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THE NATURE AND RELATIONSHIPS OF THE PALEOZOIC MICROSAURS

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ABSTRACT. An attempt is made to establish a series of characters whereby the small Paleozoic tetrapods usually termed microsaurs may be defined. A considerable number of Carboniferous and early Permian genera belong to this category, but other genera which have frequently been included do not pertain. Although the "type" microsaur, *Hylonomus*, is among the forms excluded, it seems best to retain the familiar ordinal term Microsauria for the group as here defined. The microsaurs appear to have no relationship to reptiles, but are possibly ancestral to the urodele and apodous amphibians.

FOR a number of years I have been engaged in a review of our knowledge of the older, pre-Jurassic fossil Amphibia, attempting to place them in a reasonably consistent phylogenetic and systematic framework—this not as a definitive arrangement, but with the aim of furnishing a point of departure for future work. I have from time to time made "reports of progress" in one form or another (as in Romer, 1940, 1941a) and have incorporated the results of the earlier stages of this work in the revision of my text in vertebrate paleontology (1945a). I have recently reviewed the Labyrinthodontia in rather comprehensive fashion (1947).

There remains for consideration a second major group. This I have called the Subclass Lepospondyli, using this term in a very broad sense to include the existing Urodela and Apoda (Gymnophiona) as well as various ancient fossil forms. In the labyrinthodonts the vertebral centra appear to have ossified from varied cartilaginous "arch" centers; in the lepospondyls the centrum is characteristically a spool-shaped unit structure, formed, it would seem, as a direct ossification in a mesenchyme sheath about the notochord.

A very considerable amount of material has been assigned, from time to time over the past century, to the various Paleozoic groups which I include in the Lepospondyli. Our knowledge of these forms is, however, quite unsatisfactory in almost every instance. Most are animals of small size, with a body length, generally, of but a few inches. This in itself tends to make accurate observation difficult. A majority are preserved in flattened, two-dimensional form, frequently on slabs of shale or "cannel"; this adds a further handicap. Specimens from the Coal Measures constituting a considerable proportion of the material, are frequently "diseased" through the presence of pyrite, and tend to disintegrate, thus making it impossible to verify or amplify the studies (often superficial) of the original describer. Much of the material is fragmentary in nature—disembodied heads, headless trunks, disarticulated partial skeletons, often with dubious association of various elements. As a consequence our knowledge of the Paleozoic lepospondyls is tantalizingly inadequate, despite the attention paid them in early days by such men as Dawson, Huxley, Cope, Fritsch, and Credner, and even despite valuable revisionary studies of recent years, of which those of Steen are outstanding.

A plethora of names, mainly of ordinal character, has been applied to the various components of this ancient lepospondyl assemblage. A pattern which many have followed, and to which I have very tentatively adhered, was established as a result of the report of the Miall Committee (on which Huxley presumably played an important role). In this report (Miall, 1875, p. 151) most of the amphibians to be considered here were ranged in three groups: Nectridia, Aistopoda, and Microsauria. The Nectridia are, despite skull modifications, a clear-cut group, abundant in the late Pennsylvanian and surviving into the early Permian; the double fan formed by neural and haemal arches of the caudal vertebrae is an unmistakable nectridian trademark. The group Aistopoda was formed to care for two elongate, eel-like or snake-like types found in the Carboniferous, of which *Ophiderpeton* and *Dolichosoma* are representative. There is little or no evidence that the two are related rather than parallel (cf. for example, J. T. Gregory, 1948b), but we will not concern ourselves here with this problem.

DEVELOPMENT OF THE MICROSAUR CONCEPT

In the year 1853 a paper by Lyell and Dawson (with addenda by Owen and Wyman) announced the discovery of the remains of tetrapods in tree stumps at the famous Carboniferous locality at the Joggins, Nova Scotia; Dawson published a number of later papers on additional finds. The material has been restudied by Miss Steen (1934) (who gives references to the earlier literature). Much of it pertains to a small rhachitomous amphibian, *Dendrepeton*, but in addition there are various more obscure remains to which a variety of names has been given. One named form is of importance here—the genus *Hylonomus*, with *H. lyelli* as the genotypic species. The type material is that of a small animal which Dawson believed to show reptilian affinities. For its inclusion he erected the group Microsauria. This term was retained by Cope (1869, p. 9) and by the Miall Committee in 1875; they, however, in opposition to Dawson, considered the Microsauria as amphibians rather than reptiles—an opinion followed by most (but not all) later writers.

Until this time, no forms other than those represented by Joggins material had been included in the Microsauria. Now, however, began Fritsch's classic studies of the fauna of the "Gaskohle" of Bohemia, the results of which were published in four quarto volumes beginning in 1879. Among the tetrapods from Nyran and other localities in the Stephanian of Bohemia were a number of small forms—as *Microbrachis*, *Hyloplesion*, *Seeleya*, *Sparodus*, "*Limnerpeton*"—which he associated with the Microsauria; in fact, certain remains were included in the typical genus *Hylonomus*. There followed Credner's work on the equally famous European Lower Permian locality of the Plauen'schen Grunde near Dresden. Certain small tetrapods—"*Hyloplesion*," *Petrobates*—from this locality were interpreted by Geinitz and Deichmüller (1882) and by Credner (1885, 1890) as related to Fritsch's and Dawson's microsaurs and indeed one of the two forms concerned was assigned (on very slight grounds) by Credner to Dawson's genus *Hylonomus*. In this country, Cope described the fauna of the Linton (Ohio) cannels (1875, etc.); most amphibians from this deposit are labyrinthodonts, nectridians or aistopods, but many of the Linton forms have been referred at one time or another to the microsaurs (Moodie, 1916, Romer, 1930, Steen, 1931). Unpublished work by L. I. Price indicates that a number of small Texas Lower Permian tetrapods, often confused with the captorhinomorph reptiles, are related to the supposedly characteristic microsaurs—these including *Pariotichus* (s.s.), *Cardiocephalus*, *Gymnarthrus*, *Euryodus*, and possibly others. Still further forms have been assigned to the general microsaur category by one writer or another. Most workers treating of this assemblage of forms have retained Dawson's name

Microsauria, although the writer (1933, pp. 112, 436) used Micramphibia as more appropriate. Watson (1929) in describing some small skulls from the Scottish Lower Carboniferous—*Adelogyrinus*, *Dolichopareias*—coined the new ordinal name Adelospondyli. This term, applied primarily to the Scottish genera and to *Lysorophus* of the American Permian, was mainly based on the fact that in these forms, in contrast to various other lepospondyls, neural arch and centrum are suturally separate. However, Miss Steen's work (1938) shows that this sutural situation is spread widely but sporadically and variably through much of the extent of the microsaurs. As Westoll notes (1942a) the neurocentral suture proves to be an unreliable taxonomic character, and Adelospondyli appears to be essentially a synonym of Microsauria—as this term is currently used. Although various authors have made various additions or subtractions, the circle of forms currently regarded as belonging in the Microsauria is essentially that given by me in the recent edition of my text (1945a, pp. 591-592).

