watson (1925, Fig. 21), the arch attaches solely to the pleurocentrum even in the proximal caudal region, as well as more anteriorly. In *Cricotus* the arch tends to rest somewhat more on the intercentra in this part of the column.

As an interesting parallel to *Spondylerpeton*, the neural arch in *Amia* becomes associated, in the posterior caudal region, with the "intercentral" element bearing the hæmal arch.

In the Rachitomi the caudal central elements are more primitive than the dorsals, as Williston has pointed out. It is possible that the same was true in the Embolomeri, suggesting that the intercentrum was the major central element in the ancestral amphibians, that the amniote condition is due to a continuous increase of the pleurocentrum at the expense of the centrum in the earlier as well as the later stages of their evolution, and that the later labyrinthodonts, in which a reversal of this process took place, are to be considered as a side branch, the main current of labyrinthodont evolution tending in the reptilian direction.

Fragmentary Remains of Labyrinthodonts

Williston, in 1897, described a labyrinthine tooth from the Pennsylvanian near Louisville, Kansas. He quite naturally referred it to the Labyrinthodontia in the narrower sense of the term (i.e., Stereospondyli), since the history of the group was not at all well worked out at that time, while Moodie (1916, pp. 198–199, Pl. XXI, fig. 6) refers it definitely to *Mastodonsaurus*. It is quite probable that it is the tooth of an embolomerous amphibian; but these deposits are rather late in the Pennsylvanian, and the form might well have been one of the Rachitomi; surely, however, not a stereospondyl.

A phalanx from the Pennsylvanian of Breese, Illinois, has been figured by Moodie (1916, Pl. XXII, fig. 3), and from its size it probably belongs here.

Non-labyrinthodont Remains Ascribed to this Group

Moodie (1916) assigns *Dendrerpeton* and *Platystegos* (Dawson, 1895) of the Joggins erect trees to the labyrinthodonts. I am not personally familiar with this material. However, Dawson figures the vertebræ of *Dendrerpeton;* they are holospondylous and cannot pertain to a member of the present group. In *Platystegos* the vertebræ are described as "biconcave"; it is probable that had they been of embolomerous type (and thus in contrast to those found in the better-known forms from the tree stumps) their peculiar structure would have been noted by Dawson. There is nothing in Dawson's description of the skull (it has not been figured) to show that is a labyrinthodont. Indeed, as far as the description goes, it might well apply to *Stegops*, of the Linton fauna, which is apparently an aberrant branchiosaur.

REPTILIA

It is obvious that the evolution of the reptiles must have been under way at the time when the Linton cannel was being formed, for the deployment of the group was already far advanced when our next glimpse of tetrapods is obtained in the Round Knob Formation, some-

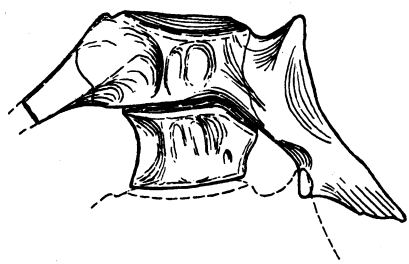

Fig. 25. Vertebra of *Spondylerpeton*, × 1.

what later in the Pennsylvanian series of the same region. Remains of reptiles, however, would not normally be expected to any extent in a pool deposit of this sort. One form from Linton—"*Eosauravus*"—is generally recognized as a reptile, and there are a very few additional specimens which may be placed in this category.

Tuditanus punctulatus Cope

T. punctulatus Cope, 1874, pp. 271–272; 1875, p. 392, Pl. xxxiv, fig. 1; 1896, p. 303; Moodie, 1916, pp. 85–86, Fig. 19.

Isodectes punctulatus Cope, 1897, pp. 88–90, Pl. iii, fig. 3; Williston, 1908, pp. 395–400; Moodie, 1909*a*, pp. 11–16, Pls. iv, v.

[1]*See Dawson's* "Air Breathers," 1863, etc.

Eosauravus copei WILLISTON, 1910, p. 272.
TYPES.—*T. punctulatus*, 6926, *E. copei*, NM, 4435.

