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TETRAPODS OF THE PENNSYLVANIAN NODULES FROM MAZON CREEK, ILLINOIS

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ABSTRACT. A revision of the Pennsylvanian amphibians and reptiles from Mazon Creek, Illinois, reveals that *Amphibamus* (including *Miobatrachus* and *Mazonerpeton*) belongs to the rhachitomous labyrinthodont family Dissorophidae. *Micrerpeton* (including *Eumicrerpeton*) is the larva of a labyrinthodont possibly different from *Amphibamus*. *Sauropleura*, a nectridian, is recorded for the first time from this locality. *Spondylerpeton*, an embolomere, the aistopod *Phlegethontia*, and the captorhinomorph reptile *Cephalerpeton* conclude the list of determinable genera. *"Mazonerpeton" costatum* is probably not a tetrapod and *"Amphibamus" thoracatus* is non-vertebrate.

The close similarity between Paleozoic vertebrate faunas of North America and Europe is attributed to rapid initial dispersal of newly evolved animals and cannot be regarded as evidence of a closer migration route than the Bering Strait land-bridge. Comparison with the diverse present-day amphibian and reptilian faunas of Europe and North America is misleading as these are composed, with few exceptions, of ancient families whose range was formerly far more extensive than at present. On the other hand, none of the faunal evidence opposes some more intimate connection; it is quite indeterminate as to the position of the migration route.

REMAINS of tetrapods are extremely scarce among the numerous fossils from the famous nodule beds at Mazon Creek, near Morris, Illinois, but the perfection of their preservation in comparison to approximately contemporary remains from cannel coals gives them unusual importance. Most authors who have studied these specimens have commented upon the remarkable preservation. Eye pigments, and according to Moodie, body color markings as well, impressions of body outline, and perfect molds of the bones filled with powdery kaolinite are characteristic; impressions of the filled intestines have been recovered in several specimens. The history of the discovery and description of these fossils has been told by Moodie (1912a, and 1916, pp. 12-15); Cope was first to describe amphibian remains from these nodules, but many of the specimens lay undescribed in various museums until Moodie undertook his researches upon the Carboniferous fauna which culminated in the 1916 monograph. Subsequently certain of these specimens have been restudied by D. M. S. Watson (1940; see also Westoll, 1944) and the writer (Gregory, 1948); and Olson (1946) has reviewed the entire vertebrate fauna of this locality, pointing out needed revisions in Moodie's list. A critical re-examination of all known tetrapod specimens from the locality in the light of recent advances in knowledge of the relationships and structure of Paleozoic vertebrates form the basis for the present summary of the fauna.

Dr. David H. Dunkle has most kindly placed a number of undescribed specimens in the Lacoe Collection of the U. S. National Museum at my disposal for study and description. Dr. E. C. Olson has loaned types preserved in the Chicago Natural History Museum. I am indebted to Dr. E. H. Colbert and others of the staff of the American Museum of Natural History for the privilege of making comparisons with material from Linton, Ohio. Professor A. S. Romer of Harvard University has most kindly permitted me to read the manuscript of his paper on the "microsaurs." The illustrations have been prepared by Miss Shirley Glaser, staff artist of the Peabody Museum of Natural History. To all these I wish to express my gratitude for their invaluable assistance.

AGE AND CORRELATIONS

The Mazon Creek nodule beds are in the shales overlying the Morris, or No. 2 Coal which lies at the base of the Carbondale formation, middle Allegheny Series, at the base of the floral zone of *Pecopteris* and *Neuropteris flexuosa*. It is correlated with zone H of Dix in England and zone D of the late Westphalian of Germany. Thus it is somewhat earlier than the comparable faunas from Linton, Ohio and the "Gaskohle" of Nyrany, Bohemia, but may be nearly contemporary with that from the Jarrow Colliery, Kilkenny, Ireland. Further discussion of the correlation may be found in Westoll (1944, pp. 8-10) and Romer (1947, pp. 323-325).

Faunal list.

Class Amphibia
    Subclass Apsidospondyli
        Superorder Labyrinthodontia
            Order Rhachitomi
                Family Dissorhophidae

Amphibamus grandiceps Cope
=*Mazonerpeton longicaudatum* Moodie
=*Miobatrachus romeri* Watson
Family incertae sedis
Micrerpeton caudatum Moodie
=*Eumicrerpeton parvum* Moodie
Order Embolomeri (?)
Family Cricotidae
Spondylerpeton spinatum Moodie[1]

Subclass Lepospondyli
Order Nectridia
Family Urocordylidae
Sauropleura sp.
Lepospondyli ? incertae sedis
Order Aistopoda
Family Dolichosomidae
Phlegethontia mazonensis Gregory
Class Reptilia
Order Captorhina
Family Protothyrididae
Cephalerpeton ventriarmatum Moodie
Indeterminate specimens
Erierpeton branchialis Moodie
Erpetobrachium mazonensis Moodie
"*Mazonerpeton*" *costatum* Moodie

A comparison of the faunal lists for Mazon Creek given by Moodie and Olson with that above reveals a striking diversity of opinions about the relationships of the various forms. Moodie recognized 10 species of tetrapods, which he distributed among 8 genera and 5 families. Olson also recognized 10 species, but arranged them very differently. In the present summary only 6 genera and species are recognized, with 3 of the previously described forms listed provisionally as indeterminate. "*Amphibamus thoracatus*" Moodie is found to consist of plant impressions; *Erierpeton branchialis*, *Erpetobrachium mazonensis* and "*Mazonerpeton*" *costatum* are based upon nondiagnostic fragments. *Mazonerpeton longicaudatum* and *Miobattrachus romeri* are considered synonyms of *Amphibamus grandi-*

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[1] Olson, 1946, p. 302, lists "*Spo. mazonensis* Moodie," an obvious lapsus.

ceps Cope. *Eumicrerpeton parvum* is synonymous with *Micrerpeton caudatum.* Two Orders, the Nectridia and Aistopoda, which have not previously been recognized in this assemblage, have been identified among hitherto undescribed specimens.

To those who would object to this drastic reduction in the nominal list of Coal Measures Amphibia, on the grounds that then as today, favorable habitats must have been teeming with batrachians many of which have left no trace, it must be emphasized that the Mazon Creek locality is a small area whose deposits indicate uniform conditions. The small sample of the fauna which is likely to be preserved at one spot would consist of several individuals of the more common forms, and perhaps a few of the less abundant or less aquatic types. It would fail to capture the closely related species which may have inhabited similar environments to the north, east, south, or west. At this locality, and at one time, the fauna would not be likely to contain more than one species of any genus. Therefore, it is closer to the truth to regard the morphological variation among obviously closely related forms from a single locality as an indication of the variability of the species rather than possible interspecific variation. Several specimens resemble the type of *Amphibamus grandiceps* so closely that their inclusion in that species is not likely to be seriously questioned. Less mature forms, however, depart considerably from the proportions of the typical specimens and frequently are insufficiently preserved to show crucial characters. Such larvae are, after all, indeterminate, and have been lumped as "branchiosaurs." Some of these small forms show features which are at least strongly suggestive of *Amphibamus,* and it is quite possible that *Micrerpeton* really consists of larvae of that species. That adults and larvae of the same species of labyrinthodont may occur together is demonstrated by the abundant series of growth stages of *Archegosaurus* from Lebach, the occurrence of *Melanerpeton* and *Diplovertebron* at Nyrany, and at other localities (some reviewed by Romer, 1939). There is no assurance that all the *Amphibamus* material is not immature; one can only trace its development up to the largest individuals preserved, whose size is comparable to modern small amphibians.

ENVIRONMENTAL IMPLICATIONS

Westoll (1944, p. 107) pointed out the frequent association of nectridians, aistopods, and haplolepid fishes in a facies fauna which he regarded as indicative of stagnant shallow waters full of accumulating plant debris and lacking in oxygen. At that time the Mazon Creek occurrence of haplolepids seemed an exception to this type of association which required special explanation; the subsequent discovery of both aistopods and nectridians at this locality brings the assemblage into line with the hypothesis. However, the Mazon Creek fauna differs from others of this facies in being preserved in shale instead of coal, and in the numerical predominance of labyrinthodonts instead of nectridians. As these shales immediately overlie the coal, they do not necessarily represent a greatly different environment from that under which coal accumulated. The profusion of coal-swamp plants indicates similar floral conditions. A slight increase in the amount of clay brought in by the streams might bring about the transition from coal to shale deposition without rendering the waters uninhabitable to the coal-swamp fauna.

In discussing *Phlegethontia* (1948b, pp. 652-654) I suggested that this aistopod may have been snake-like in habits, and not aquatic. The greater frequency of these animals in the cannel coals than elsewhere does not favor such an hypothesis. The scarcity of reptiles in these assemblages suggests that they were not members of the same association as the labyrinthodonts, nectridians, and fishes, but rather were inhabitants of the shores of the pools (or possibly trees). The relative infrequence of aistopods compared to nectridians at Linton might be explained on the same basis; at Mazon Creek, however, the former order is actually better represented, although no significance should be attached to the difference between such small numbers.

PALEOGEOGRAPHIC IMPLICATIONS OF THE COAL MEASURES FAUNA

Close resemblances between the Pennsylvanian vertebrate fauna of North America and that of Western Europe were first recognized by Cope (1868, p. 215). Advocates of both land bridges and drifting continents have cited them as supporting evidence for their theories (cf. Nopcsa, 1934, pp. 94-95). In comparing the common elements of the Mazon Creek and Linton faunas with those of Jarrow and Nyrany, one encounters an obstacle in the current nomenclature, which maintains generic distinctions between Pennsylvanian amphibians of North America and Europe with the sole exception of

Ophiderpeton. The family relationships between many of these animals is quite apparent, and 11 (50%) of the 22 tetrapod genera now recognized from Linton and Mazon Creek have closely related analogues at either Nyrany or Jarrow.[2] If the Cochleosauridae and Dendrerpetontidae are considered a single family for purposes of comparison, 10 (59 per cent) out of a total of 17 families of tetrapods known from the North American Pennsylvanian also occur in Europe. Two other American families, the Zatrachyidae and Hylonomidae, appear in the early Permian of Europe. Still another Superfamily of labyrinthodonts, the Micropholoidea, is represented in the two faunas by rather divergent families, the Lysipterygiidae and Chenoprosopidae.

