NOTES ON BRANCHIOSAURS.

ALFRED S. ROMER.

ABSTRACT. A small amphibian from the late Pennsylvanian of Pennsylvania exhibits typical branchiosaur features and is described as *Branchiosaurus darrahi.* A study of the branchiosaurs demonstrates that the order Phyllospondyli is non-existent; the forms assigned to it are simply small and generally immature labyrinthodonts belonging to the rhachitomous and embolomerous divisions of that group.

NO typical branchiosaurs of the type common in European deposits of late Carboniferous and early Permian age have been hitherto reported from North America. The amphibian described below (MCZ 1265) is consequently of some interest as an American form exhibiting the general organization seen in *Branchiosaurus* and other old world genera. It was obtained from a carbonaceous shale layer in the Clarksburg horizon of the Upper Conemaugh (late Pennsylvanian) near Montrose, Alleghany County, Pennsylvania, by W. C. Darrah, who presented it to the Museum of Comparative Zoölogy.

The specimen is a slab on which are displayed the skull and postcranial skeleton to the base of the tail, as seen in the accompanying plate. The skull as preserved is about 7 mm. in length, the presacral column about 25 mm. Presumably a small amount of skeletal material adhered to the counterslab, which was not recovered, but apparently nearly the complete skull and jaws are present, although somewhat crushed and disarticulated. At first sight it appeared that much of the structure could be ascertained. Closer inspection, however, proved disappointing. Little surface detail was apparent and, except where bones had been separated to leave an intervening area of matrix, no indubitable sutures were visible. This situation appears to be due to the fact that the specimen has not been preserved in "normal" fashion, but is represented only by a cast formed of bituminous material which, when examined microscopically, shows no trace of bony structure. No attempt has been made, therefore, to restore the skull or to indicate the pattern of the bony elements.

The skull has the typical short, broad shape seen in the classical *Branchiosaurus* species, with large orbits and a very short face. As in that "genus," the table is short; however, it is rather narrower and the otic notches are more prominent than in typical members of *Branchiosaurus*. Seemingly the postfrontals and postorbitals are (as in *Branchiosaurus*) quite narrow. Apparently the skull as preserved is seen from the lower side with, for the most part, the under surface of the roofing bones exposed. A strip of material near the midline may represent part of the parasphenoidal rostrum; a raised area covering most of the "table" region may represent the expanded posterior portion of that bone.

Behind the skull a fine series of six rows of gill rakers is present, showing the characteristic 1-2-2-1 arrangement of the rows. About 20 presacral vertebrae are present, represented by neural arches of branchiosaur type, and the thoracic region shows the characteristic short ribs. In the trunk region there are indications of body outline, but no scales are apparent. The girdles are poorly preserved. Much of the limbs can be seen, with an apparent phalangeal formula in the manus of 2-2-3-2 and in the pes of 2-2-3-2+-3?.

Although of little morphological interest, the specimen is important from a paleogeographical point of view and is hence worthy of being named. We assign it, as *B. darrahi* to the "genus" *Branchiosaurus*, with the contours of the otic notch and table regions as supposed specific characters.

The branchiosaurs have long been regarded as characteristic members of an independent order of amphibians, the Phyllospondyli. A review of the evidence now available indicates, however, that this supposed order is non-existent and that the branchiosaurs are feebly ossified and, for the most part, immature representatives of various groups of the Labyrinthodontia.

Typical branchiosaurs are small, imperfectly ossified, short-headed, and in many cases are seen to be gill-bearing. These features in themselves tend to indicate that branchiosaurs are larval forms, as suggested half a century ago by Gaudry (1883, pp. 258-261) and von Ammon (1889, pp. 109-111).

Credner's intensive work on these forms (1886) appeared, however, to refute such suggestions. He demonstrated a series of growth stages in *Branchiosaurus amblystomus*, in which the largest specimens which he assigned to the species were still of quite small size but had nevertheless lost their gills. They were therefore presumed to be adults. Further, his often-copied figure of the vertebrae (Credner, 1891, Fig. 25) indicated a peculiar construction of the centrum not duplicated in any other amphibians; it is to this "leaf-like" central structure that the group owes its name.

