THE STRUCTURE OF *CEPHALERPETON* AND AFFINITIES OF THE MICROSAURIA

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ABSTRACT. The type specimen of *Cephalerpeton ventriarmatum* Moodie from the Pennsylvanian of Mazon Creek, Illinois, is redescribed and refigured. New information so obtained supports the view of Baur that the Microsauria are Reptilia rather than Amphibia.

In 1912 Moodie described a microsaur from the Mazon Creek nodules which he named *Cephalerpeton ventriarmatum* and regarded as a close relative of *Amphibamus* Cope. It has been associated with that genus in most subsequent classifications. Watson (1940) showed that *Amphibamus* possessed phyllospondylous vertebrae with suggestions of rhachitomous central elements, and further showed that in it were many indications of the evolutionary trends which led to the frogs; Romer (1945, p. 591) has expressed this position by erecting the Infraclass Eoanura for its reception under the Salientia. Westoll (1944, p. 107) published notes by Watson affirming the microsaurian nature of *Cephalerpeton*, and Olson in a revised faunal list of the Mazon Creek vertebrates (1945, p. 302) regarded it as a microsaur of uncertain affinities. Romer (1947, p. 119) on the other hand has suggested that it, like other small amphibians from the Mazon Creek nodules, may be a larval labyrinthodont. In hope of obtaining further evidence upon its affinities the type specimen in Peabody Museum at Yale University has been reëxamined. By use of latex casts sufficient detail omitted from Moodie's description (1916, p. 133-134) was observed to justify redescription and additional illustration. More important is the discovery of additional evidence supporting the view of Baur (1897) that the Microsauria are not Amphibia but primitive Reptilia.

Cephalerpeton ventriarmatum Moodie

The unique type specimen of this microsaur (Yale Peabody Museum No. 796) consists of a mold of the crushed and partly disarticulated skull, the first 26 vertebrae and ribs, both forelimbs, and most of the ventral armor of scales. Portions of the body outline surrounding the arms are visible. Unfortunately the pelvis, hind limbs, and tail are missing; a reasonable estimate of the total length, assuming lizard-like proportions of the other microsaurs, is about 10 inches (25 cm.).

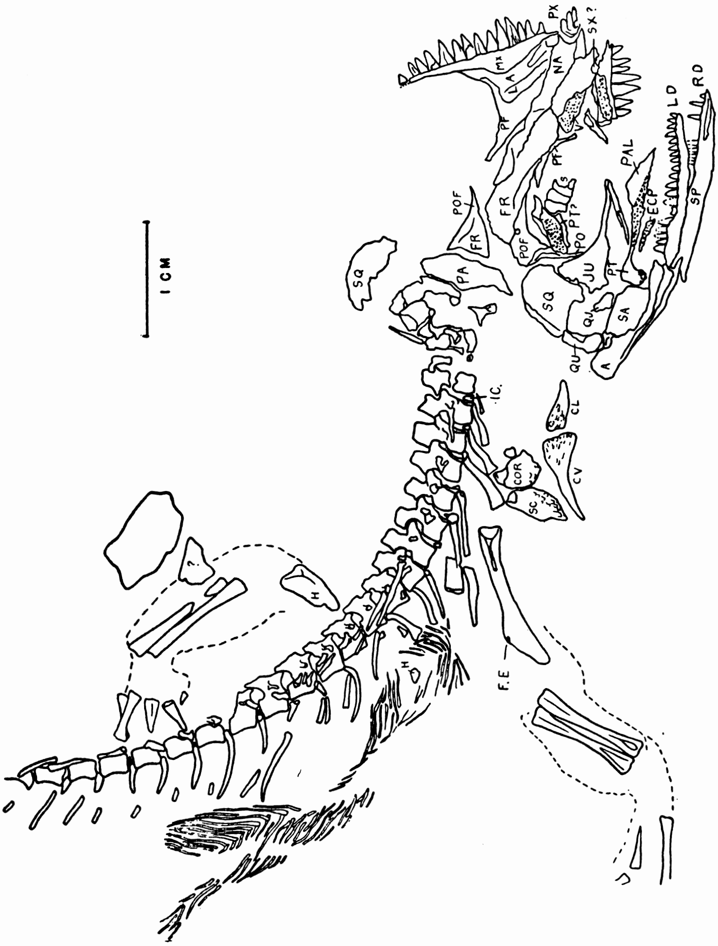

Figure 1. *Cephalerpeton ventriarmatum* Moodie, skeleton as preserved, x 1.5. Drawn from latex cast and reversed. A angular, CL cleithrum, COR coracoid, CV clavicle, ECP ectopterygoid, FE entepicondylar foramen, FR frontal, H humerus, IC intercentrum of 5th vertebra, JU jugal, LA lacrimal, LD left dentary, MX maxillary, NA nasal, PA parietal, PAL palatine, PF prefrontal, PO postorbital, POF postfrontal, PT pterygoid, PX premaxillary, QJ quadratojugal?, QU quadrate, RD right dentary, S sclerotic plates, SA surangular, SC scapula, SQ squamosal, SP splenial, SX septomaxillary?, V prevomer. Two elements adjacent to the left fore-limb are unidentified and probably do not pertain to this animal.