These identical families and closely related genera form a larger proportion of the Pennsylvanian fauna than the common elements of the Recent amphibian and reptilian faunas of Europe and America. (According to Romer (1945b, p.436) only 24 per cent of the genera and 48 per cent of the families of these Classes which today inhabit Europe also occur in North America.) Still closer similarities existed between the early Permian faunas. Romer (1945b, pp. 434-440) has argued that the higher degree of similarity between these late Paleozoic vertebrate faunas than between Recent Amphibia and Reptilia of the two regions, points to a more readily traversible connection than that provided by the Cenozoic Bering Strait land bridge. In particular, he emphasized the presence of closely related or identical genera of recently developed and rapidly evolving paleoniscid fishes, rhachitomes, and lepospondyls which imply intimate continental connections. Westoll's (1944, pp. 109-110) analysis of the environmental implications of the aistopod-nectridian-haplolepid assemblage emphasized the importance of suitable habitats along the migration route, and led him to a similar conclusion; he argued that continental drift would bring the fossiliferous areas into closer proximity than a land bridge.

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[2] This summary is based upon the following comparisons:
Spondylerpeton—Diplovertebron;
Leptophractus—Gaudrya; Branchosauravus—Cochleosaurus;
Platyrhinops—Mordex; Sauropleura—?Scinosaurs;
Ctenerpeton—Urocordylus; Ophiderpeton common to both;
Phlegethontia—Dolichosoma; Tuditanus—?Microbrachus or *Hyloplesion.* Family assignments follow Romer, 1947.

It does not follow from the greater faunal similarity that the connection was more direct than the Cenozoic Siberian-Alaskan land bridge. Present-day dissimilarity between amphibians and reptiles of temperate North America and Europe is a direct result of the antiquity of these Families. Most of these animals were well established by Cretaceous times and many are known from the fossil record to have been more widely distributed in the early Cenozoic than at present. It is unnecessary to assume continuous or even frequent intercontinental migrations during the Cenozoic to account for their present distribution. With the exception of *Bufo*, *Hyla*, and *Rana*, all of which have species which are tolerant of cold (Darlington, 1948, p. 17), and which may recently have attained a circumboreal distribution, (*ibid*, p. 21), and possibly the emydid turtles (*ibid*, p. 23) the Recent herpetofaunas of the northern hemisphere are essentially relicts, made up of animals whose ranges have notably contracted since the early Cenozoic. Darlington (1948, p. 17) points out that salamanders form an ideal example of a relict distribution; snakes, lizards, crocodilians and turtles all show evidence of contracting range during the Cenozoic and the north temperate forms are mainly related to those in the adjacent tropical areas. Pelobatine frogs have a relict distribution analagous to salamanders; *Miopelodytes* Taylor (1941) from the Miocene of Nevada shows the former greater range of European genera of this Family. Differential extinction in Europe and America has brought about present-day diversity from a once more wide-spread and homogeneous fauna.

Mammals, on the other hand, were rapidly evolving during the Cenozoic, and new adaptive types repeatedly penetrated, in both directions, from one continent to the other, as Simpson (1947) has shown in great detail. It is worthy of note that the degree of resemblance between the early Eocene mammalian faunas of Eurasia (mainly Europe) and North America is of the same order of magnitude (42 per cent genera and 89 per cent of families in common) as between the Pennsylvanian amphibian-reptile faunas under discussion. In each case a relatively recent origin and rapid expansion of range of the groups in question is indicated, and the resemblances are greater than at subsequent periods after regional differentiation has set in.

A high degree of faunal resemblance between terrestrial and freshwater vertebrates of two areas is not indicative of a long and close connection between the areas involved (a variety of the often refuted age and area hypothesis) but merely indicates that migration between the two areas is possible for the particular organisms under consideration. It is quite probable that animals which are rapidly evolving new adaptations may expand their range, within limits imposed by ecological factors and major geographic barriers, and spread throughout the available areas in negligible time geologically. The absence of competing types undoubtedly favors such rapid spread; and competition is an important limiting factor preventing the extension of range of genera now confined to Europe or North America.

Westoll's argument that the environmental requirements of haplolepid fishes and associated organisms were so specialized that the long migration route across the Bering Strait, or even across a North Atlantic land bridge would be a serious obstacle to dispersal is a more compelling argument for the drift hypothesis than mere faunal similarity. It is granted that close land connection between North America and Western Europe, such as provided by the drift hypothesis, would provide an easy migration route for these creatures; but their presence by no means proves the connection. Although present knowledge of Pennsylvanian paleogeography of Asia, in particular, is extremely scanty, the evidence which is available is not unfavorable to a suitable migration route somewhat along the lines of the present connection. Eardley (1949, pp. 664-670) shows persistent uplift and land areas extending northwestward from the central United States from Mississippian through Permian time, east of the Cordilleran seaways. This land area may at times have been continuous with a land mass which is thought to have lain north of the marine sediments of the Brooks Range in northern Alaska, and extended north of Siberia toward Europe (Eardley, 1948, p. 427, fig. 7). Such a land area would provide a path of migration between northern Asia and central North America. There are possibilities of persistent geosynclinal seas crossing this path, both at the American and European ends. During times when the seas withdrew from these areas, migration would be possible.

Data are even more scanty on the environmental conditions in the far northern parts of this route. Coals of Pennsylvanian age are not found, but most of the sediments of this age thus far known in the north are marine; corals were well developed in the Mississippian seas at 69° North Latitude, and typical Arctocarboniferous plants occur with coal seams in early Mississippian at Cape Lisburne. It therefore does not seem unreasonable that at times during the Pennsylvanian suitable environments prevailed across what is now the Arctic Ocean for the migration of the coal swamp fishes and amphibians.

Land (and freshwater) animals may sometimes furnish evidence that certain geographical relationships are highly improbable, such as Cenozoic connections between Africa and South America; and they may also indicate that at some time a traversable connection was available. But it is doubtful whether the position of any migration route can be deduced from faunal evidence independent of geographical and geological considerations. The faunal similarities between Europe and North America in the Pennsylvanian indicate beyond doubt that a migration route traversable by freshwater fishes, amphibians, and small reptiles was available between these regions at that time, but afford no evidence about its position.

SYSTEMATIC REVISION

CLASS AMPHIBIA

Subclass Apsidospondyli

Superorder Labyrinthodontia

Order Rhachitomi

Family Dissorhophidae

Amphibamus grandiceps Cope

Cope, E. D., 1865, Proc. Acad. Nat. Sci. Philadephia, 1865, 134-137; 1866, Geol. Surv. Ill. vol. 2, 135-141, 1 fig., plate 32, fig. 8.

Moodie, R. L., 1916, Carnegie Inst. Washington Publ. 238, 126-131, figs. 26-28, plate 4, figs. 5, 6; plate 3, fig. 7, plate 14, figs. 1, 2.

Watson, D. M. S., 1940, Trans. Roy. Soc. Edinburgh, 60, 195-198, fig. 1.

Mazonerpeton longicaudatum Moodie, 1912, Kansas Univ. Sci. Bull., 6, 337-341, plate 3, figs. 1, 2; plate 7, fig. 3; plate 10; 1916, 61-63, fig. 14a, plate 3, figs. 5, 6.

Miobatrachus romeri Watson, 1940, Trans. Roy. Soc. Edinburgh, 60, 198-208, figs. 2-10.

Type: Nearly complete skeleton figured by Cope, said by Moodie to have been destroyed. Neotype: Yale Peabody Museum No. 794, nearly complete skeleton in counterpart, figured by Moodie, 1916, figs. 26, 27, p. 4, and by Watson, 1940, fig. 1. A third specimen referred by Moodie (1916, plate 14) cannot now be located.

Type of *Mazonerpeton*: Yale Peabody Museum No. 795, incomplete skeleton in counterpart.

Type of *Miobatrachus*: Chicago Natural History Museum No. 2000, complete skeleton in counterpart.

The first amphibian to be found in the Mazon Creek nodules was described by Cope in 1865 as *Amphibamus grandiceps*. He first referred it to a new and distinct Order of Amphibia, the Xenorachia, which he considered intermediate between the Labyrinthodontia and Caudata; later (1875) he placed it in the Colosteidae along with *Sauropleura* and *Colosteus*. O. P. Hay described a second specimen in 1900 and pointed out that the ribs were long and slender, unlike those of typical branchiosaurs; he suggested relationship to *Hylonomus*. Moodie (1916, p. 127) concurred in this opinion, referring *Amphibamus* to the Microsauria, principally upon the character of the ribs. He erected a separate family for it and placed the small reptile *Cephalerpeton* in the same family. Romer (1930, p. 93) considered *Amphibamus* a branchiosaur and Watson (1940) referred it and the closely similar *Miobatrachus* to the Phyllospondyli but placed them in a separate family from the branchiosaurs. Romer (1945a, p. 591) followed Watson's suggestion of relationship to the frogs and placed these genera in the Salientia as a primitive Order Eoanura. Case (1946) separated *Amphibamus* and *Miobatrachus* in his classification, referring the former to the Microsauria on the basis of Moodie's description of the vertebrae and ribs, and followed Watson in referring the latter to the Phyllospondyli. The present study had its inception as an effort to resolve this problem by a restudy of the specimens.

It would be superfluous to redescribe the more perfect specimens of *Amphibamus* in detail after Watson's thorough account of its morphology. Discovery of both postparietals and horned tabulars (or supratemporals) in all extant specimens of the animal requires a revision of his reconstruction of the skull table, and some reconsideration of the relationships of the genus. Evidence for this will be set forth, and the diagnostic characters of the several specimens will be reviewed to determine their relationship to one another and to the now lost type figured by Cope (1866, plate 32, fig. 8).