The type of *Tuditanus punctulatus* is a specimen showing the anterior part of the body of a small tetrapod, the general appearance of which is well shown in Cope and Moodie's illustrations. The skull is crushed and probably was somewhat broader anteriorly than is suggested by the figures. The postcranial skeleton was apparently poorly ossified, and the impressions are rather faint, making details obscure. There is a long stem on the interclavicle, a rather unusual feature for an amphibian. The carpus appears to have been unossified, and the phalanges are displaced. The vertebræ seem to be holospondylous, and I have observed no intercentra. The ribs are long and curved. The body was long and slender; there are 23 vertebræ preserved without the sacrum having been reached.

A second specimen long referred to this species was described by Cope in 1896 and 1897; it has since been discussed by Williston and Moodie. This is almost unquestionably the posterior part of the body of a primitive reptile, and Williston has made it the type of a new genus and species as *Eosauravus copei* (incidentally this form is, of course, quite unrelated to *Sauravus*, which is a nectridian amphibian).

Williston removed this second specimen from *Tuditanus* on the ground that in the latter the carpus was unossified and ossification was poor, which convinced him that the specimen was amphibian in character. But if we add to this the fact that the type of *Tuditanus* is smaller than that of *Eosauravus*, another explanation appears probable, namely, that the first known specimen is an immature individual, *Eosauravus* an adult, of the same species.

The *Tuditanus* type cannot be assigned to any known member of the Linton amphibian fauna. It certainly is not a lysorophid, or an aistopod, or a nectridian, and it does not appear to be comparable with any of the branchiosaurs. On the other hand, there are no known features which would debar it from consideration as a reptile. The stemmed interclavicle is suggestive of that group and the general form of the body is highly comparable to that of *Eosauravus*. It may be that future finds will prove these two types to be distinct, but for the present it appears to me advisable to consider them as cospecific.

Eusauropleura digitata (Cope)

Sauropleura digitata COPE, 1868, p. 216; 1869, pp. 14–15; 1875, p. 403, Pl. XXXVII, fig. 1; MOODIE, 1916, pp. 157–158.
TYPE.—6865.

The type specimen exhibits the ventral side of the trunk, covered with a well developed armor of scutes, apparently rather thin and oat-shaped; some of the more lateral ones appear to be subcircular in outline. No trace is to be seen of the vertebral column, but, as noted by Cope, the ribs indicate that the centra were not elongate. The ribs are stout and considerably curved, and the heads are dilated, but I cannot be sure that there is a distinct tubercle.

The limbs, however, are the most interesting feature of the specimen. In the hind leg is seen the femur and apparently traces of the tibia and fibula. The front legs are nearly complete, with humerus, radius and

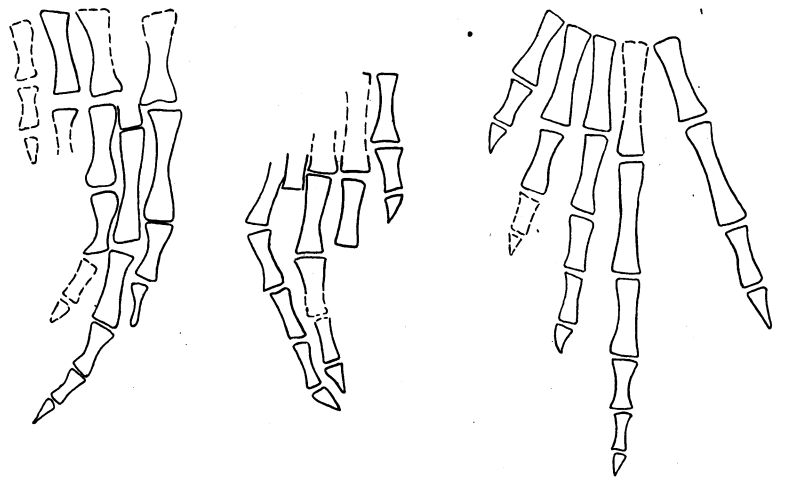

Fig. 26. *Eusauropleura digitata.* Left manus, right manus and restoration. In the first two figures the dotted lines restored after Cope. × 1½.

ulna all present. The carpus appears to have been unossified, but the metacarpals and phalanges are, for the most part, well preserved. Cope notes that the phalangeal formula was 2, 3, 4, 5, 3 (3, 4, 5, 6, 4 in his notation, which included the metacarpals). In the present condition of the specimen, some of the phalanges visible to Cope are no longer visible, but the parts that remain are sufficient to prove the point. The left manus shows traces of four fingers, of which the first two are imperfect; the two outer ones, however, have five and three phalanges, and are obviously the fourth and fifth digits. On the opposite side there are also traces of four toes. The inner one has two phalanges; the next is imperfect; the third has four; the fourth has five. These are obviously digits one to four, and the phalangeal formula was without question 2, 3, 4, 5, 3.