THE MICROSAUR CONCEPT

The current microsaur concept embraces a variety of tetrapods, mainly from the late Pennsylvanian but extending downward stratigraphically into the Mississippian and upward into the Lower Permian. All are of small size—many are tiny. All appear to have spool-shaped, "holospondylous"— *i.e.* lepospondylous—vertebral centra, and in this are in contrast with typical labyrinthodont amphibians. We may note that in distinction from other lepospondyls the vertebrae lack the peculiar fan-shaped caudal arches which are the trade-mark of the nectridian; the body shape, where known, is relatively normal and hence in contrast with the snake-like types currently placed in the Aistopoda (*Lysorophus* and its allies, if considered microsaurs, are atypical in this as well as other regards). Beyond these few obvious features there is at present in the literature no further definition of a microsaur. This situation suggests that we are dealing with an amorphous, ill-defined assemblage with nothing to guarantee that it is a natural unit. Further, there is little to distinguish microsaurs on this basis from the reptiles—a point of major importance, since confusion may occur (and has occurred) between the two groups, and since at various times part or all of the microsaurs have been claimed to be reptiles or related to them.

We shall not at this point concern ourselves with the nature of the Nova Scotian *Hylonomus* "type" of the microsaurs, for, as we have noted, the concept of the group Microsauria rapidly passed from one based on *Hylonomus* to one derived from a series of forms, mainly European, which are not necessarily similar to *Hylonomus* (and, as noted elsewhere, are apparently quite distinct). Of such forms *Microbrachis* of the Stephanian of Nyran is the best known, since it is represented by abundant material which has been carefully redescribed by Miss Steen (1938, pp. 227-234, figs. 15-20, plates 1, 3). *Microbrachis* has certain characters of the skull table which are not repeated in other microsaurs and hence may be recognized as specializations; it otherwise appears to occupy a reasonably central position in the modern concept of a microsaur (and is so considered by Westoll, 1942b). Features seen in *Microbrachis* and its close allies which can be of aid in deciding whether or not other forms belong in the same broad category are here listed and commented upon.

1. *Size small.* The specimen restored by Steen has a length of about 12 cm.; some individuals of *Microbrachis* were moderately longer. This size appears to be about an average for Carboniferous microsaurs (some terminal Lower Permian forms were considerably larger).

2. *Body moderately long and slender. Microbrachis* and various other microsaurs have rather salamander-like proportions, with an elongate trunk (here about four times the skull length); a high number of presacral vertebrae (here 38 presacrals, but a somewhat lower count in other known cases); rib contours indicating a relatively narrow trunk.

3. *Spool-shaped vertebral centra; no trunk intercentra; caudal chevrons?; neural arch pedicel relatively high and narrow anteroposteriorly; neural arch not expanded transversely nor swollen; neural spine little developed.* The vertebrae and ribs of *Microbrachis* are figured by Steen (1938, fig. 19C) and Schwarz (1908, fig. 35). In various other microsaurs the centra may be less elongate; cf. for example, Fritsch, 1879, plate 40, fig. 1 (*Seeleya*). Trunk intercentra have not been reported in any form here regarded as a microsaur; it is, however, not impossible that such structures were present in

cartilage in some cases. Steen reports poorly preserved caudal chevrons in one specimen of *Microbrachis*. Since, however, they do not appear in other individuals of this or in related forms, and since some confusion with caudal ribs is not impossible in a small and poorly preserved specimen, judgment may be suspended on this feature. The narrow base of the neural arch and lack of any degree of spine development is a striking feature of Nyran microsaurs in general, as may be seen in various of Fritsch's figures on his plates 37, 39, 40, 44, etc. There is no evidence in the material of the expanded, swollen type of neural arch so typical of the cotylosaurs and of the seymouriamorphs.

4. *Ribs two-headed, capitulum often articulating with facet or low process on the centrum, tuberculum articulating with transverse process.*

5. *Interclavicle with very broad but short fan-shaped head and short slender stem.* The girdles are too poorly preserved in most microsaurs for accurate diagnosis. The interclavicle is, however, of a unique type; see Steen, 1938, fig. 19B; Fritsch, 1879, plate 47, figs. 1-3.

6. *Limbs relatively short and feeble; manus three-toed.* The limbs of *Microbrachis* and of such other typical microsaurs as have at all adequate limb material preserved are relatively short and slender compared with those of many labyrinthodonts and are seen to be especially feeble if compared with those of contemporary reptiles. That the three-toed nature of the manus of *Microbrachis* is not exceptional or based on faulty material appears to be confirmed by a similar three-toed condition in *Hyloplesion* (Steen, 1938, fig. 22A).[1]

7. *Scales with a characteristic radiate striation; ventral scales sub-oblong, with a pronounced posterior ridge; dorsal scales rounded.* This type of radiate scale ornamentation is, as far as I am aware, confined to microsaurs and is widespread in this group. The scales of *Microbrachis* (Fritsch, 1879, plate 47) are slightly atypical in that the ridges of the striate pattern are heavier and coarser than is normal; for other and perhaps slightly more typical scales from Nyran, cf. Fritsch, 1879, plate 32, figs. 2, 5; plate 35, figs. 5-7; plate 37, figs. 1, 9-11; plate 39; plate 40; plate 41, figs. 2, 3, etc. In some cases (as

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[1] I know of no evidence for the restoration by Fritsch (1879, figs. 94, 103, 105, 108, 112) of microsaurs with a five-fingered hand.

Sparodus crassidens, Fritsch, 1879, plate 10) the pattern may assume a more circular rather than a radial arrangement.

8. *Skull greatly elongate postorbitally; otic notch absent.* In the series crossopterygians-amphibians-reptiles there has been, as pointed out by Westoll (1938) and the writer (Romer, 1941b, pp. 156-159, fig. 4) a notable shift in skull proportions as regards the relative length of the preorbital and postorbital segments; there has been, along this main evolutionary line, a steady reduction of the relative length of the postorbital region

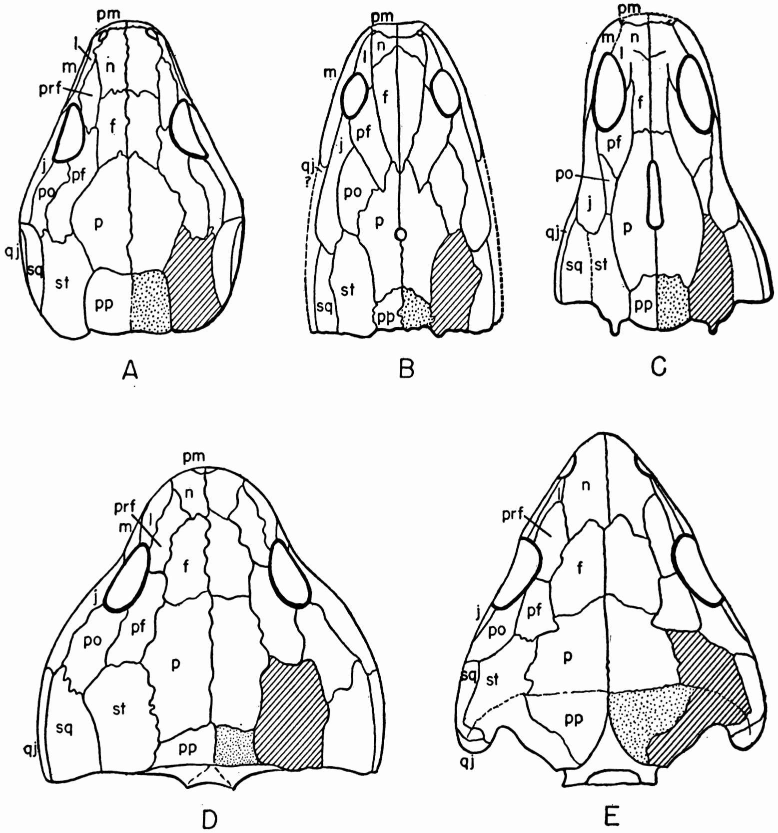

Figure 1. Dorsal views of various microsaurs: *A, Euryodus, B, Dolichopareias, C, Adelogyrinus, D, Pantylus, E, Ostodolepis.* Abbreviations: *f,* frontal, *j,* jugal, *l,* lacrimal, *m,* maxilla, *n,* nasal, *p,* parietal, *pf,* postfrontal, *pm,* premaxilla, *po,* postorbital, *pp,* postparietal, *prf,* prefrontal, *qj,* quadratojugal, *sq,* squamosal, *st,* supratemporal, *t,* tabular. On right side, supratemporal hatched, postparietal stippled. *A* after Olson, *B, C* after Watson, *D* composite of various specimens, *E* after Case.