Characteristic features of the genus shown in the type figure include the large skull with truncate muzzle, wide internarial and interorbital regions, large orbits, short postorbital region, large otic notch, short presacral vertebral column, caudal chevrons, well developed limbs, and pentadactyl pes. All these features are equally characteristic of the three other well preserved specimens of *Amphibamus*, namely, Y.P.M. 794 (neotype), C.N.H.M. 2000 (type of *Miobatrachus*), and the specimen figures by Moodie (1916, plate 14, figs. 1, 2), now lost. They are sufficient to establish the identification of neotype with the type beyond reasonable doubt.

Figure 1 shows a revised reconstruction of the skull roof of Y.P.M. 794. Latex impressions from this specimen clearly show both postparietal and a horned tabular at the back of the skull table which Watson did not figure. Aside from these details the reconstructions agree in essentials. Additional preparation has developed scapulae and portions of the pelvis which are closely similar to those figured for "*Miobatrachus*," but

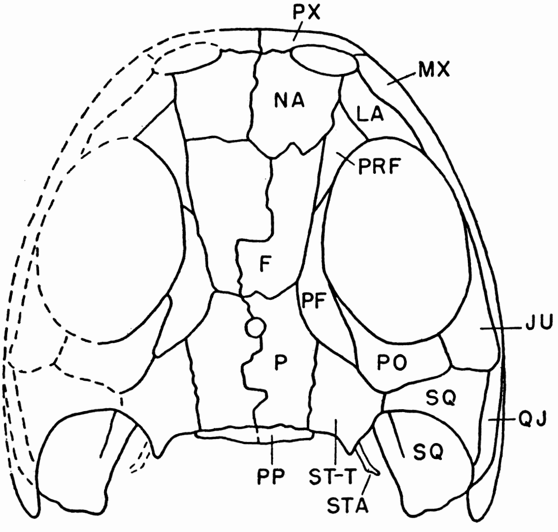

Fig. 1. *Amphibamus grandiceps* Cope. Reconstruction of skull roof of Y.P.M. No. 794, x 4. F frontal, JU jugal, LA lacrimal, MX maxillary, NA nasal, P parietal, PF postfrontal, PO postorbital, PP postparietal, PRF prefrontal, PX premaxillary, Q quadrate, QJ quadratojugal, STA stapes, ST-T supratemporal-tabular.

slightly more fully ossified. Apparently the ilium stood more vertically than in Watson's reconstruction and met the ischium in the acetabluar region. A strong sacral rib runs from the 20th vertebra toward the ilium, directed somewhat backward. The limbs and scutellation also closely resemble "*Miobatrachus*." As the vertebrae are seen mainly from the dorsal surface in this specimen, the critical structure of the centra cannot be determined. The anterior ribs are slender, nearly straight, and slightly expanded distally; posteriorly they become shorter and very thin. Chevrons are present in the caudal region.

Moodie's plate 14, figs. 1 and 2, (1916), shows another well-preserved specimen which displays the large, broad head with large orbits, short temporal region, and prominent otic notch characteristic of *Amphibamus*. Measurements of this specimen, taken from the figure, are given in the third column of table 1. O. P. Hay described this in 1900, and gives its total length as 62 mm., slightly higher than I obtained from the figure, sug-

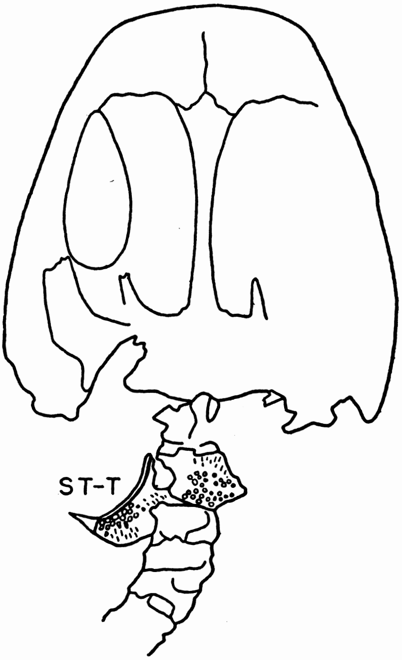

Fig. 2. *Amphibamus grandiceps* Cope. Portion of the type of *Miobatrachus romeri* Watson, C.N.H.M. 2000, showing displaced supratemporal-tabulars behind skull, x 4. Lettering as in figure 1.

gesting that the reproduction may not be exactly natural size. However, the measurements clearly show that the proportions are closely similar to those of the type and neotype. Although the illustrations are inadequate to demonstrate the presence of tabular and postparietal, these elements were visible, for Hay (1900, p. 122) says, "Jugal, supratemporal, squamosal, and epiotic (= tabular) appear to be clearly distinguishable, the latter extending prominently backward."

Miobatrachus romeri:—Comparison of Watson's restoration of this specimen with his own drawing of Y.P.M. 794 shows close similarity in outline of skull, position and size of orbits and parietal foramen, and arrangement of roofing and palatal bones. The tabular region of the skull roof is concealed beneath impressions of palatal structures on both sides of the specimen; this possibly is the result of these bones having been broken from the skull prior to burial. Impressions of detached bones similar in outline to the tabulars of Y.P.M. 794 lie a few millimeters behind the skull, adjacent to the vertebral column (fig. 2). No mention of these elements is made by Watson. A transverse suture between parietal and postparietal may be seen, and the latter element is well developed. Identification of these elements in the "*Miobatrachus*" skull, and the close similarity of all other observable parts of skull and postcranial skeleton with corresponding structures in Y.P.M. No. 794 seems sufficient evidence to warrant reference of these specimens to the same species.

Mazonerpeton longicaudatum Moodie:—Re-examination of the type of this species has revealed so many discrepancies with Moodie's account that redescription seems desirable. Only the posterior roofing bones of the skull are preserved (fig. 3).

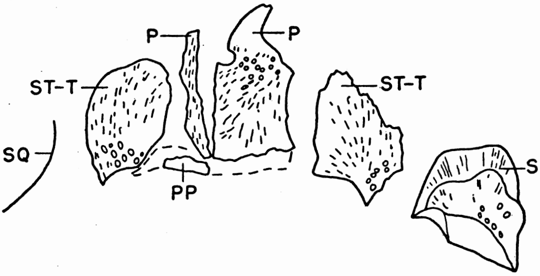

Fig. 3. *Amphibamus grandiceps* Cope. Skull roof of the type of *Mazonerpeton longicaudatum* Moodie, Y.P.M. No. 795, x 4, showing external surface as preserved in counterpart. Lettering as in figure 1.

Ornamentation of pits and ridges on the dorsal surface of the skull roof, preserved on the counterpart, indicates that the areas which Moodie described as orbits are in fact the impressions of the lower surfaces of the right squamosal and left tabular; the orbits actually lay anterior to the portion of the skull preserved in the nodule. Roofing bones are slightly separated from one another along the sutures, a feature which together with the small size of the animal suggests immaturity. Interparietals have only a small exposure on the skull table, and are imperfectly preserved. Elongate parietals (2.0 X 4.4 mm.) are united along a straight median suture and are pierced by a large (0.75 mm.) parietal foramen slightly forward of their center; the left parietal is broken longitudinally and both are incomplete anteriorly. Tabulars are large elements, possibly including the supratemporal although no trace of a suture could be found. They extend forward three-fourths the length of the parietals, (as far forward as the parietal foramen) and are nearly as wide as long. Their occipital margin curves back laterally to a short projecting horn. The large size of these elements and presence of a horn, suggests *Stegops*, in which the tabulars differ in the presence of posteromedial projections as well as a lateral horn, and in more pronounced radial arrangement of sculpture.

The squamosals are convex laterally and concave posteriorly adjacent to the otic notch. The posterior corner projects ventrally below the lower margin, covering the quadrate.

Close behind the right forefoot lies the displaced left lower jaw (fig. 4); its medial and lower surface is well preserved from the angle forward for the greater part of its length. This jaw is slender, especially anterior to the weak coronoid process. The articular cotylus projects inward, and a very short retroarticular process is present. Behind and below the articular expansion and inside the angular process is a large foramen. A suture between the angular and articular-prearticular runs just inside of the lower edge of the jaw from a point below the rear of the articular surface forward for several millimeters. There is a slight suggestion that the angular process is formed of surangular instead of angular, in the usual Amphibian fashion (see Romer, 1947, p. 61), and as Watson (1940, p. 202) has described in *Miobatrachus*. No indications of Stegops-like spines are visible on the ventral border of the angular.