SKULL

Although the skull is crushed and incomplete in the posterior region, a reasonably accurate reconstruction (Fig. 2) has been made. No reliable data were available to determine the traverse width, the squamosal and quadrate obviously being flattened out into the plane of the skull roof and partly separated from adjacent bones. Uncertainty also exists as to the palatal structure, as is discussed below.

The skull is seen from dorsal aspect, the impression being mainly of the inner surface of the roofing bones. There is no basis for Moodie's statement (1916, p. 133) that the skull bones are unornamented, as their outer surface is not preserved. The fragment of the left lower jaw which presents its lateral surface shows some trace of sculpture, and there are pits upon the outer surface of the clavicles, suggesting that *Cephalerpeton* possessed some type of sculpture on its dermal bones.

In a few places the matrix filling the interior of the skull has broken away exposing some of the palate. These glimpses, however, are inadequate for complete interpretation.

From tip of premaxillary to condyles, as preserved, the skull length is 27.7 mm.; possibly it was slightly shorter in life. The transverse width from midline to quadrate, 13.5 mm., is almost certainly too great, so the width of the skull must have been well below 27 mm. In form it was triangular, narrower than long, tapering sharply in front to a pointed snout. The large orbits are centrally located, the external nares small and anterior.

Bones of this skull roof: Moodie (1916, p. 133) figured the left premaxillary with two teeth; close examination reveals the roots of a third. No trace of an ascending process is visible; presumably it was small as the external nares are small and nearly terminal.

Part of the right and the entire left maxillaries are preserved as impressions of the inner surface. The bone is low and slender, tapering to points at each end. The narrow alveolar shelf terminates smoothly just inside the bases of the teeth without trace of the palatine suture. Moodie (1916, p. 133) figures and describes thirteen teeth; a small tooth is present anterior to those figured, making the total 14. On both sides the first three teeth are relatively small and slender. Following these are two enlarged "canines," behind which the teeth are somewhat smaller and variable in size. All teeth show fluting suggestive of labyrinthodont structure. The maxillary forms a portion of the border of the external naris. A distinct suture separates its facial portion from the lacrimal.

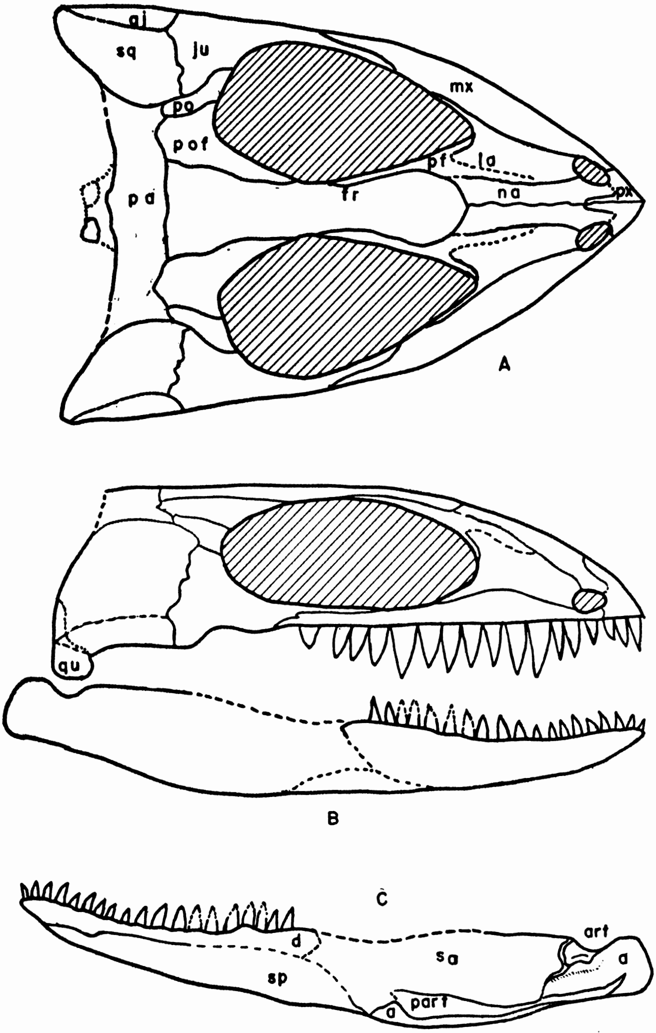

Figure 2. *Cephalerpeton ventriarmatum* Moodie, restoration of skull, x 3. A. dorsal aspect. B. Lateral aspect. C. Medial aspect of lower jaw. *Art* Articular, PART prearticular, other abbreviations as in figure 1.