That Credner's largest forms are actually adults is, however, far from certain. As is indicated by comparison with modern amphibians, the absence of functional internal gills (as inferred in "*Branchiosaurus*" from the disappearance of the gill rakers) does not necessarily mean the attainment of adult size or even the completion of metamorphosis. Further, as will be seen below, there are present in Credner's material much larger animals which, except for differences in proportions expected with growth, cannot be distinguished from "*Branchiosaurus*."

As regards the vertebral structure upon which the group is essentially founded, the work of Bulman and Whittard (Bulman, 1928; Whittard, 1930; Bulman and Whittard, 1926) shows that Credner's description was incorrect. There are well-ossified neural arches, comparable to those of young rhachitomous amphibians, but the central region is unossified. Whittard (1930, Fig. 4) figures *Branchiosaurus* as having this entire region filled by a large unreduced notochord. But in every vertebrate above the hagfish level cartilaginous central elements of some sort appear even in early embryonic stages, and we have no reason to believe that cartilaginous centra were absent here. Upon our inferences as to the nature of these cartilages rests the determination of the proper phylogenetic position of the branchiosaurs.

It has been obvious to all recent workers on the phyllospondyls that the forms assigned to that "order" are very similar to the Labyrinthodontia, and differ structurally in no respect except in feebler ossification (Watson, 1921; Steen, 1938, p. 275). However, one difference was still believed to be diagnostic—a difference in time of phylogenetic development of morphological trends. It was assumed, for example, that Carboniferous labyrinthodonts were generally characterized by a "closed" palate and that the large interpterygoid vacuities seen in the rhachitomous and stereospondylous groups were not developed within the Labyrinthodontia until Permian times. When, therefore, small Carboniferous forms with unossified centra and with large interpterygoid vacuities were discovered, it was believed that they could not be labyrinthodonts and they were, therefore, assigned to the Phyllospondyli (Watson, 1921, etc.). It was mainly upon such grounds that many Linton amphibians were assigned to this "order" by both the writer (1930) and Steen (1931).

This presumed precocious "advance" of the phyllospondyls as contrasted with the labyrinthodonts proves, however, to be fallacious. Forms with a rhachitomous palate (as *Eryops*, *Edops*) are known from American redbeds of Stephanian age; similar labyrinthodonts are present in the Stephanian of Czecho-Slovakia; and an open palate was already present in the middle Pennsylvanian in the true labyrinthodont *Dendrerpeton* (Steen, 1934). We thus lack any basis on which the phyllospondyls may be distinguished from labyrinthodonts.

Of what nature were the cartilaginous centra present in branchiosaurs? Those of the older Amphibia in which ossification has taken place may be classified into two types—the holospondylous, spool-shaped centra found in the lepospondyls (in a broad use of that term), and the various modifications of the two-ringed embolomerous pattern which are characteristic of the Labyrinthodòntia. Except in the case of a few problematical forms, no branchiosaur shows the slightest trace of morphological features comparable with those of any member of the varied lepospondyl groups; on the other hand, as we have noted, the structure of the branchiosaurs is exceedingly close to that of the labyrinthodonts. We may reasonably infer that these unknown central cartilages were intercentra and pleurocentra of labyrinthodont type. Lack of bony centra may be due to (1) aquatic habits and consequent lack of need of strong support, (2) small size, with similar implications, (3) immaturity, with associated incomplete ossification. In many cases all three factors are probably present.

That the branchiosaur material includes the larvae of the contemporaneous larger labyrinthodonts is a conclusion which is almost inescapable on theoretical grounds. Large rhachitomous and embolomerous forms were abundant in these Carboniferous and Permian deposits. Obviously they must have developed ontogenetically from small larvae. The quiet pool environment represented by such localities as Niederhässlich and Nyran is exactly the situation in which these larvae might be expected. But unless *Branchiosaurus* and its allies are these larvae, young labyrinthodonts are unknown in these deposits.

Attention should be called to Bystrow's studies on the development of the dermal roof of the labyrinthodont skull (1935, particularly Fig. 36). He comments on the fact that the structure of the dermal elements indicates that long-headed amphibians begin their lives as short-headed types. The reconstructed youthful skull type which he figures is exactly that seen in typical branchiosaurs.