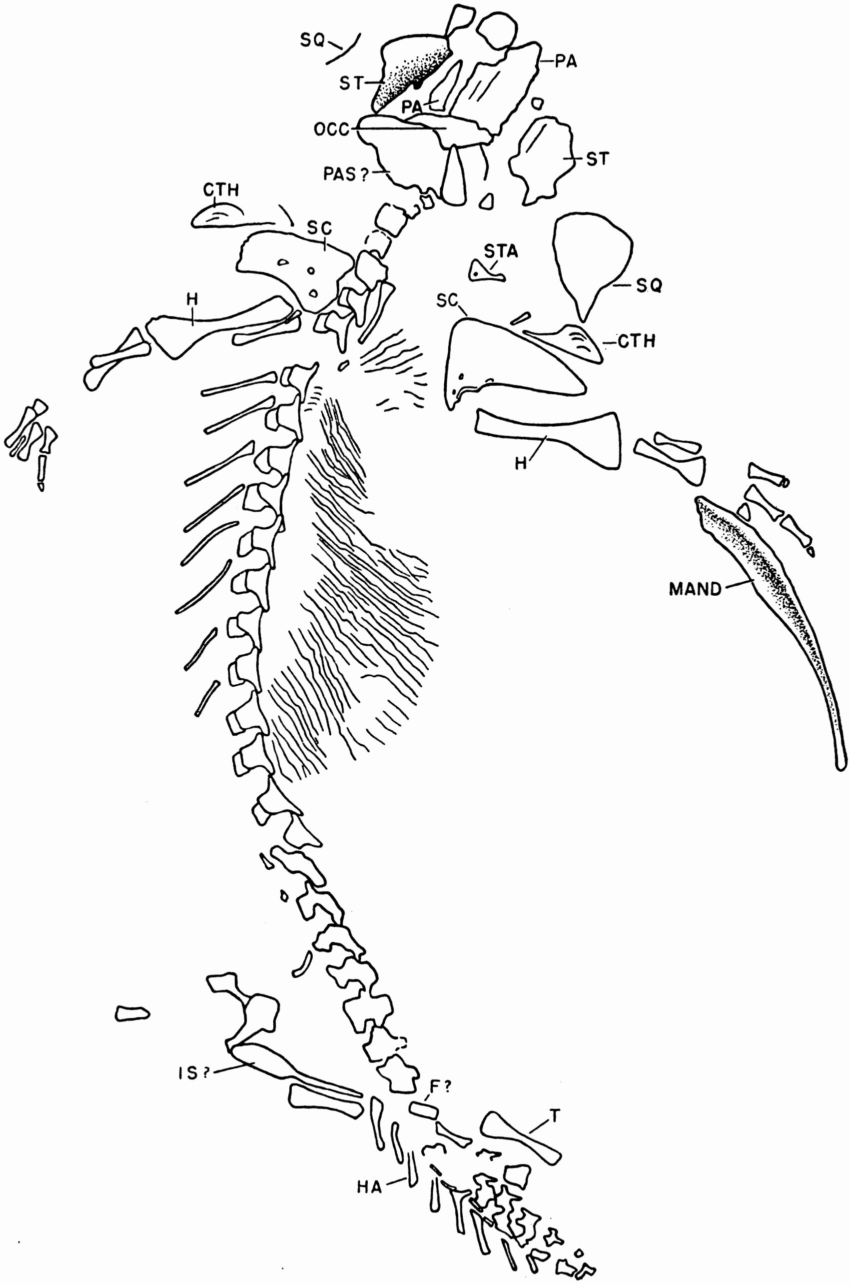

Fig. 4. *Amphibamus grandiceps* Cope. Type specimen of *Mazonerpeton longicaudatum* Moodie, Y.P.M. No. 795, x 3. CTH cleithrum, F femur, H humerus, HA haemal arches, IS ischium, MAND mandible, OCC occipital surface of skull, PA parietal, PAS parasphenoid, SC scapulocoracoid, ST supratemporal (possibly including tabular), STA stapes, SQ squamosal.

A well developed sloping occipital surface is sharply differentiated from the ornamented skull table; this region, unfortunately, is poorly preserved, and no details can be made out.

Moodie described the surface ornamentation of the skull roof as consisting of sharp tubercles and pits, which is essentially correct. In the peripheral portions of the bones there is a slight tendency for the pattern elements to be elongated, but as this is a small individual, growth characteristics of the sculpture are not pronounced. On the squamosal the sculpture radiates from the posterodorsal area. Around the anterior margin of the bone is an extensive band without pattern, indicating extensive overlap of the adjacent cheek bones along their sutures.

A displaced stapes lies behind the skull. It has a round footplate, relatively large stapedial foramen, and short straight shaft.

Moodie states that there are four or five cervical vertebrae. The anterior vertebrae are so poorly preserved that it is difficult to be sure of the number present, and no morphological detail by which they might be differentiated from those of the dorsal region is visible. He also states that "the number of dorsal vertebrae is identical with that of *Branchiosaurus* of Saxony" (1916, p. 61), which is reported to vary from 20 to at least 28, and he identified the 28th vertebra as sacral (p. 63). Twenty-two vertebrae lie anterior to the first bearing haemal chevrons; if one assumes that the sacral vertebra lay immediately in front of this, there were twenty-one presacrals.

Attempts to clean out the impressions of some of the dorsal vertebrae to learn their external form were not completely successful; the neural spines are low, and rather heavy transverse processes are directed downward along the sides of the pleurocentrum to articular facets for the ribs. Some indications of a separate intercentrum were seen. Watson's interpretation of the vertebrae of "*Miobatrachus*" would fit these limited observations satisfactorily. Caudal vertebrae (fig. 5) are exposed from the side and consist of three pieces: a neural arch, with almost no spine but long and dorsally extending zygapophyses; a short pleurocentrum, closely attached or fused to the neural arch; and an elongate but weakly ossified intercentrum. Haemal arches articulate beneath the anterior part of the intercentrum. Altogether the vertebral structure is strongly suggestive of the Rhachitomi, which accords with Watson's observations on *Miobatrachus.*

The ribs are slender and two-headed.

Both scalpulocoracoids are preserved, the right exposed from the lateral and the left from the medial aspects. This bone (fig. 5) is similar in form to that of other Paleozoic temnospondyls, with inwardly curving coracoid plate, screw-shaped glenoid, and supraglenoid, supracoracoid, and glenoid foramina distributed as in *Eryops.* The dimensions follow:

	mm.
Height scapula and coracoid	**6.3**
Height scapular blade above top glenoid	4.5
Length (anteroposterior)	4.4

Fig. 5. *Amphibamus grandiceps* Cope. A. Scapulocoracoid, and cleithrum of Y.P.M. 795 (type of *Mazonerpeton longicaudatum* Moodie), lateral view, x 8. B. Two proximal caudal vertebrae of same specimen, about x 8.

The right clavicle is preserved only in cross section and appears as a thin line running from the anterior point of the scapulocoracoid inward toward the vertebral column; it cannot be determined whether or not it was expanded in typical labyrinthodont fashion. Both cleithra are preserved, lying near the anterior edges of the scapulae; they are expanded dorsally and bear faint concentric ornamentation which is suggestive of the growth lines on a clam shell. Ventrally they taper to a narrow point which lies close against the anterior edge of the scapula. Moodie identified a small bone lying directly beneath the vertebrae and parallel to the column as interclavicle. This bone is the size of a rib and the anterior expansion is not unlike the head of other ribs of *Mazonerpeton*; in view of the dissimilarity of this bone to the interclavicles of labyrinthodonts it seems more likely that it is a rib and that the dermal girdle is not completely preserved.

Humeri are somewhat as described by Moodie, slender bones with the expanded ends placed at right angles to one another. There is a conspicuously developed pectoral process. The ends of these bones are imperfectly ossified and no indication of either ect- or ent-epicondylar foramina are visible. Dimensions are given in table 1.

The radius is both shorter and more slender than the ulna; the latter bone is stout and about one-half the length of the humerus; on the right side a moderately developed olecranon process can be observed. The epipodials differ from those of *Amphibamus* in their unequal size, and from those of *Cephalerpeton* in their shortness, being about one-half the length of the humerus instead of over two-thirds the length of the latter. The total length of the front leg to the end of the first phalanx is 16 mm.

The carpus is unossified; remains of three digits are preserved on the right side, the bases of four metacarpals and the distal phalanges of one toe on the left. The last toe on the right side is covered by the end of the lower jaw. Moodie interpreted the fourth toe as the first. The phalangeal formula is 1 - ? ->1-2.

Fragments of pelvis are visible on the right side but it has not been possible to elucidate their structure. Moodie (1916, p. 63) states that the left ilium is preserved: "It is elongate and cylindrical, its upper end adjoining the 28th vertebra."

Excavation along this element has uncovered a more extensive plate which meets a similar bone of the opposite side in V-shaped contact characteristic of the ventral elements of the primitive tetrapod pelvis; whether they are ischia or pubes cannot be ascertained from the parts exposed. *Amphibamus* (and "*Miobatrachus*") lack ossified pubes, but these elements might be present in a larger and more fully ossified form such as that under consideration. The anterior position of these elements in relation to the limb bones suggests pubes rather than ischia. No other pelvic elements have been identified.

The bone labeled femur in Moodie's figure 14a (1916) strongly resembles a tibia in its form, and a much larger bone exposed on the left (convex) side of the specimen passing beneath the vertebral column to appear again on the right is more probably the right femur.

The rear feet are not preserved.

Ventral scales are arranged in rows running outward and backward from the midline similarly to the pattern found in most "branchiosaurs" and other scaled Paleozoic amphibia; in a small anterior area the rows run forward and outward similar to those of "*Miobatrachus*." The scales were rounded, over-lapping, and marked with concentric striations, which give the appearance of "crescentic bundles of finer rods" mentioned by Moodie.

Comparisons: *Mazonerpeton* was described as a branchiosaur and has generally been accepted as such; Romer (1947, p. 119) suggested that it is a young rhachitome, which the present study confirms. The possibility that it might represent a larger individual of *Amphibamus*, suggested by the general form of the otic notch, shape of the posterior part of the lower jaw, number and observable features of the dorsal vertebrae, and the arrangement of the ventral scales, is confirmed by the detailed form of the posterior cranial elements, particularly the horned tabular—supratemporal. It differs from typical *Amphibamus* in having a coossified scapulocoracoid and relatively short radius compared to the ulna. Both of these characters are due to the greater maturity of this individual, indicated by its larger size.

Although this is the largest known specimen of *Amphibamus*, it still presents many characters of immaturity and may well be a larval form. We have no information at present as to the adult size and proportions of this animal.

Relationship to *Cephalerpeton* is excluded at once by the shorter vertebral column and especially by the temnospondylous nature of the vertebrae, by the presence of an otic notch and other skull features, by the coossified scapulocoracoid, relatively short forelimb, presence of only four toes in the manus, and differences in scutellation. It is obviously not a microsaur.

Relationship to the nectridian *Diceratosaurus* is excluded by the temnospondylous vertebrae, and also by the relatively small interparietals and form of the tabular horns.

Relationships: That *Amphibamus* is not a microsaur is evident from Watson's descriptions. The rhachitomous vertebrae, short vertebral column, and many other features contrast strongly with the lepospondyls. Watson (1940) demonstrated that the vertebral column of "*Miobatrachus*" resembled that of the Anura in the great development of the neural arch, presence of relatively small ventral blocks of the centrum, and reduced number of presacral vertebrae from that of primitive stegocephalians. He further pointed out resemblances to *Protobatrachus* in the structure of the palate, shoulder girdle, and pelvis. According to his interpretation of the skull roof there was also a trend toward the Anura in the loss of the tabulars and postparietals. On the basis of this analysis, Romer (1945a) erected a new order Eoanura for *Amphibamus* and "*Miobatrachus*."