The nasals are broad, separated in the midline posteriorly by the acute wedge of the frontals. There is a suggestion of a space between their anterior ends for the premaxillary. They bound the small nares above.

A small bone sliver is visible in the right naris which may be the septomaxillary.

Elongate, slender frontals are excluded from the boundary of the orbit by the prefrontal and postfrontal. They are separated by a median suture for their anterior half, and are about equal in width throughout their length. The parietals are broken and partly missing from the specimen. No pineal foramen is visible, but there is ample opportunity for it to have been present in some of the missing portions. No suture can be distinguished between the two parietals, whose combined width is about twice that of the frontals. A small remnant of the occipital surface is preserved; it slopes posteriorly from the rear edge of the parietal. There is no trace of postparietals or tabulars, nor of a temporal series, but again the degree of preservation of this region makes it unwise to aver their absence. Moodie (1916, p. 133) states that the supratemporal is quite large, but unfortunately did not label this element in his figure. The present interpretation may be observed in Fig. 1.

Oval orbits, somewhat longer than high, are situated midway between occiput and snout. The length as preserved, 11.5 mm., may be slightly greater than in life owing to separation of the circumorbital series.

Anteriorly the orbit is bounded by a large lacrimal which extends forward to the external naris. Just above its suture with the maxillary it is greatly thickened on the inner surface for about two thirds of the distance from orbit to naris; beyond this point the ridge becomes a groove opening into the nasal cavity. This ridge thus appears to be a bony canal surrounding the lacrimal duct, which in all probability was closed externally. If correctly interpreted, this is most unusual for an amphibian. The orbital margin of the bone is turned inward to form a smooth margin of some depth.

The prefrontal is much smaller than the lacrimal, and not everywhere separable from it. It formed most of the anterior border of the orbit, dorsal to the above mentioned ridge on the inner surface of the lacrimal. Like that bone, its orbital margin is turned inward. It extends posteriorly along the margin of the frontal to about the middle of the orbit, tapering to a narrow point. An anterior process reaching toward the nasal is undoubtedly discernible.

The postfrontal is larger than prefrontal, forming part of the skull roof behind the orbit, and extending forward as a slender process beside the frontal to contact the prefrontal. The postorbital is small, almost confined to the orbital rim. A large jugal has a slender suborbital process and an extensive development behind the lower portion of the orbit where it forms the cheek roof anterior to the squamosal. Identification of the quadrato-jugal is uncertain. A small bone is present in its position just above the lower jaw; this, however, could also be interpreted as the lower edge of the squamosal as no sutures can be seen.

The squamosals are large plates, taller than long, slightly convex, and thickened posteriorly to support the quadrates. Dorsally they appear to have been in contact with the parietal without intervention of a temporal series.

The right quadrate is incompletely preserved. Its condyle projects below the lower margin of the cheek and is strongly cylindrical. A dorsal process is indistinguishable from the posterior border of the squamosal. Medially there are indications of a pterygoid process, whose extent, however, is concealed.

Bones of the palate: Various interpretations are possible of the two denticle-covered bone fragments at the anterior end of the palate. The medial one, lying just beneath the nasal, might be the anterior portion of a broad parasphenoid, or it could be interpreted as part of an extensive prevomer plate. Two rows of fine denticles parallel its lateral border, and the remainder of its palatial surface is covered with somewhat irregularly arranged small teeth.

An opening was obviously present between this bone and the fragment exposed next to the right maxillary; this might have been either an unusually large internal naris, or, more likely, the anterior end of a large interpterygoid vacuity. If the latter interpretation is correct, the lateral fragment is probably the anterior end of the palatine, but if the nares were really large, and extended this far back, it could well be part of the prevomer. It is covered with denticles quite similar to those of the medial element.

More posteriorly, on the right side, is a slightly displaced fragment consisting of the posterior end of the palatine, covered with similar denticles on its palatal surface, and, at the posterior end, the transverse flange of the pterygoid. This flange turns downward sharply from the plane of the palate, is thickened at its lower edge, and bears a row of teeth slightly larger than those covering the flat surfaces of the palatal bones. Just anterior to the flange, the palatal surface of the pterygoid is smooth, but farther forward, along its suture with the palatine, the denticulation characteristic of the latter bone extends onto the pterygoid. A small ectopterygoid lies just lateral to the pterygopalatine suture; it also is denticulate.