This is of considerable interest. In general the amphibian manus has but four digits, and the presence of five is taken as indicative of reptilian nature. Watson has recently shown that in the small embolomerous labyrinthodont *Diplovertebron* the manus possessed five digits, but even here the formula was only 2, 3, 3, 3, 4. The specimen in all probability pertains to a reptile, or at least to some group intimately associated with the reptilian ancestry.

This form is usually considered as being the type species of *Sauropleura*, but as I have noted previously, the name belongs to a group of urocordylids. The present form is apparently not related to the amphibians usually included with it in the genus *Sauropleura* (*Colosteus*, etc.), and it is unfortunately necessary to adopt a new term, *Eusauropleura*, for this type.

FISH REMAINS PREVIOUSLY DESCRIBED AS THOSE OF AMPHIBIANS

There are several forms from Linton, which are, or have been by early writers, considered as pertaining to the amphibian fauna, but which do not appear to be of this nature. These will be considered briefly.

Cercariomorphis parvisquamis Cope

C. parvisquamis Cope, 1885, p. 405; Moodie, 1915*a*, pp. 463–464; 1916, pp. 137–138, Pl. xxiv, figs. 2, 3, Pl. xxi, figs. 3, 4.

Type.—2560.

This form (of which Moodie has given excellent figures) appears, in the type specimen, to show a disturbed body region and a tail, covered by small scale-like structures which in the best preserved regions are arranged in rather regular rows. A "*Diplodus*" tooth is visible, but it has been presumed to have been accidentally associated. The specimen has been considered an example of a completely scaled amphibian.

It seems, however, upon reexamination, that the specimen is not an amphibian at all. In the Newberry collection from Linton in the American Museum are numerous specimens of pleuracanths, in which, associated with "*Diplodus*" teeth, are considerable portions of the calcified cartilaginous skeleton of these "sharks." These are usually badly crushed, but show in places the superficial areas of calcified plates which covered the surface of the cartilages. In some regions these plates are polygonal; in others, however, they are rhomboidal, with a size and pattern which, upon direct comparison, cannot be distinguished from that of the supposed scales of *Cercariomorphis*. It thus appears that the supposedly accidental association of the *Diplodus* tooth is proper, and that this "scaled amphibian" is a portion of the skeleton of a

pleuracanth shark. The tail-like structure is probably a stripped fin axis (for which analogy can be found in Fritsch's material), but of this I cannot be certain.

Eurythorax sublævis Cope

E. sublævis Cope, 1871*a*, p. 177; 1875, p. 401, Pl. xl, fig. 4; Hussakof, 1916 pp. 127–129; Moodie, 1916, p. 170, Fig. 37.

Described from a single plate, regarded by Cope as an interclavicle of an amphibian, but shown by Hussakof to be a lungfish operculum.

Peplorhina exanthematica Cope

Conchiopsis exanthematicus and *Peplorhina anthracina* Cope, 1873, pp. 342–343; 1875, p. 410, Pl. xxxv, fig. 6, Pl. xlii, Figs. 4–6; Newberry, 1873, pp. 245–246; 1873*b*, pp. 76–77.

Cope in 1873 described *Conchiopsis* (with several species) and *Peplorhina anthracina*, and said that these forms were fish. Newberry stated that most of the *Conchiopsis* remains were those of cœlacanths, but that *C. exanthematicus* was identical with *P. anthracina*, and that the creature was an amphibian. Cope, however, persisted (apparently correctly) in regarding it as a fish. The palatal teeth and dipnoan head plates suggest a relationship to *Conchopoma* of the Permian. At any rate, it does not appear to be an amphibian.

Sauropleura longipes Cope

Sauropleura longipes Cope, 1874, p. 270.

Tuditanus longipes Cope, 1875, pp. 398–399, Pl. xxvi, fig. 2; Moodie, 1916, pp. 89–91, Fig. 20.

Type.—6940.