The present interpretation of the skull roof of *Amphibamus* removes the most striking feature of Watson's comparison with *Protobatrachus* and the Anura.

It is possible that the preponderance of the neural arch in the vertebrae of *Amphibamus* foreshadows the anuran condition as Watson suggested, but it would be dangerous to trace the phylogeny of frogs solely on this structure which is so difficult to determine, and, in *Amphibamus*, not greatly different from other rhachitomes. The palate of *Amphibamus* is quite similar to that of the edopsoid rhachitomes except for larger interpterygoid vacuities and relatively broader posterior expansion of the parasphenoid. In the latter feature, particularly, it does approach *Protobatrachus* more closely than most other labyrinthodonts. Nevertheless, the resemblance is not surely the mark of relationship, for the proportions of the basal expansion of the parasphenoid are in part related to general skull proportions, and similarities may be found between *Proto-*

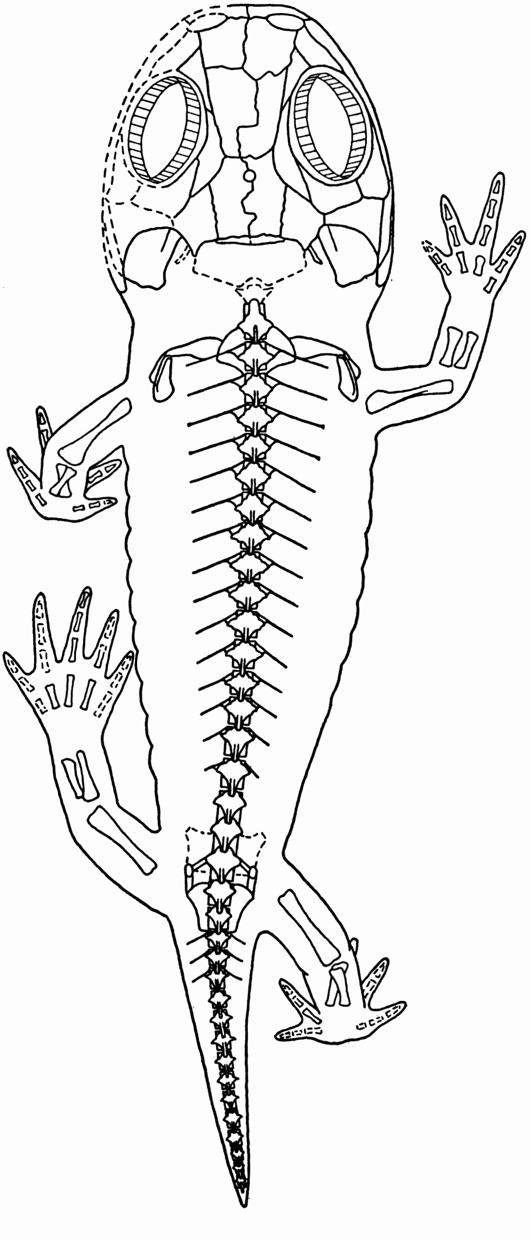

Fig. 6. *Amphibamus grandiceps* Cope. Restoration of skeleton x about 2½. Modified from Watson (1940).

batrachus and other short-headed labyrinthodonts such as *Dvinasaurus* and *Stegops*. *Amphibamus* remains as plausible an ancestor as any for the Anura, but lacks positive features indicative of such relationship.

The typical rhachitomous labyrinthodont skull roof pattern of *Amphibamus* suggests that this genus may properly be included in the Labyrinthodontia regardless of its relationships to the Anura. Distinctive characters for family assignment are the relatively large and centrally placed orbits, the large supratemporal apparently united with tabular, large otic notch, and relatively short distance between otic notch and posterior border of the orbit.

The large pointed tabulars at once suggest the horned zatrachyids, among which the closest resemblance is to *Acanthostoma*. But *Amphibamus* lacks any trace of spines on quadratojugal and angular, and its tabular horns are simple and less developed than those of *Stegops*, the nearest zatrachyid both in age and geographic position. Moreover, the orbits are considerably larger relative to skull size than in *Stegops*, and much larger than in the later zatrachyid genera. There is no trace of an internasal fenestra (also absent in *Stegops*).

Posteriorly projecting tabulars and relatively large otic notches also characterize the Dissorophidae, particularly the Pennsylvanian genera *Platyrhinops* and *Mordex;* these genera have somewhat larger orbits than the zatrachyids. Further close resemblances to *Amphibamus* are found in the short postorbitals, broad frontals and nasals. Perhaps more important is the short vertebral column; in *Cacops* there are only 21 presacral vertebrae. There are differences in the palate, notably the relatively larger prevomers and correspondingly shorter interpterygoid vacuities in *Platyrhinops*, but these are not of such magnitude as to preclude family relationship (and the prevomers of "*Miobatrachus*" seem quite large). No trace of dorsal plates of dermal armor occurs in *Amphibamus*, but this specialization of Permian dissorhopids may not yet have developed in the Pennsylvanian. Altogether, the resemblances seem sufficient to justify reference of *Amphibamus* to the Dissorhophidae.

Two other possible relatives of *Amphibamus* may be noted. Professor A. S. Romer has pointed out to me that the specimen of *Limnerpeton laticeps* Fritsch (1883, plate 36, fig. 1) from Tremosná belongs to the same group as *Amphibamus*. (The type of that species appears to be the Nyrany specimen figured in plate 31, which Steen (1938, p. 261) has shown to be different.) Its vertebrae consist of *Amphibamus*-like neural arches and small ventral plates similar to those figured by Watson in "*Miobatrachus.*" The lepospondylous vertebrae indicated in Fritsch's figure 91 do not appear to exist. Free haemal arches, which Miss Steen regarded as indicative of adelospondylous vertebrae, are known to be characteristic of the rhachitomous *Amphibamus.* The form of the scapula is quite like that of the genus under consideration; resemblances also may be found in the posterior end of the parasphenoid. Fritsch's figure suggests a large otic notch. Little can be seen of the skull structure in the electrotypes of the specimen. It may be noted that the scales (Fritsch, p. 149, fig. 90) have concentric striae like those of *Amphibamus* and in strong contrast to the radial pattern characteristic of microsaurs.

Another possible relative of *Amphibamus* is *Ricnodon limnophyes* Steen (1938, p. 227, figs. 13, 14.) This may be a differently crushed specimen of the Nyrany form described as *Mordex calliprepes* Steen (1938, p. 260, fig. 42) with which it agrees in (1) large tabular (+ supratemporal ?) bearing a small posterior horn; (2) presence of an interfrontal bone; (3) large, wide nasals; (4) moderate exposure of postparietals on skull roof; and (5) palate greatly studded with denticles.

Mordex has been referred tentatively to the trematopsids by Romer (1947, p. 167), but he figures it (*ibid,* p. 158) in comparison with the dissorophids with which it agrees equally well except for the presence of a small interfrontal. *Ricnodon limnophyes* has a larger interfrontal, and as figured by Steen lacks the large otic notch. But its squamosal is a peculiar shape and may be distorted, eliminating the notch. These two forms agree with the dissorophids and zatrachyids in various respects but perhaps are closer to the former family. They lack the elongate external nares of the trematopsids and the internaral fenestra of these and the Zatrachyids.

In view of the close similarity in age, facies, and composition of the Mazon Creek and Linton faunas, it may well be asked whether any trace of *Amphibamus* occurs at the later locality. As pointed out above, *Platyrhinops mordex* (Cope) appears to be a primitive dissorophid and resembles *Amphibamus* in many details of skull pattern. However, *Platyrhinops* has considerably shorter interpterygoid vacuities and larger prevomers;

also its orbits are relatively smaller. Generic distinction between these forms seems reasonable on the basis of our present limited knowledge of them.

SUMMARY

Amphibamus grandiceps Cope is known from five specimens, the three referred by Moodie in 1916 and the types of *Mazonerpeton* and *Miobatrachus.* It is a typical rhachitomous labyrinthodont with enlarged, horned Supratemporal-tabulars and small postparietals, belonging to the family Dissorhophidae. Evidence from the largest specimen suggests that all known material is immature.

TABLE 1

Measurements in millimeters of	*A. grandiceps* type [from Cope's figure]	*A. grandiceps* Y.P.M. 794	Moodie, pl. 14, figs. 1-2	*Miobatrachus romeri* type CNHM 2000	*Mazonerpeton longicaudatum* type, Y.P.M. 795
Length skull to rear margin table	16.8	13.7	15.5	12.8	—
Width skull	17.5	15.7	15.8	12.5	about 14
Post pineal length	5.8	3.7	4.5	4.2	3.5
Length orbit	7.0	6.4	6.6	about 6.6	—
Interorbital breadth	4.5	4.2	3.9	3.4	—
Ratio, $\frac{\text{skull length}}{\text{total length}}$	.26	.21	.25	$<.24$	—
Ratio, $\frac{\text{width of skull}}{\text{length of skull}}$	1.04	1.15	1.02	0.98	—
Length, tip snout to pelvis	50	55	about 40	43	48 from back skull
Total length	64	65+	—	>52[1]	75±[2,4]
Length dorsal vertebral segment	—	1.9	—	1.6	2.1
Length humerus	5.4	4.7	—	4.4	6.0
Distal width humerus	—	2.1	—	1.5	—
Length radius	—	2.6	—	2.0	2.1
Length ulna	—	2.6	—	2.3	3.2
Ratio, $\frac{\text{length ulna}}{\text{length humerus}}$	—	0.55	—	0.52	0.53
Length femur	7.5	6.5	—	5.9	7.0
Length tibia	4.2	3.8	—	3.2	4.0
Ratio, $\frac{\text{length tibia}}{\text{length femur}}$	0.56	0.60	.67[3,4]	0.54	—

1. Tail incomplete.
2. Estimated on basis of skull length 14 mm.
3. According to O. P. Hay.
4. Approximate.

Family incertae sedis

Micrerpeton caudatum Moodie

Moodie, R. L., 1909, Jour. Geol. 17, 39-52, figs. 1-6; 1916, Carnegie Institute Washington Publ. 238, 52-57, plate 2, plate 5, fig. 4.