Another section of the pterygoid is visible in the posterior part of the right orbit. It is a broad, flat bone, with a squamous suture, presumably for the parasphenoid, at one end, and indications of the transverse wing separating from the posterior or quadrate portion at the other. The palatal surface, again, is closely denticulate. This section of the pterygoid is highly suggestive of the advanced labyrinthodonts, and seems out of place in association with the reptile-like downturned transverse flange. It has been displaced somewhat and may be incorrectly interpreted. An alternate possibility is that it represents the palatine of the opposite side. If pterygoid, its sutural union with the parasphenoid is most un-reptilian in contrast to other characters of *Cephalerpeton.*

The form of the palatal vacuities must remain conjectural until more information is obtained about the parasphenoid and prevomers. The narrow palatine suggests that they extended far forward and may have been of large size.

Sclerotic plates: Three sclerotic plates are visible in the right orbit, as described by Moodie. They are rectangular, slightly convex outward, and overlap counterclockwise.

Lower Jaw. Both halves of the lower jaw are preserved, the right complete and in articulation with the quadrate, but covered in its middle portion by the left dentary. Teeth are most readily studied on the latter bone, but some of the right teeth can be made out. In the dentary there are at least 17 sharp, conical teeth. The first three are small, the fourth slightly enlarged, but far less than the upper fourth and fifth teeth. The next five teeth are small and subequal, but the eleventh and twelfth are again large and appear to be the strongest in the jaw. Posteriorly the size is less certain, but there are indications that the remaining teeth are larger than those in the anterior part of the jaw.

The dentaries are slender, rounded at the tip, and were only ligamentously connected in life. The length of the right dentary is 17.5 mm. Below the alveolar ridge it narrows to a thin, vertical lamella on the outer side of the jaw. A thin splenial lies medial to it for the greater portion of its length, enclosing Meckel's canal. The splenial, however, tapers to a point beneath the fourth tooth, leaving the anterior end of the canal as an open groove. Its posterior end is rounded, beneath the posterior end of the tooth row. A large, dorsally grooved angular supports the articular region and extends forward to above the posterior end of the splenial. On the outer side it is surmounted by a large surangular, posteriorly by articular, and medially by a small, perhaps incompletely preserved, prearticular. The articular is widened transversely and bears a concave cylindrical cotylus for the quadrate. The conspicuous retroarticular process is distinctly reptilian in form.

Summary: *Cephalerpeton* possessed a pointed triangular skull with large orbits centrally located. The skull roof appears to have lacked intertemporal and supratemporal, and also the posterior row of postparietals and tabulars. There is no indication of pineal foramen nor otic notch, but this may be due to incomplete preservation. A closed lacrimal canal was present. The palate was covered almost everywhere with small denticles. It appears to have had rather large interpterygoid vacuities, but possessed a reptile-like downturned transverse pterygoid process. The maxillary dentition is slightly anisodont with a tendency toward canine development.

The available information on the skull of *Cephalerpeton* is strongly suggestive of reptilian affinities. The loss of the temporal bones, presence of a lacrimal canal, downturned transverse flange of the pterygoid, and jaw with strong retroarticular process, are reptilian characters not found in paleozoic Amphibia. Further information about the nature of the braincase and palate is needed finally to determine its systematic position.

POSTCRANIAL SKELETON

Vertebral column: Twenty-five of the presacral vertebrae are preserved. The total presacral count in *Microbrachis* *pelikani* Fritsch is 38 (Steen, 1938, p. 230); in *Hyloplesion longicostatum* Fritsch there are 30 or 31 presacrals (ibid. p. 235). No other microsaurs are sufficiently preserved to make vertebral counts possible, but *Cephalerpeton*, which shows no trace of approaching the pelvis or hind limbs in the preserved specimen, fits well with the known members of the Order and could easily have had 30-40 presacral vertebrae; it definitely had more than the 24 which Romer (1947, p. 63) regards as primitive for the labyrinthodonts. This long vertebral column is an important difference from *Amphibamus*, with which Moodie erroneously associated the genus; that form has only 19 presacrals, a reduction from the primitive condition which Watson has shown is associated with other characters suggestive of Anuran ancestry.

The cervical region is not distinctly set off from the dorsal. However, the six most anterior vertebrae bear shorter ribs than those farther back, with a gradual increase in size and length of the ribs in the posterior cervical region. *Cephalerpeton*, then, at least shows a tendency toward development of a definite neck with seven cervical vertebrae so characteristic of primitive reptiles and mammals.