This species is perhaps the most perplexing of the many rather problematical specimens from Linton. The type is now in poor condition, and it is doubtful if it ever was as clear as shown in Cope's somewhat diagrammatic figure. Little is visible in the lower portion of the specimen (as figured by Cope), which was here roughly excavated. There is no trace of the supposed series of vertebræ seen at the left of the figure. The squamation shown by Cope is clearly visible only at the upper right-hand corner, and here it is certain, by direct comparison, that it consists of cœlacanth scales. The supposed limb bones are remarkably large for such a seemingly frail axial skeleton (incidentally, the right "femur" is about 50 per cent. longer than shown in the figure when excavated); they are remarkably alike in appearance and without any of the usual characters of amphibian limb bones. I believe that this

specimen is a poorly preserved cœlacanth, the fin supports of which are the apparent limbs. The only evidence to the contrary is the fact that there are distinct, although rather faint, impressions of vertebral structures in the central region of the specimen, whereas there is normally little or no ossification of the centra in later members, at least, of the cœlacanth group.

DISCUSSION

In the descriptive portion of this paper, I have attempted to clarify the confused mass of taxonomic terms that obscures the true nature of the Linton tetrapods, and to gain some understanding of the structure and appearance of the forms which inhabited this pool. As suggested in the preface, these have proved to be comparatively few in number. Instead of about sixty forms of tetrapods, there are less than twenty of whose presence we can be certain. There are a number of cases (the "*Molgophis*" group, for example) in which tentative associations of postcranial material may prove incorrect, and in the writer's effort to simplify the picture he may have been over hasty in relegating a few forms founded on poorly preserved or fragmentary material to the synonymy. However, the story is, surely, much clearer than it has been in the past.

Summary of the Fauna

The Linton forms, as I understand them, include the following:

Cocytinus, a small elongate form, probably with tiny limbs and a peculiar skull, obviously a perennibranchiate type, related to *Lysorophus* of the Permian.

Two aistopods, *Ophiderpeton* and *Phlegethontia*, slim, elongate, limbless amphibians, with elongate skulls of peculiar structure.

Two small long-tailed members of the nectridian genus *Sauropleura*, probably somewhat similar to the last in superficial appearance, although possessing small limbs and differing radically in morphology and relationships; and *Ctenerpeton*, a larger relative, with somewhat better-developed limbs.

A small "horned" nectridian, *Diceratosaurus*, with a depressed body, rather small limbs and a very long tail.

Two primitive branchiosaurs, one (*Pelion lyelli*) large, a second (*Branchiosauravus tabulatus*) considerably smaller, both tending towards the short skull type of the group.

Colosteus, one of the larger forms, with a maximum length of the comparatively elongate skull of about eight inches, the eyes placed somewhat anteriorly; resembling the labyrinthodonts in many respects, but apparently an aberrant offshoot of the branchiosaur stock.

Erpetosaurus, a much smaller relative, with larger orbits.

Stegops, a branchiosaur with an extremely peculiar "spinescent" type of skull, already highly specialized but close to the ancestry of certain larger Permian amphi-

bians; and two types related to this form, one ("*Tuditanus*" *mordax*) perhaps somewhat less specialized, a second (unnamed) with an elongate skull.

Three labyrinthodonts, the largest members of the fauna, one (*Macrerpeton*) a loxommid with elongated orbits, already degenerated to a presumably secondary aquatic existence; a related form similar to the European *Orthosaurus;* and *Leptophractus*, belonging to a line which ended with the aquatic *Cricotus* of the Permo-Carboniferous.

A primitive reptile, *Tuditanus*, and a second type, *Eusauropleura*, with a reptilian phalangeal formula, but very incompletely known.

It is unfortunate that our knowledge of the fauna is confined almost exclusively to forms which were mainly or entirely waterliving types. Of the group of animals known at Linton, few probably left the water for any great length of time; some (as the aistopods and *Cocytinus*) obviously must have spent their entire lives in that element. The evolution of the primitive reptiles was certainly under way at this time, and the already divergent groups known at the close of Pennsylvanian times must have been in the course of differentiation. But it is only in exceptional instances that the study of this material from the pools gives us a glimpse of the picture of truly terrestrial conditions.