I shall cite a number of concrete cases which tend strongly to indicate that "phyllospondyls" are actually labyrinthodonts, although small, aquatic and in many cases demonstrably larval in nature.

(1) *Stegops—Acanthostoma—Zatrachys—Platyhistrix.* A number of forms from the Linton deposits of the Pennsylvanian were assumed by both Steen and the writer to be phyllospondyls. This assumption was based for the most part on feeble evidence. In the case, however, of *Stegops* (Romer, 1930, pp. 114-118; Steen, 1931, pp. 860-865, 889), a small spinescent form, the phyllospondyl nature of the animal seemed quite certain, for *Stegops* is very similar to *Acanthostoma* of Europe, an accepted phyllospondyl. The writer pointed out that *Stegops* was also obviously allied to the redbeds amphibians *Zatrachys*, *Platyhistrix*, and *Dasyceps* (in which the vertebral structure was unknown) and hence concluded that those large animals were giant phyllospondyls. Steen denied this relationship on the ground that the redbeds animals must be labyrinthodonts. This difference of opinion was due to the fact that both of us were incorrect in our major premise, viz., that *Stegops* and *Acanthostoma* were phyllospondyls. It now appears that this whole group of forms are actually labyrinthodonts. New Texas material at Harvard shows labyrinthodont central elements associated with *Zatrachys* vertebrae. Re-investigation of *Acanthostoma* by Steen (1937) proved that that genus had labyrinthodont centra, and suggested that certain dubious structures seen in *Stegops* are also labyrinthodont centra (Steen, 1938, pp. 274-275, Fig. 45). In this case, then, forms which seemed definitely phyllospondyls prove to be definitely labyrinthodonts. Presumably ossification of the central elements took place slowly and appears only in the larger individuals. Young ones show no trace of ossification below the neural arches; that is, they are "phyllospondylous."

(2) *Melanerpeton* — *Diplovertebron.* *Melanerpeton* of Fritsch from Nyran and Niederhässlich is an unquestioned "branchiosaur," recently restudied by Steen (1938, pp. 256-259). As she points out, it is distinguished from other branchiosaurs in several characters, particularly the presence of an

intertemporal and a long stalked interclavicle, reptilian in appearance. The intertemporal is suggestive of conditions in the anthracosaurs and seymouriamorphans. The interclavicle is exceedingly characteristic, for (cf. Steen, 1938, Fig. 41, this paper Fig. 1) there is not only the main expansion of the head of it but an unusual smaller expansion at the proximal end of the stem. It is of interest that exactly this same type of interclavicle is also present in another amphibian in the same deposit, but of rather larger size—*Diplovertebron* (Fritsch, 1885, Pl. 53, Fig. 10). This animal is a labyrinthodont with an intertemporal element present. The skull (cf. Jaekel, 1902; Watson, 1926, Fig. 31) is more elongate than in *Melanerpeton.* But, as we have noted, adult skulls appear in general to be longer than those of larvae. *Melanerpeton* of Nyran is very probably a larval *Diplovertebron.*[1]

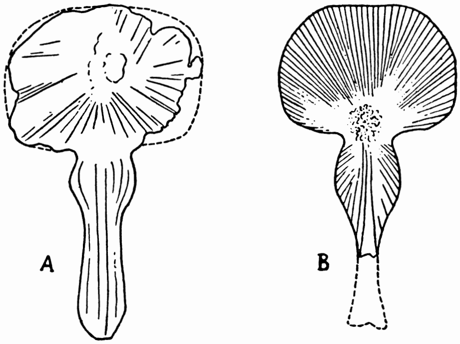

Fig. 1. Interclavicles of A. *Melanerpeton* (from Fritsch, 1879, pl. 7, fig. 1), and B. *Diplovertebron* (from Fritsch, 1885, pl. 53, fig. 10).