(disregarding obviously secondary reversals among certain temnospondyl labyrinthodonts). The short face and long postorbital region of *Microbrachis* (and other microsaurs) shows a remarkably primitive condition (figs. 1, 2).

9. *Skull roofing pattern generally primitive, but tabular absent from roof and a very large supratemporal interposed between parietal and squamosal.* The pattern of the temporal region, when preserved, offers the best diagnostic character of this group (figs. 1, 2). In various other amphibians—notably the Rhachitomi—there is a trend for reduction of bones on the skull table, so that in addition to loss of the intertemporal the posterior elements may undergo reduction at the expense of the more anterior ones. But in no known labyrinthodont is the tabular completely excluded from the skull roof; here it is absent in all known cases, although the postparietal persists dorsally. In contrast to the reduction of the tabular we find the supratemporal highly developed as a major component of the skull roof.

In regard to the skull table *Microbrachis* (fig. 2B) appears to be somewhat aberrant; such a form as *Euryodus* (fig. 1A) shows what is apparently a more primitive condition. In such forms the postparietals, strongly reduced in *Microbrachis*, are persistently large. Further, while the supratemporal is a large

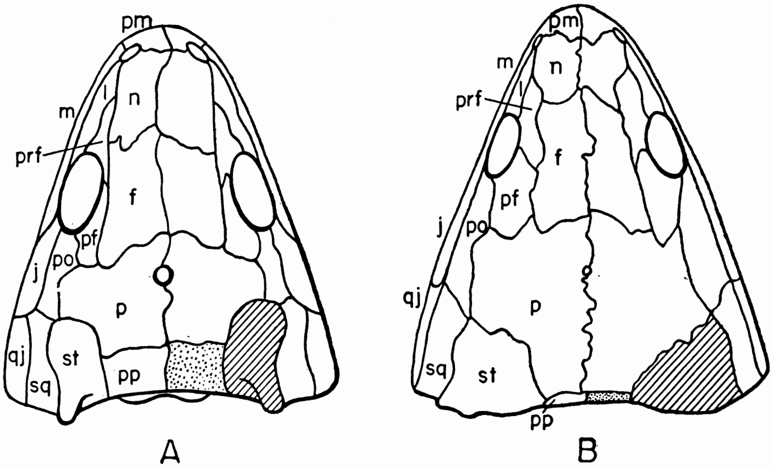

Figure 2. Dorsal views of skulls of *A, Hyloplesion, B, Microbrachis.* Abbreviations and conventions as in figure 1. *A* partly after Steen, posterior elements restored from Fritsch's data; *B* after Steen, but postparietal (present in smaller individuals only) retained.

element in *Microbrachis*, it is still more prominent in other microsaurs shown in figs. 1 and 2, stretching forward to a broad contact with postfrontal and postorbital—a contact almost entirely lost in *Microbrachis*.

Whether the element here termed supratemporal is really that element or the tabular is not, of course, entirely certain (particularly in the absence of knowledge of the occiput in most microsaurs). But presumably the process of modification in skull table pattern was parallel to that seen in certain labyrinthodonts, in which the tabular may be nearly pushed off the skull roof, while the supratemporal remains an element of substantial size (Romer, 1947, fig. 22, etc.). It is important to note that in these labyrinthodonts the postparietal is reduced *pari passu* with the tabular, whereas in microsaurs the former element is much more resistant to reduction.

10. *Palate essentially primitive in nature, with slender cultriform process of parasphenoid; movable basal articulation of braincase and palate, narrow interpterygoid vacuities.* Unfortunately little is known of braincase structure in *Microbrachis* or indeed in any microsaur. The occipital condyle (unknown in *Microbrachis*) appears to have been generally primitive in nature—technically single, but broadened and trending (as in other amphibians) toward the double type.

The items listed above give us a diagnosis which may be applied to Paleozoic tetrapods as a possible test of inclusion in or exclusion from the microsaur group. It is unfortunate that this list of characters seen in *Microbrachis* is incomplete and to some degree superficial. However, the forms to be surveyed are in almost every case still more poorly known than is *Microbrachis* itself and we must grasp at any available straw. Of the characters listed, the skull table pattern is apparently most useful in cases where the skull is known; in fragmentary or poorly preserved material, the scale type is a useful clue.

IDENTIFIABLE MICROSAURS

1. *Microbrachis*, as discussed above.

2. *Hyloplesion.* In the late Pennsylvanian Gaskohle fauna of Bohemia described by Fritsch, a number of other microsaurs are identifiable. Best known is *Hyloplesion longicostatum*, represented by complete skeletons as well as more fragmentary materials (Fritsch, 1879, pp. 160-161, plate 27, fig. 5; plate

36, fig. 2; plates 37, 38; plate 39, figs. 1-9; Steen, 1938, pp. 234-237, figs. 21, 22, 44B; plate 1, fig. 1; plate 4, fig. 3). In general the skull is quite similar to that of *Microbrachis.* Steen figures a small tabular, but this interpretation is certainly questionable and Fritsch's figures and galvanotypes strongly suggest that the supratemporal extended back to the posterior end of the table as in other microsaurs (fig. 2A). *Hyloplesion* is less specialized than *Microbrachis* in that the postparietals are well developed. The postcranial skeleton, including vertebral count and structure, squamation, etc., all agree well with *Microbrachis.* The presence of a three-toed manus, as in that genus, may be noted.

3. "*Limnerpeton.*" This genus of Fritsch's is a dumping ground for poorly known amphibians. Some of the remains are those of labyrinthodonts (Romer, 1947, pp. 143-144) and some are quite obscure.[2] A majority of the *Limnerpeton* species seem, however, to fit in well with the microsaur pattern in scales, vertebrae and other details. Such are: *L. macrolepis, L. elegans* and *L. obtusatum* (Fritsch, 1879, plates 32-35, etc.).

4. *Seeleya* (Fritsch, 1879, plate 40, fig. 1; plate 41, figs. 1-3). This is a very tiny Nyran form, obviously pertaining to this group but with relatively short vertebrae. *Orthocosta* (Fritsch, 1879, plate 39, figs. 10, 11; plate 44, figs. 1-3) is a probable synonym.

5. *Sparodus.* Somewhat more doubtful is this genus (Fritsch, 1879, plates 8-10). Two species are described; their congeneric nature is none too certain. *S. crassidens,* from Kounova, exhibits microsaur squamation. Both, but particularly *S. validus* from Nyran, have a strong palatal dentition which was compared by Cope (1881, p. 79) with that of *Pantylus* of the American Permian.

6. *Ricnodon.* The fragmentary material assigned to this genus by Fritsch (1879, pp. 167-171, figs. 106-108, plates 42, 43, 44, figs. 4-15) shows microsaur vertebrae and scales. However, the skull described by Watson and by Steen (1938, p. 227, figs. 13, 14, plate 7) as *R. limnophyes* is not microsaurian in nature and evidence for assignment here is very weak.