Relative Abundance

It is of some interest to attempt to determine the relative abundance of the various forms composing this fauna. I have listed below the number of specimens pertaining to each genus in the material available, although the figures are to be regarded as approximates only: *Colosteus* (+ the "*Pleuroptyx*" material) 48, *Sauropleura* 37, *Ophiderpeton* 17, *Ctenerpeton* 14, *Erpetosaurus* 13, *Branchiosauravus* 8, *Leptophractus* 8, *Diceratosaurus* 6, *Cocytinus* 4, *Macrerpeton* 4, *Pelion*, 3, *Phlegethontia* 3, *Stegops* 2, *Eusauropleura* 2, *Tuditanus* 2, "*Tuditanus*" *mordax* 1. The large aberrant branchiosaur *Colosteus* and the elongate nectridians of the *Sauropleura* type are by far the most abundant forms. The large limbless aistopod *Ophiderpeton* is moderately abundant, as are relatives of the two leaders, *Ctenerpeton* (related to *Sauropleura*) and *Erpetosaurus* (a small relative of *Colosteus*).

If the material be arranged by larger groups, the figures are as follows: Phyllospondyli 75, Nectridia 57, Aistopoda 20, Labyrinthodontia 12, Lysorophia 4, Reptilia 4. The branchiosaurs and nectridians taken together constitute more than three-fourths of all specimens, while reptiles and lysorophids are rare. Taken together with our knowledge from other types of evidence, these figures suggest that the branchiosaurs and nectridians were then at the height of their development, while the

embolomeres, aistopods and lysorophids, groups probably of greater antiquity, were on the wane.

It is remarkable that in the Linton material there is no trace of any "microsaur" or "normal" lepospondyl. This is in contrast with the condition at Nyřan, apparently; but it is possible that certain of the supposed lepospondyls from that locality are in reality branchiosaurs.

Amphibian Vertebræ

While the nature of the vertebral column of the labyrinthodonts seems to be well understood through the work of Williston and Watson especially, that of the "holospondylous" types is still a matter for debate. All the smaller Palæozoic amphibians are usually divided into lepospondyls and phyllospondyls; but the former group is obviously a dumping ground for forms and groups which may have little connection with each other. Abel (1919) has recently attempted to redistribute the material into "Gastrocentrophori," etc., but it is obvious that his groups are still more artificial than the older ones.

The comparative degree of specialization of the various types in the Linton fauna, together with the suggestion made above (in the discussion of *Spondylerpeton*) that the main line of vertebral evolution in the early amphibians was the development of the pleurocentrum at the expense of the intercentrum, gives rise to a possible line of speculation as to the nature of the "holospondylous" centra.

Of all the non-labyrinthodonts in the fauna, the branchiosaurs are, on the whole, closest in cranial structure to that group. The chevrons, in certain forms at least, are intercentral in position, suggesting that the centrum is the pleurocentrum and that the branchiosaurs have branched off from an ancestor common to them and the labyrinthodonts in which the pleurocentrum was the dominant element.

The Nectridia are somewhat more specialized than the branchiosaurs. The caudal chevrons are attached to the centra, suggesting that these elements are intercentra, and that the nectridians and labyrinthodonts separated at an earlier time, when the intercentra were still the predominating elements.

In the aistopods and lysorophids, chevrons are unknown. But if the above reasoning be followed, the fact that the origin of these groups is obviously more remote than that of the branchiosaurs or nectridians, suggests strongly that the centra of their vertebræ are homologous with the intercentra.[1]

[1]Cope (1886a) long ago suggested that the centrum of the smaller Palæozoic amphibians was the intercentrum.

This reasoning tends to support, to some extent, the customary union of the smaller non-branchiosaurian amphibians in one group; but such common features as they may possess are few.

The line of thought used above gives, of course, too simple a picture and neglects the many complexities possible in the ontogeny of vertebræ.

Environment of the Linton Amphibians

Case (1917) has discussed the environmental conditions surrounding the Linton fauna, but it may be of interest to review the situation in the light of a better understanding of the amphibian forms concerned. Vegetable material must, of course, have been the ultimate source of food supply, but none of the amphibians was adapted to this sort of diet. Water-living invertebrates were presumably numerous, although their remains are exceedingly rare, owing (as Case suggests) to an intense competition for food in the small remnant of a once large pool in which the Linton fish and amphibians presumably met their death. Fish were abundant, especially several species of small palæoniscids, which appear to have been invertebrate feeders, as were presumably the moderately abundant cœlacanths and the comparatively rare dipnoans.