Eumicrerpeton parvum Moodie,
1910, Amer. Naturalist 44, 367-375, figs. 1-4;
1911, Proc. U. S. National Museum 40, 429-431, fig. 1;
1916, C. I. W. Publ. 238, 57-60, plate 3, figs. 1, 2; p. 65, fig. 15 b, c.

Type: Walker Collection (no. 12313), Chicago Natural History Museum no. UR 38, almost complete skeleton and impressions.

Type of *Eumicrerpeton*: Yale Peabody Museum no. 803, imperfect impression. Referred Y. P. M. 802 and U. S. N. M. no. 4400 (figured by Moodie), and U. S. N. M. nos. 4319, 4432.

The type skull of *Micrepeton* is broken off transversely just in front of the orbits (fig. 7), and shows no trace of the "minute nostrils" mentioned by Moodie. Sutures are indistinct; the median suture, those separating the circumorbital series from frontal and parietal, a doubtful transverse suture between frontals and parietals, and on the left side a possible suture around the postorbital are all that could be determined. In a few places where the bone has broken away from the matrix the impression of minute ornament pits can be observed. Several significant features of the external skull structure may be determined.

Most important of these is the well-developed otic notch, best seen on the left side of the counterpart specimen. It is deep and slopes back strongly exactly like that of *Amphibamus*. There is

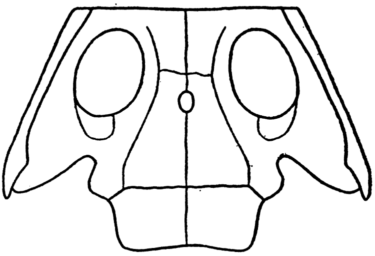

Fig. 7. *Micrerpeton caudatum* Moodie. Skull of type, C.N.H.M. UR 38, x 5.

a long, sloping occiput, now crushed into the plane of the skull roof. The orbits are of moderate size, oval, directed outward as much as upward, separated from the frontal by the prefrontal and postfrontal bones. A few tiny wedge-shaped bones in the left orbit may be fragments of the sclerotic plates. Between the posterior halves of the orbits lies the large parietal foramen. Impressions of the cheek bones are not sufficiently continuous to reveal its structure, nor is aught but the outline of the lower jaw visible.

A suggestion of an impression of the expanded posterior end of the parasphenoid, bearing minute teeth, is seen on the counterpart specimen.

Moodie's reconstruction (1909, fig. 5) is inaccurate and suggests far more than can be observed.

Twenty vertebrae lie between the skull and the point where the femur crosses the vertebral column; although the sacral vertebra could not be identified with certainty, a presacral vertebral count of 19 or 20 is probable. Cervical vertebrae have short stout transverse processes. Impressions of the vertebrae are incomplete, but in the posterior dorsal region impressions reveal low neural spines, strong zygopophyses, and extensive neural arches reaching low on the sides of the vertebrae. The structure is like that described by Watson in *Miobatrachus* except that the ventral elements could not be distinguished. Direct comparison of the specimen with the type of *Miobatrachus romeri* confirms the resemblance. The proximal caudal vertebrae consist of large neural arches and well developed intercentra bearing elongate haemal arches. These are separated by a space which presumably contained the notochord.

Two slender curved ribs are preserved.

Limb bones are poorly preserved; Moodie has indicated their general positions. I cannot agree with his identification of the elements of the shoulder girdle, which are exceedingly indistinct and unidentifiable. There is no trace of the pelvis.

The ventral armature consists of a series of overlapping rows of small lenticular scales which diverge posteriorly from a median row of larger scutes; the impression is not so clear as that in the *Miobatrachus* specimen but is exceedingly similar to it.

The lateral line of the tail and color bands which Moodie described (1909, pp. 47-49, figs. 4-6) can no longer be observed. Certain features of the specimen suggest that the "color bands" may have been impressions on the rock due to internal structures rather than rows of pigmented scales. Round, slightly overlapping scales can be seen on the tail, especially on the counterpart.

Discussion of the relationships of *Micrerpeton* is best deferred until after certain additional specimens have been mentioned.

Eumicrerpeton parvum Moodie:—Both of the Yale specimens (Y.P.M. no. 802 and 803) are impressions of the lower surfaces of larvae which show little besides body outline and the cast of the intestine. The skulls are slightly broader than long, have large orbits well separated by a broad skull roof, and appear to have had otic notches. On the larger specimen, no. 803 (fig. 8), there is a suggestion of a triangular area of parasphenoid teeth at the back of the palate, and a slender parasphenoid bar between large interpterygoid vacuities.

Clavicles and interclavicles cannot be separated; together they form a transverse girdle a short distance behind the skull, the outer ends of the clavicles curving backward. Nothing can be seen of the primary shoulder girdle, which may have been entirely cartilaginous in such young stages. Short portions of

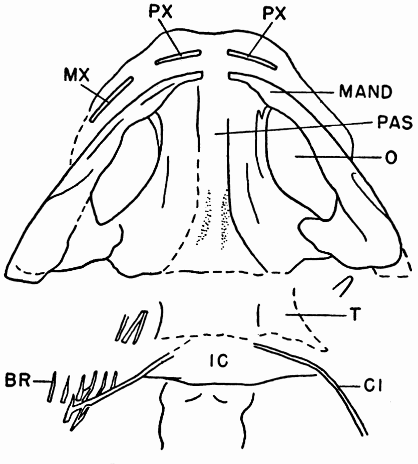

Fig. 8. *Micrerpeton caudatum* Moodie. Skull of type of *Eumicrerpeton parvum* Moodie, Y.P.M. No. 803, x 6. BR possible branchial filaments. CL clavicle, IC interclavicle, O orbit, MAND lower jaw, PAS parasphenoid, PX premaxillary, T skull table.

the humeral shafts were ossified, and in no. 802 there is a suggestion of one bone in the left forearm. No trace of the pelvis is to be seen in that specimen, and only a poor indication of the left thigh. In no. 803, a portion of the shaft of the femur may be seen.

Far better preserved is U. S. N. M. no. 4400 (fig. 9), which shows clear skeletal impressions in addition to the cast of the digestive tract which largely occupied Moodie's attention. The large supratemporal-tabular with a small posterior horn is definitely visible on both sides of the skull table. Behind the sharp boundary of the skull table are impressions of the sloping occipital surface, but the rear outline of occiput and condyles are obscure as in all these specimens. Postparietals cannot be distinguished. The interorbital and nasal regions are broad; the large parietal foramen lies between the rear half of the orbits. Tuberculation on the skull roof is indicated, but the squamosals appear smooth at this stage.

No useful data concerning postcranial skeleton can be obtained; the general appearance has been described by Moodie.

These three specimens, and the two to be mentioned below, appear to be somewhat differently preserved individuals of *Micrerpeton caudatum*. The short, broad skulls, anteriorly placed pineal foramen, and large orbits close in front of the otic notch indicate relationship to that form. Details of skull pattern in U. S. N. M. no. 4400 agree with and supplement those of the type. Similarities in proportions are evident from measurements given in table 2.

U. S. N. M. no. 4319—Undescribed branchiosaur.—This is the smallest individual branchiosaur so far recovered from Mazon Creek, its total length being about 23 mm. In spite of small size, considerable details of skull structure are preserved, and neural arches of the vertebrae are well developed. The fracture of the nodule does not include the levels of the limb bones, although traces of the left forelimb outline may be seen. The skull is short, broad, with large and widely separated orbits and a large parietal formen lying between the middle of the orbits. The skull table projects well behind the quadrate articulation, and is drawn out laterally into tiny tabular horns.

Sutures between nearly all the roofing elements can be distinguished, only the quadratojugals, maxilla and premaxillae being obscure or missing. The anterior portion of the skull roof is missing, but the entire outline may be seen on the lower impression.

The supraoccipital is broad, slightly rounded at its dorsolateral angles, and faintly groved near the midline.

Interpterygoid vacuities are extremely wide. The parasphenoid rostrum is fairly wide, of uniform width, similar to that in such stereospondyls as *Metoposaurus*. There are no traces of teeth along the anterior process, but a triangular patch lies just at its base where the bone expands to floor the braincase, as in *Amphibamus*.

About 22 vertebrae are preserved, and there are indications that the last are in the pelvic region. Thus the column is similar in length to *Amphibamus*.

Identification of this small animal is difficult. Its resemblances to *Micrerpeton* and "*Eumicrerpeton*" are sufficient to justify references to the same species of *Branchiosaur*. Observable details of the skull roof pattern agree well with *Amphibamus*, but the form is so small and the characters shown are so generalized "stegocephalian" that it would be difficult to assert that it could not be the larva of some other labyrinthodont.

U. S. N. M. no. 4432:—This small and imperfect specimen shows but few traces of the skull. The double-headed ribs are well preserved and show, on the more anterior ones, a slight distal expansion. About sixteen vertebrae and one forelimb are preserved. Measurements are given in the table.

Relationships: *Micrerpeton* resembles *Amphibamus* in the following respects:

1. Well-developed otic notch
2. Sloping occiput
3. Large orbits
4. Type of ornamentation
5. 19 or 20 presacral vertebrae
6. Known structure of vertebrae
7. Ribs
8. Details of ventral scutellation
9. General size of limb bones
10. Haemal arches

Observable differences between *Micrerpeton* and *Amphibamus* include:

1. Skull length 1/8 to 1/5 total length, compared to about 1/4 total length in *Amphibamus.*
2. Skull width appreciably greater than skull length instead of about the same.
3. Tail longer.
4. Pineal foramen between orbits instead of behind them.
5. Possibly less developed horn on tabular (or supratemporal).