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[2] *"Limnerpeton" laticeps* (Fritsch, 1879, plate 36, fig. 1) is strikingly similar to *Amphibamus* and *Miobatrachus,* presumed ancestral "frogs."

7. "*Hylonomus*" of Niederhässlich. Certain small tetrapods present in the early Permian Niederhässlich deposits near Dresden, first described by Geinitz and Deichmüller (1882, plate 8, figs. 1-9) were identified as belonging to Fritsch's genus *Hyloplesion*. Credner (1885, pp. 724-736, plate 29) assigned this material to Dawson's genus *Hylonomus* (quite incorrectly, one may believe); later, however, he realized that two quite distinct animals were represented. One, *Petrobates*, will be considered later; the second he termed *Hylonomus geinitzi* (Credner, 1890, pp. 240-247, 255-258, plate 9, figs. 1-11), pointing out, however, its close similarity to Fritsch's *Hyloplesion*. This animal (once the *Petrobates* material is sorted out) conforms in most regards to the typical microsaur structure defined earlier. The vertebrae and clearly dichotomous ribs are comparable to those of *Microbrachis* and *Hyloplesion*. Intercentra are absent; so too are haemal arches in the tail. Credner's plate 9, figure 5 indicates a vertebral count of close to 30 presacrals (despite his own statement that the count was much lower). Several of Credner's figures show the characteristic fan of the interclavicle, and a low degree of development of limbs, much as in *Microbrachis* and *Hyloplesion*. The scales are closely comparable with those of *Hyloplesion*. It may be noted, however, that in addition this form has a series of tiny polygonal bony plates in the region of the pectoral girdle (Credner, 1890, plate 9, figs. 6, 9, 10, 's'). The skull is poorly preserved but Credner's plate 9, figure 6 shows clearly the presence of three elements lateral to the parietal—obviously the characteristic large supratemporal in addition to squamosal and quadratojugal.[3]

8. *The gymnarthrids*. Vertebrate specimens from the early Permian Redbeds of the American Southwest are preserved in a fashion quite different from those of the European deposits so far discussed. Instead of slabs of shale on which small skeletons may be preserved but skulls crushed, the usual matrix is a clay from which recovery of tiny skeletons is unusual but in which skulls may be preserved in three-dimensional fashion. In consequence we deal here mainly with skull material. Parenthetically, we may note that these terminal members of the

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[3] The restored composite skull figured as that of "*Hylonomus geinitzi*" by Watson (1940, fig. 11) does not agree with this; it is, however, of a type to be expected in *Petrobates*.

microsaur group tend (as do other contemporary lepospondyls) to relatively (although not absolutely) large size.

The typical microsaurs of the American Redbeds are a series of forms which include *Pariotichus*, *Gymnarthrus*, *Cardiocephalus*, *Euryodus and Isodectes;* they are known almost entirely from skull materials, these skulls averaging about 2 cm. in length. Most recently described is *Euryodus* (Olson, 1939); a resumé of the older material was given by Case (1911a, pp. 69-70, 144-145; 1911b, pp. 34-35, 36-38, 91-93). Mr. L. I. Price informs me, as a result of his unpublished studies of the group, that all are very similar in cranial structure despite variations in description. The skull pattern, as seen in *Euryodus* (fig. 1A) or *Pariotichus*, is exactly that to be expected in a typical microsaur—a short face, a very long, postorbital region, good postparietals but no tabular in the skull table, and a long and highly developed supratemporal reaching forward to a broad contact with both postorbital and postfrontal. The palate, as in other microsaurs, is one with a narrow cultriform process of the parasphenoid, movable basal articulation and narrow interpterygoid vacuities. The teeth are, in this group, blunt and medio-laterally compressed. As in certain, at least, of the other microsaurs there is no indication of emphasis of the "canine" region in the anterior part of the maxilla; instead there is here a trend toward tooth enlargement in the posterior part of the maxillary series.

9. *Ostodolepis.* Other microsaurs, less typical in nature but definitely members of this group, can be identified in the Redbeds fauna. One such is *Ostodolepis.* This was first described by Williston (1913) on the basis of vertebrae; Case later (1929) described a nearly complete skeleton. A striking peculiarity lies in the skull shape, with a domed roof and curiously pointed "snout." Case, in summarizing the features of *Ostodolepis*, found himself puzzled to assign this form to either reptiles or amphibians since it seemed to him to show many features characteristic of both classes. However, the more important of his supposed reptilian characters—such as the palatal construction—are now known to be primitive amphibian characters retained in microsaurs as in reptiles.

The skull, despite its obvious peculiarities, shows the definitive microsaur characters (fig. 1E): absence of tabulars from the skull roof, but retention of postparietals (here slanting backward on the occipital surface), and a highly developed supratemporal running from postorbital and postfrontal to the back of the skull. Ossified hyoids are present. The vertebrae are "holospondylous"; there are no intercentra[4] nor is there space for them; the neural arches are not broadened nor swollen. The imperfectly preserved interclavicle has (Case notes) an extraordinarily broad head, and thus is probably of microsaur type. The limbs are relatively small. There is preserved a system of ossified scales which Case compares with those of the microsaur *Sparodus crassidens* of Fritsch.

10. *Pantylus.* The genus *Pantylus*, mainly known from skull material from the Texas Permian Redbeds, has long been a puzzle to paleontologists; Williston (1916, pp. 165-176) is the most recent describer. The lack of an otic notch and its relatively large size (reaching a skull length of 9-10 cm.) have caused most authors to place it among the cotylosaurs. It does not, however, conform readily to the structural pattern of any cotylosaur group, and its specialized dentition, with a battery of blunt crushing teeth, tends to further isolate it. Restudy indicates that it is unquestionably a (relatively) large end form among the microsaurs, and is obviously related to *Sparodus* of earlier European deposits (Cope, 1881, p. 79; Romer, 1945b, p. 429). The proportions of the skull roof are typically microsaurian. Williston was unable to determine the pattern of the skull table; comparative study of all available material indicates the presence of the microsaur pattern shown in figure 1D. As in other members of the group, the palate retains a movable basal articulation, and interpterygoid vacuities are small. Vertebrae presumably associated are comparable to those of *Ostodolepis.* If the caudal vertebrae figured by Williston are actually those of *Pantylus* they are of considerable theoretic interest in bearing haemal chevrons. The limbs, incompletely known, were very small; plates in the form of tiny tesserae covering part of the belly are comparable to those noted for the Niederhässlich "*Hylonomus.*"

11. *Tuditanus?* Curiously, identifiable microsaurs from the Carboniferous are as rare in North America as they are abundant in Europe. Several forms thought to be microsaurs are (as noted later) true reptiles. Of the three major American

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[4] The supposed intercentra of Williston's type are not such but are apparently rib fragments.