Upon the invertebrates must have fed not only most of the fish fauna, but the smaller amphibians, such as *Cocytinus*, *Sauropleura* and most of the branchiosaurs, while forms of somewhat larger size (as *Ctenerpeton* and aistopods) may have varied this diet by devouring the smaller palæoniscids.

Among the larger forms, whose diet very probably consisted exclusively of other vertebrates, are to be included the pleuracanths, fresh-water shark-like types of considerable size, whose remains are abundant in the Linton cannel (it is interesting to note that no certain remains of osteolepid crossopterygians have been discovered in this locality).[1] The numerous palæoniscids probably formed the staple food of these larger fish, but it is likely that small amphibians may have played a part in their diet.

Of presumably similar habits were the larger amphibians, *Colosteus*, and the labyrinthodonts, fish-eaters for the most part, but preying also on their smaller amphibian relatives.

Comparison with Other Faunas

If faunas of simliar type be sought abroad, it is obvious that the closest comparison is with the Jarrow (Ireland) Coal Measures fauna,

[1]Newberry has described several species of "*Rhizodus*," all but one based on teeth which are probably those of labyrinthodonts; the remaining one appears to be founded on a lung-fish plate.

described by Huxley (1867). The forms from this locality are comparatively few in number, but with one exception each can be matched by a related form in the Linton assemblage. *Ophiderpeton* is present in both localities; *Dolichosoma* of Jarrow is related to *Phlegethontia* of Linton; *Urocordylus* presumably to *Ctenerpeton; Ceraterpeton* is a somewhat more primitive member of the group to which *Diceratosaurus* belongs; the Embolomeri are present in both localities. Only in the case of *Lepterpeton* is there no known American homologue.

The large and interesting assemblage from Nyřan, Bohemia, described by Fritsch in his "Fauna der Gaskohle," is from a late Pennsylvanian horizon, but is similar in many respects. The aistopods and nectridian forms are in general comparable to those from Linton. More advanced branchiosaurs are present, but it is probable that relatives of the more primitive and specialized Linton forms are present among the many inadequately known genera in Fritsch's material. Embolomeri are still present among the labyrinthodonts, but the Rachitomi, characteristic of the Permian, have already appeared. Primitive reptiles are present in both localities.

The contrast is much greater with the fauna from the Permo-Carboniferous of North America (and that from the Rothliegende). *Lysorophus* of the Clear Fork is the last survivor of the group to which *Cocytinus* belongs. There are no known aistopods. Two nectridian forms survive, the last of their line, *Crossotelos* of the lower portion of the beds representing the *Ctenerpeton* type, and *Diplocaulus* being the final stage of the evolution of the "horned" forms. There are no typical branchiosaurs in the red beds (the microfauna is not well known), but they were abundant in the Permian of Europe. *Platyhystrix* and *Zatrachys* are large-end members of the *Stegops* specialization. Among the labyrinthodonts, *Cricotus*, the last American embolomerous form, barely survived the end of the Pennsylvanian, while Rachitomi are the dominant group. The great abundance of the reptiles, already separable into a number of orders, is the most striking feature of the assemblage. We are in the presence of a new evolutionary stage, in which the Pennsylvanian groups are for the most part extinct or represented by a few relict types. The center of the stage is held by the reptiles and, secondarily, the Rachitomi.

The Linton amphibian fauna is in most respects a mature rather than a primitive amphibian assemblage. It is true that in most of the groups there are still many traces of inheritance of primitive features in the skull structure from a common ancestral type. But even in this

respect, *Cocytinus* was presumably highly specialized, while such forms as *Ophiderpeton*, *Sauropleura*, *Diceratosaurus* and *Stegops* are already very considerably modified. The development of different types of vertebral structures had apparently proceeded at a still more rapid rate, while the divergence in bodily proportions and limb development was extreme. Except for the higher divisions of the Labyrinthodontia, all the Palæozoic amphibian groups were already well established.

To accomplish this radiation into these various amphibian types, and into the earliest reptiles as well, must have required a very considerable period of time. The early stages in amphibian differentiation are to be sought in deposits of Mississippian or late Devonian age.

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