Evaluation of these differences is difficult. The animals do not look alike, yet most of the tangible distinctions are characters which are known to vary during growth. All specimens of *Amphibamus* lack the distal portion of the tail so that ratios of head to total length appear greater than their true value. Quite possibly complete specimens would give substantially longer lengths and bring these ratios for the two groups within reasonable limits of variability. Skulls of *Micrerpeton* and "*Eumicrerpeton*" are all crushed flat and considerably widened posteriorly. It is not possible to accurately reconstruct these, but if the depth was at all comparable with that of *Amphibamus* the width could not have greatly exceeded the length. This distinction, then, is uncertain.

Possibly more significance is to be attached to the more anterior position of the pineal foramen, but even this may change with growth.

A possibly valid distinction between *Micrerpeton* and *Amphibamus* may lie in the trend to increase of width/length ratio of the skulls with increase in size in the former genus. Such a trend would not lead to the equidimentional amphibamid skull. But this trend itself may be an artifact due to crushing.

Regression of skull length against total length is not conclusive as to trend and could well be interpreted either on the basis of growth or of different proportions. *Micrerpeton* specimens are less than 40 mm. in length compared to 50-75 mm. length in *Amphibamus,* a sufficient difference to account for substantial changes of proportions.

Finally, the most characteristic feature of the *Amphibamus* skulls is the form of the supratemporal; in *Micrerpeton* this is not determinable except in U.S.N.M. 4400, which does resemble *Amphibamus* in this feature.

The temptation is strong to throw these forms into the synonymy of *Amphibamus* and attribute the differences to differential growth. But it seems impossible at present to prove such synonymy and better advised to retain *Micrerpeton* as a separate genus of "branchiosaur."

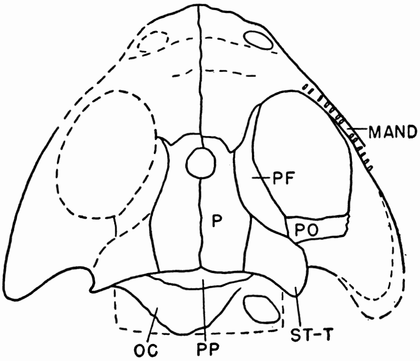

Fig. 9

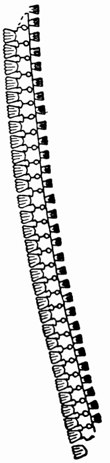

Fig. 10

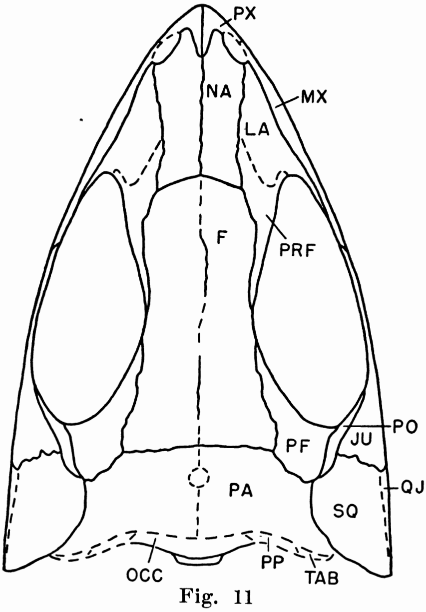

Fig. 11

Fig. 9. *Micrerpeton caudatum* Moodie. Skull of U.S.N.M. No. 4400, x 6. Lettering as in figures 1 and 4.

Fig. 10. *Sauropleura* sp. U.S.N.M. No. 18125, x 2.

Fig. 11. *Cephalerpeton ventriarmatum* Moodie, Y.P.M. No. 796. Skull roof, reconstructed, x 2½. F frontal, JU jugal, LA lacrimal, MX maxillary, NA nasal, OCC supraoccipital, PA parietal, PF postfrontal, PO postorbital, PRF prefrontal, PP postparietal, PX premaxillary, QJ quadratojugal, SQ squamosal, TAB tabular (or supratemporal).

Equal difficulties beset attempts to allocate these animals to family position within the Rhachitomi. No genera are known to me with the combination of large orbits, short faces, and such anteriorly placed pineal foramina. Some specimens of *Branchiosaurus*, as that figured by Bulman and Whittard (1926, p. 539, fig. 1), and the highly aberrant Triassic Brachyopids, are all that approach it, and the latter are obviously not related. The branchiosaur resemblance is chiefly in features of immaturity. The series of *Actinodon* skulls figured by Romer shows posterior migration of pineal foramen relative to orbits with growth, and it is possible that larger specimens of *Micrerpeton* would have longer skulls and pineal foramen behind the orbits. Such changes could bring it very close to *Amphibamus*, but other changes in proportion could give rise to quite different forms.

Consequently family assignment of *Micrerpeton* is not possible at present. It may represent young of *Amphibamus*, but this cannot be demonstrated. Here it is listed separately as a Rhachitome incertae sedis.

Indeterminate labyrinthodont
Erierpeton branchialis Moodie 1912

Moodie, 1912, K. U. Sci. Bull., vol. 6, no. 2, pp. 328-330, plate 1, fig. 3, plate 2, fig. 1.
1916, C.I.W. Publ. 238, pp. 65, 69-70, plate 3, fig. 4, text fig. 15a.

Type: Impression of skull and soft body parts in nodule, Yale Peabody Museum no. 801.

The skull impressions are susceptible to alternate interpretation from that of Moodie, who regarded them as mandible, basibranchial, and paired hypohyals. The paired impressions are strongly suggestive of pterygoids, and the median one of the anterior portion of the parasphenoid of a palate with large interpterygoid vacuities. The mandible is massive for an animal of this size, rather than slender as described by Moodie (1916, p. 70); nor is there any evidence in the impression to support his statement that the symphysis was not a complete sutural union. Most striking is the posterior prolongation of the mandible to an extent which suggests that the quadrate lay well behind the pterygoid vacuities in contrast to *Amphibamus*. Olson regarded *Erierpeton* as indeterminate, and

TABLE 2

Measurements in millimeters of	*Micrerpeton caudatum* type C.N.H.M. 12313	*Eumicrerpeton parvum* type. Y.P.M. 803	*E. parvum* Y.P.M. 802	*E. parvum* U.S.N.M. 4400	U.S.N.M. 4319	U.S.N.M. 4432
Length skull to rear margin table	—	5[2]	4.4	6.3	4.6	—
Width skull	8.6[1]	7.0	6.0	9.7	6.0	7
Post pineal length	2.1	—	—	2.3	—	—
Length orbit	2.7	—	—	2.8	1.9	—
Interorbital breadth	2.0	1.9	—	2.3	1.7	—
Ratio, $\frac{\text{skull length}}{\text{total length}}$	—	.13	.16	.17	.19	—
Ratio, $\frac{\text{width of skull}}{\text{length of skull}}$	—	1.4	1.36	1.54	1.30	—
Length, tip snout to pelvis	27[2]	23	20	29	—	—
Total length	49	39	28	38	24[2]	—
Length dorsal vertebral segment	0.9	—	—	—	—	1.2
Length humerus	3.7	1.6	—	2.5	—	3.5
Length radius	—	—	—	—	—	2.1
Length ulna	—	—	—	—	—	1.7
Length femur	3.0+	—	—	3.9	—	—

1. Probably too large, as result of crushing
2. Approximate

suggested dropping it from the faunal list. Romer (1947, p. 119) suggested that it may be a larval rhachitome of the *Eugyrinus-Pelion type.* Conceivably it might be an immature *Cephalerpeton,* but there is no positive evidence of this. What little evidence exists supports Romer's conclusion, and the name may be retained to indicate its presence, although it would be impossible ever certainly to identify another specimen with it.

Order Embolomeri Cope
Family Eogyrinidae Watson ?
Spondylerpeton spinatum Moodie 1912

Moodie, 1912, Kansas Univ. Sci. Bull., vol 6, no. 2, pp. 355-357, plate 8, figs. 1, 2; plate 9, fig. 1.
1916, C.I.W. Publ. 238, p. 179, fig. 39, plate 4, figs. 1, 2.
Romer, 1930, A.M.N.H. Bull. 59, pp. 132-133, fig. 25.

Type: Yale Peabody Museum, no. 793. Nodule containing 5 caudal vertebrae.

The pleurocentra are suturally united to both neural and haemal arches; intercentra are equal in size to pleurocentra, without apophyses. A large form not identifiable with better-known genera.

Subclass Lepospondyli
Order Nectridia
Family Urocordylidae
Sauropleura sp.

U.S.N.M. Div. Vertebrate Paleontology, no. 18125. Half nodule with incomplete impression.

A specimen in the Lacoe collection which Dr. David H. Dunkle kindly brought to my attention reveals the presence of the Nectridian genus *Sauropleura* in the Mazon Creek fauna (fig. 10). Both the anterior part of the skull and distal end of the tail are missing, and little structure can be determined beyond the highly characteristic vertebrae and gastralia. Apparently the specimen is a young individual; the preserved length of the vertebral column from the back of the skull is only 61 mm.; more than half of this is tail. The posterior width of the skull is 5½ mm.

The spines of the caudal vertebrae expand in characteristic Urocordylid fashion, their distal ends broad and nearly touching as in *Sauropleura* rather than slender and elongate as in *Urocordylus* or *Ctenerpeton.* Both neural and haemal spines bear radiating ridges which extend into minute denticulations at the ends of the spines; six ridges and serrations are present on the neural spines; the haemal spines, although slightly broader, have only four.

Closest resemblances to this animal are found in the Linton, Ohio, species, *Sauropleura pectinatus* Cope, which differs in the presence of a larger number of ridges on the expanded spines (up to 11 according to Cope, 1868, p. 216; 1875, 378). Possibly the Mazon Creek form belonged to a distinct species, but the present specimen is too imperfect to demonstrate this.