Pennsylvanian tetrapod localities—Mazon Creek, the Joggins, and Linton—no microsaurs are identifiable from the first and none is positively known from the second (although very probably present). Even at Linton there are few specimens which can even be considered for entry into this category, for most of the forms termed microsaurs by Moodie (1916) have since been shown by Steen (1931) or the writer (1930,1947) to belong elsewhere or are peripheral, rather than typical members of the microsaur group. The only specimens which merit consideration are the type of *Tuditanus punctulatus* and a second specimen which Cope assigned to this species but was made the type of *Eosauravus copei* by Williston (Cope, 1874, pp. 271-272; 1875, p. 392, plate 34, fig. 1; 1897, pp. 88-90, plate 3, fig. 1; Williston, 1908, pp. 395-400; Moodie, 1909, pp. 11-16, plates 4, 5; 1916, pp. 55-88, fig. 19; Romer, 1930, pp. 134-135, etc.). The type specimen of *T. punctulatus* consists of the anterior part of the body of a small tetrapod; the second, type of *Eosauravus*, includes much of the trunk and tail but lacks head and anterior limbs. The *Eosauravus* specimen was hailed by Williston as "the oldest known reptile" and is generally considered as reptilian; little attention has been paid to the *T. punctulatus* type, and there is no guarantee that the two are associated. Little can be made of the skull, and squamation is absent from both specimens. Evidence for reptilian nature is the assumed hind leg phalangeal formula of 2.3.4.5.4, possible presence of more than three digits in the manus and of two sacral ribs, and the presence of a stemmed interclavicle. But there is no evidence of five phalanges in toe four, and certain microsaurs have a five-toed pes with nearly as high a formula; further, it is not impossible to interpret the interclavicle as of the peculiar type seen in *Microbrachis*, etc. Arguing for a microsaurian position are the long and slender body proportions; it is clear that both specimens of *Tuditanus* must have had a higher presacral count of vertebrae than is found in early reptiles. Again, caudal chevrons appear to be absent. Still further, if Moodie is correct as to orbital position in his figure of the *Tuditanus* skull, the long postorbital region is indicative of microsaur rather than reptilian structure. More evidence is needed, but *Tuditanus* is not improbably a microsaur.

12. *Dolichopareias, Adelogyrinus.* Among the few known

amphibians of Mississippian age are two types of modest size represented by skulls and in one instance by some postcranial remains including "holospondylous" vertebrae (Watson, 1929, pp. 245-250, figs. 24-27). In both genera (fig. 1B, C) the "face" is extremely short, the postorbital region much elongate, in a fashion both primitive and comparable with that of later microsaurs. In correlation with this elongation, the postorbital bone has been dragged backward out of the orbital margin (cf. *Colosteus*, *Erpetosaurus*). In both (again as in microsaurs) postparietals are well developed, but tabulars are absent from the skull roof. In both we find instead—as in microsaurs—a single elongate element lateral to the parietal and postparietal extending from the postorbital to the back margin of the skull.[5] In *Dolichopareias* the lateral margin of the cheek is unknown, but we can reasonably regard this element as the supratemporal and assume both squamosal and quadratojugal to have been present more laterally. In *Adelogyrinus* no suture is evident between supratemporal and squamosal, a single large element occupying the position of the two. These two genera may be reasonably considered as early forerunners of the microsaurs.

The microsaur periphery. So far we have confined our survey to forms exhibiting, as far as can be determined, the characteristic features of the microsaurs defined above. There are, however, various other lepospondylous forms of the Carboniferous and earlier Permian which may be allied to the microsaurs and may perhaps be included in a broad common group with them. These may be noted in passing.

It will, I think, be generally agreed that the varied nectridians form a distinct category of lepospondyls. There remain, however, three further series of amphibians, all elongate eel-like or snake-like forms, which are lepospondylous but non-nectridian and hence possibly of microsaur affinities. The *Ophiderpeton* and *Dolichosoma* groups, of ancient lineage, but poorly known, are customarily included (for no particular reason) in a common, distinct group, the Aistopoda. A third series of elongate forms, of which *Lysorophus* of the early Permian is best known, is, in contrast, often included in the microsaurs, and definitely included in Watson's Adelospondyli.

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[5] There is no positive evidence of a tabular, despite its restoration by Bystrow (1935).

Lysorophus, however, is a very specialized form which shows few of the features cited above as characteristic of the microsaurs (cf. J. T. Gregory, 1948a, p. 564) and there is as little—or as much—reason for its inclusion here as for the inclusion of the aistopods.[6] If these forms are related to the typical microsaurs, as may well be the case, the relationship is a distant one and discussion of this matter is not pertinent to our present purposes.

TRUE REPTILES CONFUSED WITH MICROSAURS

It is obvious that the microsaurs have many features in common with the reptiles—features which have led various people to advocate their relationship to reptiles or even their inclusion in that class. Putting aside for the moment the problem of possible relationship, it is of importance to see how a microsaur can be distinguished from forms which would be agreed to by all to be definitely reptilian. *A priori*, it is highly probable that confusion between two such groups, whether related or not, might readily take place. It was once thought that reptiles made their appearance at about the beginning of the Permian; but various instances of the occurrence of true reptiles are now known well down in the Carboniferous and the finding in the Pennsylvanian of such specialized reptile types as *Edaphosaurus* and diadectids indicates that the origin of the Reptilia is to be looked for well back in the Pennsylvanian. We must be on the outlook for small Carboniferous true reptiles which, if poorly preserved or insufficiently described, might be included among the microsaurs.

If the list of microsaur characters cited above be examined, it is obvious that certain of them are found both in this group and in forms generally accepted as genuine reptiles. Both have "holospondylous" vertebrae; the ribs are similar; the microsaurs, like reptiles, have retained an essentially primitive type of palate contrasting with that of most amphibians; neither typical microsaurs nor primitive true reptiles have taken on the eel-like proportions of certain amphibian types; most reptiles have, like microsaurs, eliminated the otic notch; typical microsaurs are much smaller than the average of known early reptiles, but size is no safe criterion.

[6] As I hope to show at another time, *Lysorophus*, sometimes thought to be an ancestral urodele, is a reasonable ancestor of the Apoda.

Other features may, nevertheless, aid us in distinguishing between the two groups. On the basis of present knowledge, the presacral intercentra are indicative of a reptile rather than a microsaur, and the presence of haemal arches is perhaps diagnostic as well. Early true reptiles are all relatively short and stocky, with no more than 27 presacral vertebrae, and with stoutly developed limbs; all microsaurs in which the body form is known have much more slender and elongate trunks, with a higher presacral vertebral count (usually in the 30s) and with limbs of smaller size.[7] The pes of microsaurs is of a pentadactyl type not dissimilar to that of reptiles; the manus, in contrast, has but three digits in known instances.

The squamation is highly distinctive. The typical microsaurs have well developed ornamented ventral (and dorsal) scales; in reptiles there is a ventral "abdominal rib" system with the scales reduced to oat-shaped or rod-shaped elements.

The skull, if well preserved, can exhibit strongly contrasting features (cf. fig. 3 with figs. 1, 2). The microsaur skull is exceedingly primitive in its elongate postorbital region; reptiles are notable for major reduction proportionately of the

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[7] Even discounting the greater slenderness of limb elements to be expected in small animals.