Melanerpeton (Credner, 1883; 1885) is known from the Plauenschen Grunde, though *Diplovertebron* has not been found there. At that locality, however, is found a genus, *Discosaurus* (Credner, 1883; 1890) which appears to resemble *Diplovertebron* (and *Dendrerpeton*) in many respects and might well represent the adult of the *Melanerpeton* of that locality. In this connection it is perhaps significant that certain specimens of small amphibians from Moravia have been identified

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[1] The tabular region of *Diplovertebron* is not surely known (unless *Gephyrostegos* of Jaekel is identical, as Watson suggests), and hence we cannot be sure that the peculiar lappets present in *Melanerpeton* are retained in the adult. Steen (1934) figures similar structures in *Dendrerpeton*, a form which may be related to *Diplovertebron.*

both as *Discosaurus* (Stehlik, 1924) and *Melanerpeton* (Augusta, 1936a; 1936b). This debate is, in all probability, merely an academic one as to where the dividing line between larva and adult should be drawn.

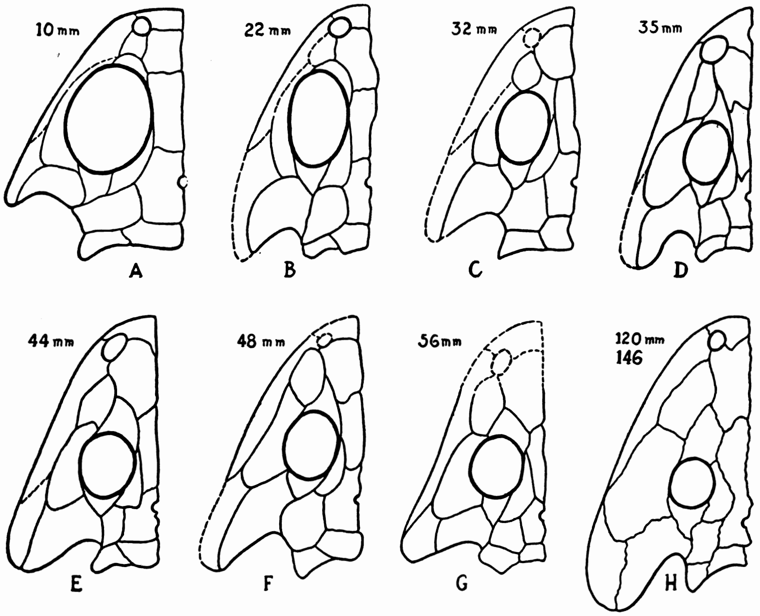

Fig. 2. A series of skulls from Niederhässlich which appear to demonstrate the development of *Onchiodon* (*Sclerocephalus*) *labyrinthicus* from "*Branchiosaurus amblystomus*." The skulls are arranged in ascending order of size (the length in mm. is indicated). A and B are "*Branchiosaurus*"; C, E, and F are "*Pelosaurus*"; and D, G, and H are *Onchiodon*. All skulls restored from Credner's figures as follows: A, 1886, pl. 17, fig. 6; B, 1886, pl. 17, fig. 16; C, 1882, pl. 12, fig. 4; D, 1882, pl. 13, fig. 8; E, 1885, pl. 27, fig. 7; F, 1885, pl. 28, fig. 1; G, 1882, pl. 13, fig. 6; H, 1893, pl. 30, restored from figs. 1 and 2.

The known *Diplovertebron* remains are of modest size; it is not impossible that still larger individuals may be represented in the fragmentary materials of large labyrinthodonts from Nyran.

(3) *Branchiosaurus—Pelosaurus—*"*Sclerocephalus*." The forms so far discussed are not, however, "typical" branchiosaurs; the case for the existence of the Phyllospondyli rests primarily upon the nature of the Branchiosauridae proper. We shall consider especially "*Branchiosaurus*" *amblystomus*, and to eliminate possibility of confusion of identity of the forms