Order Aistopoda

Family Dolichosomidae

Phlegethontia mazonensis Gregory

Gregory, J. T., 1948, Am. Jour. Sci. 246, pp. 636-663, figs. 1-6, plate 1.

Type: U.S.N.M. Div. Vertebrate Paleontology, no. 17097, nodule in counterpart with complete skeleton.

A second specimen in the U.S.N.M., no. 4313, consists of a series of 19 dorsal vertebrae and assorted ribs of a much larger individual than the type. Individual vertebrae are 3.3 mm. long from tips of the zygapophyses, and have centra 2.6 mm. long. Their height is about 3.5 mm., and width across the transverse processes 3.2 mm. Neural canals are large cylindrical, completely surrounded by bone as figured previously. A slight intervertebral space betwen centra is indicated.

The assignment of the Aistopoda to the Reptilia, suggested in the article cited above, has been questioned by Professor A. S. Romer on the grounds, first, that the reduction of the skull roof in this genus is an amphibian feature not shared by primitive Reptilia; second, that the unusually complete ossification of the braincase is more like primitive amphibians such as *Edops* (Romer and Witter, 1942) than early reptiles such as *Captorhinus* (Price, 1935); third, that such high specialization is unlikely in the Reptilia at the time of their first appearance whereas the late Pennsylvanian Amphibia had already undergone a long period of evolution and diversification; and finally that the character of several cervical vertebrae is not pertinent to distinguishing between these classes of vertebrates.

Inasmuch as the fenestration of the temporal region has occurred in both Amphibia and Reptilia, this character cannot be regarded as critical. The boundaries of the fenestra in *Phlegethontia* are more like those of some reptiles than any amphibian. And other reptiles (Pelycosaurs) with fenestrated skulls are known from somewhat later Pennsylvanian deposits (Romer and Price, 1940, pp. 33-34).

Although Romer (1949, p. 158) has stated that there were about seven cervical vertebrae in primitive tetrapods, an inspection of figures of several labyrinthodont skeletons fails to show any with more than two specialized cervicals. Elongation of the neck with resulting modification of the cervical vertebrae is characteristic of the amniotes. Even primitive reptiles have relatively short cervical regions, so that the eight modified anterior vertebrae of *Phlegethontia* are probably unique among Pennsylvanian tetrapods. They were interpreted as indicative of a long-necked (and thus probably amniote) ancestor, but reconsideration of the evidence suggests that this is more probably another independent specialization of the aistopods; no such possible ancestor is known in the Paleozoic, unless it be *Cephalerpeton*, which had a moderately extensive cervical region.

The structure of the braincase is the critical character in estimating the affinities of this Order. As was pointed out previously (Gregory, 1948b, p. 653) there is marked resemblance to snakes and to various burrowing animals in the skull of *Phlegethontia* which must be attributed to adaptive modification. However, this skull type could be easily derived from the more platybasic neurocranium of such a primitive labyrinthodont as *Edops* by constriction of the interorbital region and expansion of the otic capsule. Aside from the lack of ossification in the orbitotemporal region, the braincase of *Captorhinus* would serve equally well as a point of departure from which to derive the aistopod skull; but an accessory hypothesis of secondary ossification is then required. Consequently reference to the Amphibia is simpler, although not conclusively demonstrated.

CLASS REPTILIA

Order Captorhina

Family Protothyrididae

Cephalerpeton ventriarmatum Moodie

Moodie, R. L., 1912, Kansas Univ. Sci Bull., vol. 6, no. 2, pp. 350-352, plate 1, fig. 4; plate 7, fig. 12. 1916, Carnegie.
Institute of Wash. Publ. 238, pp. 133-134, fig. 29.

Gregory, J. T., 1948a, Am. Jour. Sci. 246, pp. 550-552, figs. 1-2.

Type: Peabody Mus. Nat. Hist., no. 796, mold of crushed and partly disarticulated skull, the first 26 vertebrae and ribs, both forelimbs, and ventral armor.

A revised restoration of the skull is shown in figure 11; it differs from my earlier attempt in the greater interorbital width and interpretation of the postorbital portion of the skull roof. The impression previously regarded as parietal is more probably a portion of the displaced supraoccipital.

Evidence that *Cephalerpeton* was closely related to the captorhinomorph reptiles led me to revive Baur's suggestion that the microsaurs were reptiles (1948a, p. 565). Professor Romer has orally disputed this view, maintaining that the microsaurs are holospondylous amphibians with a large intertemporal bone at the back of the skull, quite unlike the captorhinids. We agree that this group has nothing to do with reptilian ancestry. Although *Hylonomus* and related primitive reptiles on which the term Microsauria was founded must be excluded from the group, it will be more conducive to stability of nomenclature to continue using Microsauria in the sense of Romer (1945) than restricting it as I suggested in 1948.

Unfortunately the critical posterior portion of the skull table is missing from *Cephalerpeton.* The preserved portion agrees in pattern with *Captorhinus*, and also with some of the aberrant microsaurs (in the sense of Romer, 1945, pp. 159-160). The postcranial skeleton is distinctively reptilian in its pentadactyl manus, separate coracoid ossification, and rod-like gastralia, so that it may confidently be associated with the Captorhina. Its upper dentition closely resembles that of *Romeria texana* Price (1937, p. 97, plate 6, fig. 1) from the Wichita Group of Texas, with which the anterior portion of the skull roof agrees fairly well. Reptilian skeletons of similar size and character are known from the slightly later Pennsylvanian deposit at Linton, Ohio, as *Eusauropleura digitata* (Cope)[3] and *Tuditanus punctulatus* Cope; until skulls of these animals are discovered the degree of their relationship to *Cephalerpeton* will remain unknown.

In spite of the priority of Hylonomidae over Protothyrididae as a family name for these unspecialized small captorhinomorphs, the unsatisfactory preservation of *Hylonomus* makes it undesirable as a family type. Romer (1945, p. 592) refers (with query) *Tuditanus* and *Eusauropleura* to the *Solenodonsauridae*, a family based upon an equally poorly known genus

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[3] Romer (1950) suggests that this skeleton may possibly belong to one of the microsaurs.

of somewhat larger size. Until more is known of these reptiles, there is no good reason not to refer all the American forms to the Protothyrididae.

The Protothyrididae, like the Limnoscelidae, are extremely primitive captorhine reptiles with predaceous dentition. Their small size makes them even more ideal ancestors for later reptiles than *Limnoscelis*. The origin of these families from embolomerous labyrinthodonts is obscure; absence of an otic notch makes Seymouriamorph derivation unlikely.

Indeterminable specimens

Mazonerpeton costatum Moodie

Moodie, R. L., 1912, Kansas Univ. Sci. Bull., vol. 6, pp. 341-343, plate 2, fig. 3, plate 8, fig. 4, plate 9, fig. 2; 1916, C.I.W. Publ. 238, pp. 63-65, fig. 14b.

Type: Yale Peabody Museum no. 800; nodule in counterpart with portions of skull and skeleton.

The tetrapod nature of this imperfect specimen is questionable. A confused mass of impressions of the inner surfaces of skull bones lies at the end of the vertebral column. Portions of the condyle and margins of the foramen magnum can be distinguished. Somewhat detached from the remainder of the skull is a maxillary (labeled clavicle at the lower left of Moodie's figure) studded with numerous, closely spaced, short, conical teeth of equal size throughout.

Near the center of the nodule is a long, triangular, symmetrical element, forked at its broad end, and bearing dermal bone sculpture on the convex side. Moodie labeled this clavicle, which it cannot be; no tetrapod possesses such an element. Possibly it is a median gular of a fish.

Two "ribs" which meet by the broad, bifurcated end of the above mentioned bone differ from the heavier ribs preserved elsewhere and appear to form a symmetrical pair. Possibly they are hyoid or branchiostegal elements.

A series of thick ribs lies detached from the vertebral column. They are holocephalous, with slightly expanded distal ends. Little can be determined of the vertebral structure. There is no trace of limb bones.

The specimen presents sufficient information to show that it does not belong to any of the better preserved Mazon Creek tetrapods, but not enough to indicate its true affinities.

Moodie (1916, p. 65, fig. 15e) figured a "rib of *Mazonerpeton costatum*," Yale Peabody Museum no. 804. This cannot be identified with the type of that species. It is an indeterminate shaft lacking terminations.

Erpetobrachium mazonensis Moodie

Moodie, R. L., 1912, Kansas Univ. Sci. Bull. 6, 353-354, plate 2, fig. 2, plate 8, fig. 3;
1916, C.I.W. Publ. 238, p. 150, p. 65, fig. 15D, plate 3, fig. 3.

Type: Yale Peabody Museum no. 799. Nodule in counterpart with limb bones.

Bones of at least three limbs are present in this specimen, along with plant impressions. Preservation is too imperfect to permit determination of the bones present, or of the kind of tetrapod represented. They are fairly slender for an amphibian and larger than those of any of the better-known Mazon Creek forms, being 23 to 24 mm. long each.

Possibly to be associated with this, solely on the basis of size, is a limb bone, probably femur, preserved as impression in counterpart in U.S.N.M. no. 4377. Its length is 18.7 mm., its width at the proximal end 5.0 mm. The ends of the bone appear to have had cartilaginous extensions.

These remains are entirely indeterminate, even the class of vertebrates represented being in doubt. *Erpetobrachium* is a *nomen vanum.*

Non-vertebrate material previously described as Amphibian.

Amphibamus thoracatus Moodie

Moodie, 1911, U.S.N.M. Proc. 40, 431-433, fig. 2.
1916, C.I.W. Publ. 238, 131-132, fig. 14.

Type: U.S.N.M. Div. Vert. Pal. no. 4306, nodule in counterpart.

Moodie thought he detected a triangular skull, large interclavicle, and bones of the forelimb in this nodule, but close scrutiny fails to reveal aught but plant remains. The "interclavicle" shows parallel leaf veination, and some of the other impressions also may be plant. The supposed skull impression is such that the right lower jaw would have to be present in both halves of the nodule in different places. The "species" may safely be forgotten and dropped from further consideration of the Pennsylvanian fauna.

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