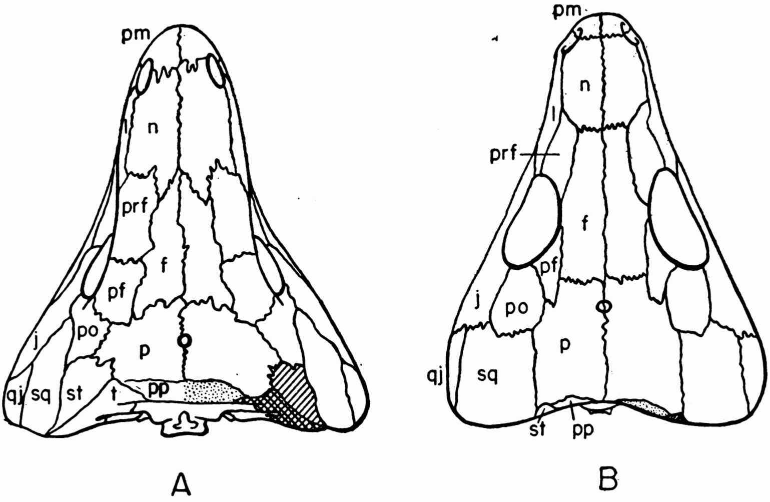

Figure 3. Dorsal views of skulls of captorhinomorph cotylosaurs: *A, Limnoscelis, B, Captorhinus,* to show contrast in skull pattern with that of microsaurs. Abbreviations and conventions as in figures 1 and 2; tabular cross-hatched.

posterior skull region. In microsaurs the otic notch has been obliterated—so thoroughly obliterated that dermal cheek and table elements are welded into a single unit. In early reptiles the notch is still retained in diadectomorphs; it is lost in captorhinomorphs, but welding of cheek and table is still imperfect, so that, as seen in *Limnoscelis* (and even in pelycosaurs) there persists a line of structural weakness between cheek and table components. The condition of supratemporal, tabular and postparietal is markedly different in the two groups. In reptiles in correlation with occipital shortening, the table exposure of both postparietal and tabular is much reduced and the supratemporal, never of great size, is reduced in parallel fashion. In microsaurs, the condition of these three elements differs greatly. The tabular is completely eliminated from the roof in every known instance, while in every form known except *Microbrachis* the postparietal remains well developed dorsally. The supratemporal is not reduced concomitantly with the posterior elements; instead, it is expanded to become a very prominent element in the pattern.

Using these diagnostic characters, it can be seen that certain forms often included in the microsaurs do not fall in this group, but are apparently proper reptiles, presumably cotylosaurs.

1. *Petrobates.* This name was applied by Credner to a small tetrapod from Niederhässlich which had earlier been confused by Geinitz and Deichmüller (1882, pp. 38-41) with "*Hylonomus*." Credner (1890, pp. 255-257) tabulates various differences between the two; and it is interesting that most of the features in which *Petrobates* differs from its contemporary are almost precisely those in which a primitive reptile might be expected to differ from a microsaurian amphibian (the skull structure is, unfortunately, poorly known). Both are small tetrapods with "holospondylous" vertebrae, but *Petrobates* is much the more stocky type, with stouter limbs and a shorter vertebral column (only about 19 presacrals as compared with a much higher number in "*Hylonomus*"); the manus is pentadactyl; haemal chevrons are present. A superficial but definitely diagnostic feature lies in the nature of the ventral squamation. Primitive reptiles as noted above are characterized by the presence of a system of V-shaped rows of slender oat-shaped or rod-shaped scales which contrast sharply with

the typical oblong amphibian scales of the microsaurs. Reptilian scales are present in *Petrobates*; "*Hylonomus*" has the microsaur type. It seems certain that *Petrobates* is a small reptile, very probably a captorhinomorph cotylosaur.

2. *Cephalerpeton*, a small tetrapod from the nodule beds of Mazon Creek, was described by Moodie as a microsaur. The specimen has been restudied by J. T. Gregory (1948a). On the basis of its structure, he argues that *Cephalerpeton* is a reptile and that hence microsaurs are reptiles. With his conclusion that *Cephalerpeton* is a reptile I am in complete agreement. But many of the features which he cites to prove its reptilian nature are crucial reptilian characters not found in typical microsaurs. The slender ventral abdominal ribs are typically reptilian and in contrast with microsaur scales. Presacral intercentra are present in the column in contrast to known microsaurs. The limbs are more highly developed than in microsaurs and in contrast to microsaurs in which the manus is known, the front foot is pentadactyl. In apparent contrast with microsaurs (but the evidence is poor) is the presence of a distinct coracoid ossification and of an entepicondylar foramen in the humerus. Significant is the reptilian nature of the ventral scales as elongate gastralia. The skull proportions, with a much abbreviate postorbital region, are those of a reptile and in sharp contrast to those of true microsaurs. It is unfortunate that the skull table is poorly preserved but it seems certain that the most diagnostic of all microsaur features—the large supratemporal—is absent from the skull pattern. Significant as well is the typical reptilian pterygoid flange described by Gregory, and the pronounced retroarticular process of the jaw. Altogether, *Cephalerpeton* appears to be a true reptile, quite unlike the typical microsaurs, and presumably a member of the captorhinomorph cotylosaurs (cf. *Romeria*). The only contradictory evidence is the fact that the neural arches do not appear to show the swollen condition normally found in cotylosaurs.

3. *Hylonomus*, type of the Microsauria of Dawson (although not of later writers), is known only from the erect trees of the Joggins—and very poorly known at that, for, as Steen (1934) points out, there is no guarantee that any of the material assigned to this genus properly belongs here apart from the type specimen and a second which is closely comparable. Both are very fragmentary and there is no skull

definitely associated. Even so, a variety of features indicate that we are dealing with a typical reptile. These include: (1) relatively large limbs; (2) caudal chevrons; (3) pelvis almost identical with that of such primitive reptiles as *Limnoscelis* (or even the pelycosaur *Ophiacodon*); (4) interclavicle of typical reptilian shape and especially (5) the scales, which are long slender rods of reptilian type and contrast strongly with those of the microsaurs of current concepts. *Hylonomus* is probably a captorhinomorph cotylosaur but might possibly be an ophiacodontoid pelycosaur.

Fritschia and *Leiocephalikon*, likewise from the Joggins, are equally poorly known (Steen, 1934, pp. 490-492), but the evidence suggests that they also are true reptiles.

The identification of *Hylonomus* as a true reptile leads to an embarrassing situation in nomenclature, for the term Microsauria was based upon this genus. If we were dealing with nomenclature on a generic or specific level, this would mean that the name Microsauria should follow its "type" and that some other term should be used for the forms discussed in this paper. But there is no "legal" compulsion upon one to do this; no advantage would be gained and, on the contrary, some confusion would result. I therefore propose to continue the use of the term Microsauria in its current sense, based upon *Microbrachis* and related forms.[8]

4. *Eusauropleura.* A specimen from the Linton Pennsylvanian sometimes considered a microsaur is that which forms the type of *Eusauropleura* (*Sauropleura*) *digitata* (Cope, 1875, p. 403, plate 37, fig. 1; Romer, 1930, pp. 135-136, fig. 26, etc.). The specimen exhibits the ventral side of the trunk of an animal, showing the ventral squamation, much of the limbs and ribs. The head is not preserved, the vertebrae are not visible and the hind leg is incomplete. Such data as can be obtained indicate that *Eusauropleura* is a true reptile: (1) the oat-shaped gastralia are of reptilian type, (2) the five-toed manus with a reptilian phalangeal formula of 2.3.4.5.3 is in contrast with the three-toed condition in known microsaurs, (3) the trunk was obviously relatively short and compact, after the primitive reptilian rather than the microsaurian pattern.

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[8] I have profited from discussion with Dr. J. T. Gregory of this problem and others connected with the microsaurs.

MICROSAURS AS REPTILE RELATIVES?

Even if we can distinguish morphologically between microsaurs and forms definitely reptilian, may it not be that these forms can still be classed as reptiles in a broad sense or as forms ancestral to them? Many workers have claimed that the microsaurs are of reptilian nature, as, for example, Dawson (1863, p. 47, etc.), Baur (1897), J. T. Gregory (1948a), Huene (1948). But if the conclusions given in the last section are accepted, the arguments of the first three of the writers mentioned are, while perfectly acceptable, beside the present point, for they are based almost entirely on forms—*Hylonomus*, *Petrobates*, *Cephalerpeton*—which appear to be true reptiles and not microsaurs in the customary sense.[9] Huene's thesis rests in great measure upon certain features of rather doubtful or debatable nature, such as the presence of caudal chevrons, the identification as a tabular of the bone here called the supratemporal, presence of single occipital condyle, and of an otic notch.