Unfortunately the anterior cervical region is incompletely preserved; a detached neural arch lying behind the occiput suggests that the atlas may have had divided arches, but further data are lacking. The posterior cervicals and dorsals are all closely similar. The centrum is spool-shaped, the articular ends are round and pierced by deep conical openings for the notochord which was constricted in characteristic "hourglass" shape. The sides of the centra are slightly concave laterally, meeting below in a rounded midventral ridge.

Thin crescentic intercentra are present in the cervical region and at least in part of the dorsal region; they have been identified following vertebrae nos. 4, 5, 7, 8, 10, 11, 17, 18, 21.

The lepospondylous centra of the microsaurs, therefore, are pleurocentra, and homologous with those of reptiles. A derivation ultimately from temnosopondylous amphibian ancestry is indicated. It is possible, in view of the similarity of urodele vertebrae to those of lepospondylous stegocephalians, that the urodeles, likewise, have centra strictly homologous with those of amniotes. A similar suggestion regarding the homologies of lepospondylous vertebrae has recently been made by von Huene

(1948, p. 44) on the basis of the presence of chevrons in the caudal region of microsaurs.

Stout neural arches arise from the anterior half of the centrum; no trace of a neurocentral suture is visible. The arches are not all swollen as in cotylosaurs but resemble those of *Hylonomous* and *Microbrachis.* The zygapophyses are strongly developed, and slope inward slightly. A round diapophysis extends out a short distance from the side of the arch for articulation with the rib tubercle. Above the level of the zygapophyses the arches narrow rapidly to a well developed, low neural spine only slightly shorter than the corresponding centrum. The spines are of uniform height and flat topped. There are no accessory articulations between the vertebrae.

Ribs: All vertebrae bear distinctly two-headed ribs with fairly stout, elongate, curved shafts. The heads articulate intercentrally; no trace of parapophyses are visible on the centra, so it is probable that the ribs articulate directly with cartilaginous or osseous intercentra. Most of the rib heads are found between adjacent centra. A strong tuberculum is given off which articulated with the knob-like diapophyses of the neural arches. Beyond this the shaft becomes compressed and broad. There is a tendency for expansion of the shaft near its distal end.

The first visible rib is borne by the fourth vertebra. It is extremely slender and short, directed backward and downward, reaching to the anterior part of the following vertebra. The rib of the fifth vertebra is considerably larger, but still directed posteriorly, and reaching only to the middle of the next segment. The sixth rib is larger and somewhat transitional to the form of the dorsal ribs. It is about twice the size of the sixth. The seventh and following ribs are subequal in size and directed more outwardly from the vertebral column.

Moodie referred *Cephalerpeton* to the Microsauria, correctly, largely on the basis of its curved, well ossified ribs. These structures do not present distinctive characters for separation of the group from labyrinthodonts or reptiles. The contrast with the imperfectly ossified ribs of modern amphibians is a matter of degree of development, and again not disproof of relationship.

Shoulder Girdle: Moodie mentions a single element of the shoulder girdle which he regards as the coracoid. He describes it as "long and spatulate at both ends, with the median portion almost cylindrical, not unlike that described by Credner (1881) for the coracoid of *Branchiosaurus*, save that the lower end of the branchiosaurian coracoid is acuminate. In the present form it is spatulate." In the figure Moodie shows the element here identified as clavicle and has it labeled clavicle. Nothing corresponding to Moodie's description can be found on the specimen unless the bone adjacent to the wide end of the clavicle is regarded as its other end which has been displaced.

Four shoulder girdle elements have been identified. The primary girdle is represented by distinct scapula and coracoid ossifications which are plate-like elements meeting at a well defined glenoid, and resembling those of small reptiles. Anterior to these lies the clavicle, and near its medial end a small element regarded provisionally as a cleithrum. Nothing resembling the interclavicle of *Microbrachis* (Steen, 1938, p. 231) can be found; apparently it became lost from the specimen, for there is no likelihood of its absence in an animal of this sort.

The scapula is incompletely preserved, its dorsal end broken away. Its blade is slender, of constant width (2.9 mm.) throughout the preserved 6 mm. length. There is a thick supraglenoid buttress above which the posterior border rises straight. The anterior surface is nearly straight dorsally but curves around gradually at the lower end adjacent to the coracoid. This ventral anterior region curves inward slightly toward the midline. The glenoid appears to be a triangular facet rather than the screw-shaped surface characteristic of most paleozoic tetrapods.

The coracoid is nearly equidimensional and rounded from the glenoid around its lateral and anterior borders to the ventral edge. A sharp bend leads to the concave posterior edge. The bone is directed inward at a large angle from the scapula, so that its lateral surface faced largely downward. There is a strong buttress from the anterior lip of the glenoid down to the lateral surface, separating a posterior depressed area below the glenoid from the remainder of the blade. No coracoid foramen can be seen, but a glenoid or nutrient foramen may be present in the aforementioned depressed area. There is no development of the coracoid posterior to the glenoid socket.