FIG. 1

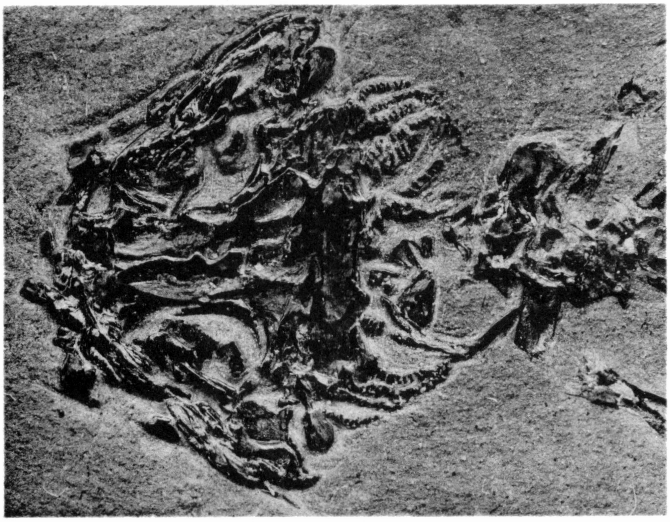

FIG. 2

Skull and skeleton of *Branchiosaurus darrahi,* n.sp. The enlarged figure of the skull, below, shows that the bony elements have been cleared from the matrix since the picture above was taken. Lower figure about 5½ times natural size. The entire animal about 2½ times natural size.

concerned will confine our discussion solely to materials described and figured by Credner (1882; 1885; 1886; 1893) from a single locality and horizon, that of the Plauenschen Grunde or Niederhässlich, near Dresden. These materials indicate that "*Branchiosaurus*" *amblystomus* consists of young individuals of the large rhachitomous amphibian usually known as *Sclerocephalus labyrinthicus* (but better termed *Onchiodon*, cf. Watson, 1919, pp. 4, 5), and that the transitional forms are those included by Credner in the genus *Pelosaurus*. In the accompanying figure (Fig. 2) we have ranged sketch restorations of skulls of these forms, all reduced to the same absolute length to facilitate comparison. These range about two fifths of an inch to half a foot in length. Throughout this series the elements present are identical and their relative positions are essentially constant (although there are a few differences which may be reasonably attributed to individual variation or imperfections in the material, and the sutures are, of course, more sinuous in the adult type). There may be seen a steady progressive change in various proportions as we proceed from small to large skulls. The skull as a whole becomes relatively longer and narrower, and the presence of zones of growth (cf. the discussion by Bystrow, 1935) both anteriorly and posteriorly results in the elongation of elements in both facial and temporal areas. The orbit, too, becomes relatively small with increasing size, the otic notch is progressively narrower and the quadrate region swings further posteriorly.

The specimens included in the figures were originally believed by Credner to belong to five different forms. The first and second (A, B) were at first thought to represent two different species of *Branchiosaurus* (*B. gracilis* and *B. amblystomus*), but the discovery of intermediate forms convinced Credner of their identity. *Pelosaurus* (Figs. C, E, F) was throughout his studies considered as a branchiosaur, but as generically distinct from *Branchiosaurus*. Figures D and G were in his earlier papers thought to be a distinct form ("*Archegosaurus*" *latirostris*) but were later identified by him as immature specimens of "*Sclerocephalus*" (H). Credner himself, then, reduced the number of forms from five to three. But it is obvious that on the bases of skull pattern and size we cannot stop here. "*Branchiosaurus*" is readily separable from the adult "*Sclerocephalus*"; but the "*Pelosaurus*" skulls neatly bridge the gap. They cannot be clearly distinguished either in size or any structural features from the "branchiosaurs" on the one hand or "*Sclerocephalus*" on the other.

This evidence furnished by the skull roof strongly suggests that we can, in this single locality, trace the ontogenetic history of the labyrinthodont "*Sclerocephalus*" from a tiny "branchiosaur" larva to the mature form. Nor is this evidence controverted by any observable facts related to palatal or postcranial structures. There are changes in proportion, increasing ossification, elongation of ribs, elongation of neural spines, appearance of centra, etc., but apart from very minor features (not worthy of citing in detail and probably associated with imperfections in material) the evidence is in agreement with the story told by the skull roof.