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[9] Baur's evidence for the reptilian nature of *"Hylonomus"* (of Niederhässlich) as well as *Petrobates*—two sacral ribs, for example—appears to rest on specimens identified by Credner as belonging to the latter genus.

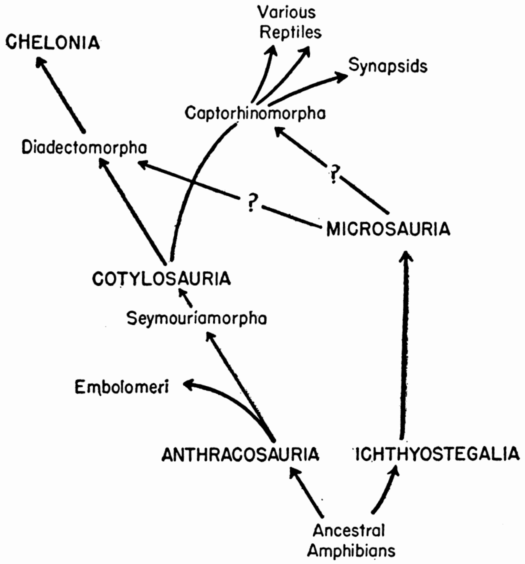

Figure 4. Phylogenetic diagram of possible origin of reptiles. Orthodox interpretation, through anthracosaurian labyrinthodonts, at the left; microsaurian derivation at the right.

Westoll (1942a, 1942b), from a somewhat different viewpoint maintains that the microsaurs, or adelospondyls, are ancestors of the captorhinomorph cotylosaurs. To properly evaluate his ideas it is necessary to view them in the light of currently accepted concepts of reptilian ancestry and phylogeny which have grown up through the work of Case, Williston, Watson and others (cf. fig. 4).

It is generally held that the reptilian pedigree stems from a point near the base of the Amphibia and leads through the anthracosaurian labyrinthodonts (these including the embolomeres) which had developed true centra and other reptile-like structures. *Seymouria* is a late representative of a group of anthracosaurs, or at least of forms of anthracosaurian derivation; it shows so many characters identical with those of reptiles as to be frequently included in the "stem reptiles" or, if not so included, is deemed ancestral to them. The reptilian basal stock is usually considered to form an ordinal group Cotylosauria. Known cotylosaurs, however, can be clearly divided into two groups, Diadectomorpha and Captorhinomorpha, as pointed out by Watson (1917) and emphasized by Olson (1947), who even argues that the two groups are so distinct that the term Cotylosauria should be abandoned. Both Olson and W. K. Gregory (1946) conclude that the turtles are descended from diadectomorphs and it is generally agreed that most, at least, of the other reptilian orders have sprung from the captorhinomorphs. Seymouriamorphs, diadectomorphs and captorhinomorphs differ in certain cranial structures, notably as regards the otic notch and adjacent elements, and the palate. *Seymouria* retains the primitive otic notch, diadectomorphs have a peculiarly exaggerated notch, captorhinomorphs have lost it; diadectomorphs have a specialized palate and dentition. In almost every other regard, however, the three groups are strikingly similar and many postcranial structures—even details of neural arch construction—are practically identical. It is difficult to escape the conclusion that the three are closely related, that the reptiles are monopryletic, and that their line of descent lies through the anthracosaurian labyrinthodonts.

Westoll's hypothesis is that the captorhinomorphs have descended from microsaurs (adelospondyls); that the seymouriamorphs are not phyletically related to reptiles; and that while the seymouriamorphs are good anthracosaurs, both diadectomorphs and captorhinomorphs (via the microsaurs) have descended from the very ancient ichthyostegalians—very different amphibians indeed. Positive and convincing proof is required if one is to deny the seemingly certain relationship of *Seymouria* to the reptiles and establish a radically different line of reptilian ascent—proof which Westoll does not furnish. He cites the presence of certain microsaur-reptile similarities, attempts to bring limb structure of microsaurs in line with that of reptiles, and compares the captorhinomorph skull table structure with that of microsaurs. The presence of certain similarities between microsaurs and true reptiles is obvious; but these similarities are matched by still greater similarities between seymouriamorphs and reptiles and counterbalanced by differences which do not for the most part exist between reptiles and their presumed anthracosaur relatives. Limb comparisons force upon him the doubtful assumption that *Eusauropleura*, *Hylonomus*, and *Fritschia* are microsaurs related to *Microbrachis*. It is possible, perhaps, to evolve the skull pattern of reptiles from that of microsaurs, but it is a hard struggle. Captorhinomorphs exhibit the general reptilian trend toward a shortening of the skull table; microsaurs are persistently primitive and show absolutely no trend of this sort. In the captorhinomorphs, postparietal, tabular and supratemporal show concomitantly the expected reptilian drift in skull table structure—posterior movement and reduction in size. Not so in microsaurs, for while the tabular is eliminated in all known microsaurs, the supratemporal has expanded to unusual size and the postparietal generally resists reduction. I can think of no Paleozoic amphibian forms (except for some of the eel-like lepospondyls) which, on the basis of skull table structure, are more unlikely reptile ancestors than the microsaurs. It is true that captorhinomorphs and microsaurs have in common one advanced feature in this region of the skull—elimination of the otic notch. However, this creates more difficulties than it solves; for, unless reptiles are (most improbably) polyphyletic, it involves development of the diadectomorph notch in secondary fashion. I have tried (1946) to explain how this might have happened; but my attempted explanation has not, I think, been satisfactory to my colleagues (nor, indeed to myself).

THE PHYLOGENETIC POSITION OF MICROSAURS

As to the ancestry of the Microsauria, descent from the ancient ichthyostegids is not unreasonable. Westoll (1942b) has advocated this pedigree, and I had independently reached the same conclusion. The evidence is, of course, incomplete and based essentially on the skull roof pattern and proportions. The postcranial skeleton of ancestral ichthyostegids has not been described. It is highly improbable that they had "holospondylous" vertebrae, but this is no bar to microsaur derivation, for it is obvious that vertebrae of this sort have arisen more than once among amphibian groups.[10]

In the discussion above, our attention has been concentrated on "typical" microsaurs. The question of the relationships to them of various specialized holospondylous types of the Paleozoic—the *Lysorophus*, *Ophiderpeton* and *Dolichosoma* groups, particularly—is worthy of further study, although it is probable that firm conclusions must await the discovery of new materials.

If reptilian relationship be denied, are the microsaurs terminal members of their line, or are they, in some sense or other, to be considered as ancestral to any later amphibians? As noted earlier, *Lysorophus*, a member of the microsaurian "periphery," is a possible ancestor of the Apoda. This form is often considered to be an ancestral urodele. It is, one would think, too far gone in body elongation and limb reduction to be seriously thought of in this light. But may not some other microsaur have to be the urodele ancestor? In most regards the "typical" Microsauria are reasonable urodele ancestors. The one strong objection lies in the palatal structure. The urodele palate was unquestionably formed by modification from a primitive amphibian type, with small interpterygoid vacuities and a movable articulation with the braincase. But one would expect late Carboniferous or early Permian ancestors of the urodeles to exhibit a trend in the modern direction (such as is shown in contemporary labyrinthodonts and even *Lysorophus*). The typical Microsauria show no such trend; on the contrary they are persistently primitive in this regard.