The form of the primary girdle bears no resemblance to that figured by Steen for *Microbrachis*.

The clavicle lies slightly separated from the scapula but in approximately its normal position. Dorsally it consists of a narrow rod which lay anterior to the scapular blade. This widens gradually below and turns medially, following the contour of body and primary girdle. The lower end is a broad spatulate plate bearing a distinct ornamentation of rows of small pits on its outer surface. It will be noted that this clavicle closely resembles that of *Microbrachis pelikani* figured by Steen (1938, fig. 19).

Closely adjacent to the ventral end of the clavicle lies a smaller element with a pattern of pits on its outer surface indicating a dermal origin. Although in the approximate position of an interclavicle, its form and lack of symmetry clearly indicate that it cannot be that element, nor is it the clavicle of the opposite side, for it is smaller than and of different form from the bone just described. Most likely it is a cleithrum of the right side, displaced from its proper position at the top of the scapula. The ornamented oval area lay above the scapula, and the unornamented narrower portion extended downward toward the clavicle.

The retention of such a well-defined cleithrum is a primitive feature not at all unexpected in such an early form. Separate coracoid elements, however, are not known in Amphibia. This is an advanced, reptilian character, as is the simple structure of the glenoid.

Forelimb: The front limb of *Cephalerpeton* was well developed for an animal of this size. Faint impressions of the fleshy portions are preserved, but probably are too compressed to give a reliable indication of its bulk; the humerus exceeds the radius and ulna in length (ratio: 10:7), as in modern salamanders and some of the less agile lizards. The metapodials are relatively elongate. Unfortunately the phalanges are not preserved.

The humerus is 15 mm. long. Its shaft is slender, and the proximal and distal surfaces are expanded in planes at approximately 90° to one another. An entepicondylar foramen is present, as in *Hylonomus lyelli* (Steen, 1934, p. 488, Moodie, 1916, pl. ix). A moderate deltoid ridge extends down the shaft over one-third its length. The ends terminate rather abruptly and evidently were extended by cartilage in life.

Radius and ulna are subequal in size and extremely simple in form, being slightly flattened rods with gradual expansions at either side. Their lengths are 10 mm. (right) and 11 mm. (left) respectively, and the diameter at the distal end is 1.8 mm. Like the humerus, their ends are truncate and were continued by cartilage to the articular surfaces. There is a space of three or four millimeters between the ends of the humeri and the epipodials, which suggests that these cartilaginous epiphyses must have been fairly extensive. On both sides the radius and ulna lie closely adjacent to each other, their ends touching.

The unossified carpus occupied a space of 4 to 5 mm. between the epipodials and metapodials.

There were five digits in the hand. Only the metacarpals are preserved; on the left side the proximal ends of all five can be seen, the fifth partially concealed beneath the shaft of the fourth. Only two are preserved on the right, and only the first in its entirety. They are extremely long and slender, the incomplete second metacarpal of the right manus being 7 mm. long.

The only really progressive character in the forelimb of *Cephalerpeton* is the presence of an entepicondylar foramen in the humerus. Primitive amphibia generally lack this, having an open notch, although some specimens of *Eryops* have been found in which the notch is bridged over. Nevertheless, in such a small animal, this must be regarded as more reptilian than amphibian. The presence of five digits in the manus is not distinctive of either Reptilia or Amphibia, for it probably was arrived at as a typical number early in the history of the tetrapods: those amphibia in which the number is reduced from five are to be regarded as specialized. (Evans, 1944, p. 82).

Gastralia: The skin impressions of *Cephalerpeton* fail to show any indications of scales except in the ventral abdominal region. Here a dense set of elongate scales set in chevron arrangement, the apex directed forward in midline, extends from the region just behind the front limbs to the posterior end of the specimen. Three pairs of longitudinal rows of transverse scales are present, the two medial rows interdigitating in the midline where the scutes interlock by means of hook-shaped projections. The two lateral pairs of each set are short, straight rods, pointed at the ends. The scutes in the middle region of the belly are larger than those just behind the front limbs.

RELATIONSHIPS

Relationship to Amphibamus: Moodie placed *Cephalerpeton* in the Amphibamidae, distinguishing it from *Amphibamus* by its larger size, larger and more centrally placed orbits, anisodont teeth, and absence of otic notch. Watson (1940) has shown that *Amphibamus* is not a microsaur but closely allied to the ancestry of the Anura, and possesses not lepospondylous but aspidospondylous vertebrae resembling the rhachitomous type in arrangement of the central elements. *Cephalerpeton* may further be distinguished from *Amphibamus* by the far larger number of presacral vertebrae, the presence of five digits in the manus, the ossified scapula and coracoid, and the type of ventral armor. They belong to widely separate groups.