It may be inquired why this seemingly simple developmental story escaped Credner's attention. It did not escape him; it was considered, but rejected for two reasons. He did not observe the lacrimal in *Branchiosaurus* and hence believed that its presence in *Pelosaurus* was a valid generic difference. He further believed that *Pelosaurus* possessed the peculiar structure of the centra which he thought characteristic of branchiosaurs in general, and (given this premise) reasonably concluded that the rhachitomous central elements of the "*Sclerocephalus*" specimens could not have developed from such a type. But both his premises are now known to be incorrect. *Branchiosaurus amblystomus* is now known to possess a lacrimal (Bulman and Whittard, Fig. 1) and, indeed, it can be seen in Credner's own figures; and we now know Credner's supposed branchiosaur type of centrum to be non-existent. There is thus no bar to free acceptance of this entire ontogenetic story.

In the Autun region, the Niederhässlich story is repeated almost exactly (Gaudry, 1878; 1883, pp. 251-279; Thevenin, 1906; 1910). The small larval types are named *Protriton* (with *Branchiosaurus* considered a synonym); for somewhat larger forms Credner's term *Pelosaurus* is used by Thevenin; the larger specimens are "species" of *Actinodon* and *Euchirosaurus*. Gaudry pointed out the possibility of an ontogenetic series in the material, but since little morphological detail was then known wisely avoided drawing a positive conclusion. Thevenin, it is interesting to note, states that he constructed a series of skull figures of Autun forms, as we have done with the Niederhässlich ones. He comments on the interesting series of proportional differences exhibited, but concluded that no ontogenetic series is represented. His reasons are in part those cited by Credner, but he also cites skull elongation, reduction of eye size, etc., as evidences of distinctness. These, however, are characters which are definitely related to increase in size, and it seems certain that "*Protriton petrolei*" is the young of *Actinodon.*

(4) *Archegosaurus.* For nearly a century there have been known from the Permian of Lebach in the Saar region tiny amphibians with gill rakers, a feebly ossified skeleton, a vertebral column consisting only of neural arches and, indeed, almost every feature of a typical branchiosaur (von Meyer, 1858, Pl. 14, etc.). But these have never been called branchiosaurs, for it was early recognized that they were larval forms of the rhachitomous labyrinthodont *Archegosaurus decheni.* Remains of that long-snouted amphibian constitute almost all of the numerous tetrapod specimens recovered from this locality. Von Meyer's plates show specimens exhibiting every size stage from presumed adults with heads a foot long down to forms with a skull length of about 20 mm. (Fig. 3). The gilled larval forms are highly comparable with "*Branchiosaurus*" in every respect except one—the snout is somewhat elongated, with a skull length about 2.3 times the width of the skull table, whereas in "*Branchiosaurus amblystomus*" the comparable figure does not exceed 1.7. This, however, is readily explainable. "Normal" branchiosaurs appear to be larvae of labyrintho-

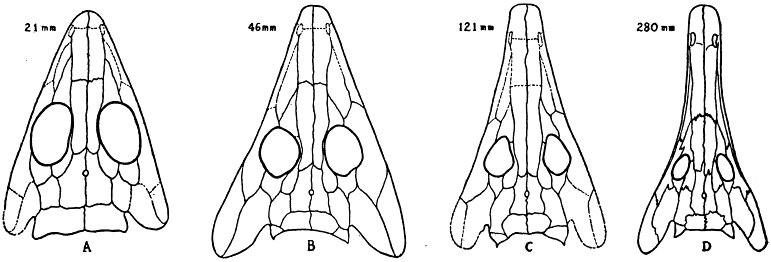

Fig. 3. A series of skulls showing the ontogenetic changes seen in *Archegosaurus decheni,* as demonstrated by von Meyer. The skulls are arranged in ascending order of magnitude (the length in mm. is indicated) and reduced to the same absolute length. This series differs from that shown in fig. 2 in that the tendency toward great elongation of the facial region is already apparent in even the smallest known specimen. All skulls restored from von Meyer (1858) as follows: A, pl. 14, fig. 5; B, pl. 14, fig. 13; C, pl. 12, fig. 1; D, pl. 8a.

donts with a "normal" skull shape; the larval *Archegosaurus* belongs to a form with an attenuated snout, and hence a trend in this direction would be expected at an early stage.