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[10] Note that even among the stereospondyls the brachyopids have evolved a "holospondylous" centrum by elaboration of the intercentrum.

REFERENCES

Baur, G., 1897. Ueber die systematische Stellung der Microsaurier: Anat. Anz., Band 14, pp. 148-151.

Bystrow, A. P., 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere: Acta Zool., Band 16, pp. 65-141.

Case, E. C., 1911a. Revision of the Amphibia and Pisces of the Permian of North America: Carnegie Inst. Washington Pub. No. 146, pp. 1-148.

————, 1911b. A revision of the Cotylosauria of North America: Carnegie Inst. Washington Pub. No. 145, pp. 1-122.

————, 1929. Description of a nearly complete skeleton of *Ostodolepis brevispinatus* Williston: Contr. Mus. Pal. Univ. Michigan, vol. 3, pp. 81-107.

Cope, E. D., 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America: Am. Philos. Soc. Trans., vol. 14, pp. 1-252.

————, 1874. Supplement to the extinct Batrachia and Reptilia of North America. I. Catalogue of the air-breathing Vertebrata from the Coal-measures of Linton, Ohio: Am. Philos. Soc. Trans., vol. 15, pp. 261-278.

————, 1875. Synopsis of the extinct Batrachia from the Coal-measures: Ohio Geol. Survey Rept. 2, part 2 Paleontology, pp. 349-411.

————, 1881. On some new Batrachia and Reptilia from the Permian beds of Texas: U. S. Geol. and Geog. Survey Terr. Bull., vol. 6, pp. 79-82.

————, 1897. On new Paleozoic Vertebrata from Illinois, Ohio, and Pennsylvania: Am. Philos. Soc. Proc., vol. 36, pp. 71-90.

Credner, H., 1885. Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Theil V: Zeitschr. Deutsch. Geol. Ges., Jahrg. 1885, pp. 694-736.

————, 1890. Die Stegocephalen und Saurier aus dem Rothliegenden Plauen'schen Grundes bei Dresden. Theil IX: Zeitschr. Deutsch. Geol. Ges., Band 42, pp. 240-277.

Dawson, J. W., 1863. Air-breathers of the coal period, Dawson Brothers, Montreal.

Fritsch, A., 1879. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Prague. Published in parts, 1879-1901.

Geinitz, H. B., and Deichmüller, J. V., 1882. Nachträge zur Dyas II: Mitt K. Min.-Geol. u. Praehist. Mus. Dresden, Heft 5, pp. 1-46.

Gregory, J. T., 1948a. The structure of *Cephalerpeton* and affinities of the Microsauria: AM. JOUR. SCI., vol. 246, pp. 550-568.

————, 1948b. A new limbless vertebrate from the Pennsylvanian of Mazon Creek, Illinois: AM. JOUR. SCI., vol. 246, pp. 636-663.

Gregory, W. K., 1946. Pareiasaurs versus placodonts as near ancestors to the turtles: Am. Mus. Nat. History Bull., vol. 86, art. 6, pp. 265-326.

Huene, F. R., 1948. The systematic position of the Microsauria: AM. JOUR. SCI., vol. 246, pp. 44-45.

Lyell, C., and Dawson, J. W., 1853. On the remains of a reptile(*Dendrerpeton acadianum,* Wyman and Owen), and of a land shell discovered in the interior of an erect fossil tree in the coal measures of Nova Scotia: Geol. Soc. London Quart. Jour., vol. 9, pp. 58-63.

Miall, L. C., 1875. Report of the Committee, consisting of Professor Huxley, Professor Harkness, Henry Woodward, James Thomson, John Brigg, and L. C. Miall, on the structure and classification of the Labyrinthodonts: Brit. Assoc. Adv. Sci. Rept., Belfast Meeting, 1874, pp. 149-192.

Moodie, R. L., 1909. Carboniferous air-breathing vertebrates of the United States National Museum: U. S. Nat. Mus. Proc., vol. 37, pp. 11-28.

————, 1916. The Coal Measures Amphibia of North America: Carnegie Inst. Washington Pub. No. 238, pp. 1-222.

Olson, E. C., 1939. The fauna of the *Lysorophus* pockets in the Clear Fork Permian, Baylor County, Texas: Jour. Geology, vol. 47, pp. 389-397.

————, 1947. The family Diadectidae and its bearing on the classification of reptiles: Fieldiana: Geology, vol. 11, pp. 1-53.

Romer, A. S., 1930. The Pennsylvanian tetrapods of Linton, Ohio: Am. Mus. Nat. History Bull., vol. 59, pp. 77-147.

————, 1933. Vertebrate paleontology, University of Chicago Press, Chicago.

————, 1940. Review of 'Die fossilen Amphibien' by O. Kuhn: Jour. Paleontology, vol. 14, pp. 389-391.

————, 1941a. Evolution of the Amphibia: Geol. Soc. America Bull., vol. 52, p. 1931.

————, 1941b. Notes on the crossopterygian hyomandibular and braincase: Jour. Morphology, vol. 69, pp. 141-160.

————, 1945a. Vertebrate paleontology, revised ed., University of Chicago Press, Chicago.

————, 1945b. The late Carboniferous vertebrate fauna of Kounova (Bohemia) compared with that of the Texas redbeds. Am. Jour. Sci., vol. 243, pp. 417-442.

————, 1946. The primitive reptile *Limnoscelis* restudied: Am. Jour. Sci., vol. 244, pp. 149-188.

————, 1947. Review of the Labyrinthodontia: Harvard College Mus. Comp. Zool. Bull., vol 99, pp. 1-268.

Schwarz, H., 1908. Ueber die Wirbelsäule und die Rippen holospondyler Stegocephalen (Lepospondyli Zitt.): Beitr. Paläontologie Oesterr.-Ungarns u. des Orients, Band 21, pp. 63-105.

Steen, M. C., 1931. The British Museum collection of Amphibia from the middle Coal Measures of Linton, Ohio: Zool. Soc. London Proc., 1930, pp. 849-891.

————, 1934. The amphibian fauna from the South Joggins, Nova Scotia: Zool. Soc. London Proc., 1934, pp. 465-504.

———, 1938. On the fossil Amphibia from the gas coal of Nýrany and other deposits in Czechoslovakia: Zool. Soc. London Proc., ser. B, vol. 108, pp. 205-283.

Watson, D. M. S., 1917. A sketch classification of the Pre-Jurassic tetrapod vertebrates: Zool. Soc. London Proc., 1917, pp. 167-186.

———, 1929. The Carboniferous Amphibia of Scotland: Palaeont. Hungarica, vol. 1, pp. 221-252.

———, 1940. The origin of frogs: Royal Soc. Edinburgh Trans., vol. 60, pp. 195-231.

Westoll, T. S., 1938. Ancestry of the tetrapods: Nature, vol. 141, pp. 127-128.

———, 1942a. Ancestry of captorhinomorph reptiles: Nature, vol. 149, p. 667.

———, 1942b. Relationships of some primitive tetrapods: Nature, vol. 150, p. 121.

Williston, S. W., 1908. The oldest known reptile—*Isodectes punctulatus* Cope: Jour. Geology, vol. 16, pp. 395-400.

———, 1913. *Ostodolepis brevispinatus,* a new reptile from the Permian of Texas: Jour. Geology, vol. 21, pp. 363-366.

———, 1916. The Osteology of some American Permian vertebrates. II: Walker Mus. Contr., vol. 1, pp. 165-192.

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