Relationship to the microsaurs: Dawson (1863, p. 65) established the Order Microsauria for *Hylonomus*; Cope (1868, p. 210) regarded the Order as batrachian rather than reptilian and referred numerous genera to it. Fritsch (1883), added *Hyloplesion*, *Seeleya*, *Orthocosta*, and *Ricnodon* to the *Hylonomidae*, and erected separate families Limnerpetonidae and Microbrachidae for the corresponding genera which are now generally regarded as members of this group. Recent studies by Steen (1934, 1938) have placed the morphology of *Hylonomus*, *Microbrachis*, and *Hyloplesion* on a firm footing; the other genera are poorly known. These are the typical microsaurs which are perhaps best placed in the family Microbrachiidae, *Michrobrachis* being far better known than *Hylonomus*.

Cephalerpeton possesses in common with typical microsaurs the abnormally large number of presacral vertebrae, long two-headed ribs, similar form of vertebrae, well developed limbs, and chevron arrangement of elongate scales on the abdomen. In the loss of the postparietal row and temporal bones from the skull roof it shows closer affinity to *Microbrachis*, "*Hylonomus*" *geinitsi*, and *Scincosaurus* than to *Hyloplesion*. Thus, according to Watson's view of microsaurian evolution, it is to be regarded as an advanced member of the Order in spite of its early appearance.

Cephalerpeton seems to differ from *Hylonomus lyelli* Dawson in the smaller number of maxillary teeth; otherwise it can be scarcely distinguished on the basis of available descriptions of that inadequate type. *Tuditanus punctulatus* Cope and *Eosauravus copei* (Williston) from Linton, Ohio, are microsaurs which resemble *Cephalerpeton* rather closely. As figured by Moodie (1916, p. 87, fig. 19) the orbits of *T. punctulatus* are considerably smaller than in *Cephalerpeton* and are separated from the frontals by well developed pre- and post-frontal elements. Romer (1930, p. 135) pointed out the reptilian features of the type of *Tuditanus* and the probability of its association with the postcranial skeleton known as *Eosauravus copei* which has been widely mentioned as the "oldest reptile." He did not mention their agreement in all these features with the microsaurs, to which Moodie had referred *Tuditanus*, and to which group they most probably pertain. *Cephalerpeton* may be a synonym of *Tuditanus*, but until the skulls of both genera are better known, it would be premature to change the nomenclature.

Content of the Microsauria: Watson (1930, p. 245) proposed the Order Adelospondyli with *Adelogyrinus* as type and referred to it *Lysorophus*, *Cocytinus*, and *Pleuroptyx*. Subsequently Steen referred the typical microsaurs *Hylonomus* and *Microbrachis* to this Order, and stated (1938, p. 272) that Watson had found the diagnostic neurocentral suture in the vertebrae of *Hylonomus lyelli.* Association of the microsaurs and lysorophids seems highly unsatisfactory; the lysorophid palate differs widely from that of typical microsaurs in its broad parasphenoid and backwardly prolonged dentigerous prevomers. Until far stronger proof of relationship can be found they must be considered separately in any discussion of the affinities of these animals. Other adelospondyls such as *Gymnarthrus*, *Cardiocephalus*, *Euryodus*, and *Adelogyrinus* differ from typical microsaurs in possession of a supratemporal bone and absence of a pineal foramen; they may be related to the microsaurs, but this is far from certain. The limbless Aistopoda, which have been regarded as a distinct Order by some and as microsaurs by others, show sufficient resemblance to the Microsauria to warrant tentative inclusion within that order. On the contrary, the urocordylids and diplocaulids (Order Nectridia), sometimes (for example, by Moodie) included in the Microsauria, are widely different in structure of skull and vertebrae, and cannot be closely related.

The following remarks on the relationships of the microsaurs apply primarily to the Microbrachiidae; further investigation of the other families is needed to confirm their relationship to this group.

Relationship of the microsaurs to the Reptilia: Cope (1868, p. 210) referred the Microsauria to the Amphibia on the grounds that the supposed reptilian characters of dermal scales, parietal fontanelle, and ossified ribs were all found in the Labyrinthodontia, and further because of the presence of two occipital condyles and deeply biconcave vertebrae resembling those of Salamanders. Fritsch (1883) accepted the Microsauria as members of the stegocephali. Credner (1890, pp. 257-258) raised the question of the relationships of *Hylonomus geinitzi* Credner and *Petrobates truncatus* Credner, pointing out the reptilian features of these forms and suggesting that they might include the ancestors of the reptiles. Following this lead, Baur (1897) declared that these genera were in fact reptiles, and pointed out the additional reptilian character of two sacral vertebrae and ribs. He also emphasized that the persistantly notochordal vertebrae and stegocrotaphic skull were shared by primitive reptiles and stegocephalians, and that the scales of some microsaurs were homologous with the gastralia of others and of reptiles. Moodie (1909a) accepted the reptilian relationships if not nature of the microsaurs, but later (1916, p. 76) rejected this view in favor of their belonging to the Amphibia, apparently because he believed there were only four toes in the manus.

Subsequent writers have treated the group as amphibian, except von Huene, who recently (1948) has argued again for their reptilian affinities. Westoll (1942 a, b) recognized the relationship of the microsaurs to the captorhinomorphs and suggested that they were ancestral to that Order.

Reptilian characters of *Cephalerpeton* which are not found in Amphibia other than microsaurs include:

1. Lacrimal duct piercing canal in lacrimal bone (also in *Seymouria*).
2. Pterygoid with downwardly directed transverse flange.
3. Lower jaw with well developed retroarticular process (known in *Benthosuchus* among the Labyrinthodontia, but otherwise distinctly reptilian).
4. Vertebral column with minute, crescentic intercentra between the lepospondylous pleurocentra. (In this connection the presence of caudal chevrons articulating intercentrally in *Hyloplesion* and *Hylonomus* may be noted.)

5. Neck region of about 7 cervical vertebrae with short or immovable ribs.
6. Pectoral girdle with separate scapular and coracoid ossifications.
7. Ventral scales becoming internal, rod-like, gastralia.
8. Absence of temporal series from skull roof.
9. Absence of otic notch.
10. Pentadactyl manus (primitive for Amphibia).

Reptilian characters shown by other microsaurs, not preserved in *Cephalerpeton*:

1. Basicranium with reptile-like basipterygoid processes, slender anterior process of parasphenoid. (Similar among amphibians only to seymouriamorphs and equally resembling undoubted early reptiles such as the captorhinomorphs.)
2. Two sacral vertebrae.
3. Ilium with posteriorly directed spine but no separate vertical process as in labyrinthodonts.
4. Well ossified pubis, (known in labyrinthodonts, but not generally in small amphibia; the form of the pelvis is more reptilian than stegocephalian).
5. Interclavicle with long posterior process.
6. Relationship of neural arch to centrum noted by Watson.

Cope's objection that the vertebrae were more like those of salamanders than of reptiles was written before the discovery of early Permian reptiles, which have vertebrae much like those of the microsaurs. The double occipital condyle is not invariably associated with a broad parasphenoid; moreover it is not certainly present in microsaurs. At present not one microsaur character is known which could not belong to a primitive reptile as well as to an amphibian. In addition they possess numerous characters mentioned above which are generally regarded as distinctly reptilian.

On the basis of this evidence it seems that the Microbrachiidae is a family of primitive reptiles rather than of Amphibia. Von Huene (1948) has independently suggested this while the present studies were in progress. In arrangement of skull bones, microsaurs seem close to the captorhinids; both families have large expansion of the jugal on the face behind the orbit. The neural arches of the vertebrae, however, are not swollen like those of the captorhinids and resemble more those of primitive pelycosaurs. It has long been realized that the known Captorhinomorpha, except *Limnoscelis*, while exceedingly primitive in most respects, possessed certain specializations of the teeth which made them improbable ancestors of later reptiles, although the generally ancestral position of the group to all later reptiles has not been questioned. Microsaurs, occurring as they do slightly earlier than the captorhinids, and lacking the specialized durophagous dentition of the Captorhinidae, as well as the peculiarly swollen "cotylosaurian" neural arches, form even better generalized ancestors of the Eureptilia.

The Microsauria lack the distinctive vertebrae of the Captorhinomorpha, and therefore are best regarded as a separate Order under the infraclass Captorhina (Olson, 1947). The classification may be summarized as follows:

- Class Reptilia
    - Subclass Parareptilia
    - Subclass Eureptilia
        - Infraclass Captorhina
            - Order Microsauria
                - Families Microbrachiidae
                    - Gymnarthridae
                    - Dolichosomidae
            - Order Captorhinomorpha
                - Families Captorhinidae
                    - Limnoscelidae
        - Infraclasses Synapsida, etc.

Whether the microsaurs possessed amniote embryonic development must, of course, remain unknown. Their occurrence in coal swamp deposits suggests at least a partly aquatic mode of life. As we are unable to demonstrate whether they underwent amphibian or reptilian development, their systematic position must be estimated from morphological characters. These rather clearly connect them most closely to the most primitive true reptiles, the Captorhinomorpha. Whether amphibian or reptile, they are the most ancient and most primitive members yet found of the amniote line.

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