The neural arches of the adult *Archegosaurus* bear a well-developed spine; in the larval forms the spine is low and rounded. The changes in neural arch proportions seen here are exactly comparable to the differences between these structures in "*Branchiosaurus*" and "*Sclerocephalus*."

(5) *Actinodon* ("*Archegosaurus*") *latirostris.* In the Lebach deposits a relatively small amount of material was early identified as pertaining to a second species of amphibian, originally described as a second species of *Archegosaurus*, but later recognized as distinct and assigned to *Actinodon.* The material is less complete than in the case of *Archegosaurus*, but here also von Meyer (1858, pp. 219-220, Pls. 9, 10, etc.) recognized that a series of growth stages could be identified. *A. latirostris* is a relatively short-headed form, and in consequence the growth stages known begin with a small skull which is quite close to "*Branchiosaurus*" in its proportions (Fig. 4). In this series there is little relative increase in the length of the skull table, but a moderate elongation of the muzzle. In the smallest skull the length is about 1 2/3 times the breadth of the skull table; in the largest specimen shown (probably not adult) the figure is about 2 2/3. The series is closely comparable to that illustrated for "*Branchiosaurus*" *amblystomus.* We have here a demonstration of the fact that a labyrinthodont may begin its existence with a typical "branchiosaur" skull.

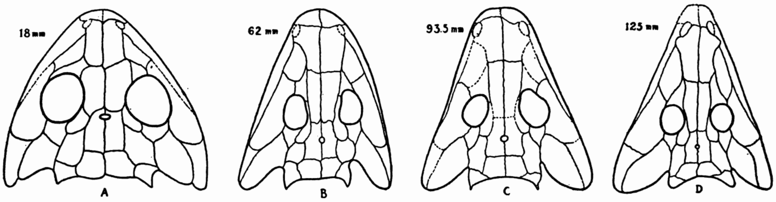

Fig. 4. A series of skulls showing the ontogenetic changes demonstrated by von Meyer in *Actinodon latirostris*, and closely comparable to the series seen in fig. 2. All skulls restored from von Meyer (1858) as follows: A, p. 220; B, pl. 10, fig. 4; C, pl. 9, fig. 5; D, pl. 9, fig. 1.

(6) *Other supposed phyllospondyls.* We have seen that there is no known character by which the phyllospondyls can be separated from the labyrinthodonts; that adult labyrintho-

donts may have "phyllospondylous" vertebral columns; that accepted branchiosaurs may in certain cases be shown to be larval labyrinthodonts of both embolomerous and rhachitomous groups; that accepted labyrinthodonts may be shown to arise from gilled larvae of a branchiosaurian nature. The forms considered above are but part of the better known members of the supposed order Phyllospondyli, but they sufficiently prove, I believe, that the group is non-existent, and that, therefore, the systematic position of the other forms which have been thought to be phyllospondyls should be reconsidered.

A matter for practical consideration is the taxonomic disposition of the branchiosaurs. We have pointed out in several instances the probable adults to which various of these larvae have given rise. But in many cases specific or even generic identity of young and adults is incapable of positive proof. For example, *Branchiosaurus darrahi* is found close to horizons and areas in which *Eryops* has been reported. It is possible that this little form is an *Eryops* larva, but the case cannot be proved. I suggest that the family Branchiosauridae be provisionally retained and placed in the Rhachitomi as a "dumping ground" for typical larval forms, and that *Branchiosaurus* and other genera may be conveniently placed here as "form genera" analogous to those used by paleobotanists for various disassociated parts of plants. Non-typical larval forms had best be associated with the groups in which comparable adults are placed; *Melanerpeton*, for example, should be associated with *Diplovertebron* in any classification.

Of the numerous Linton forms regarded as branchiosaurs by the writer and Steen, *Stegops* has already been discussed. The obscure vertebral remains associated with *Erpetosaurus* are now regarded by Steen (1938, p. 275) as indicating its rhachitomous nature. *Colosteus* is obviously related to the last and hence is likewise to be considered as a labyrinthodont. *Pelion* and *Branchiosauravus* may be larvae of *Leptophractus lancifer* or similar types. *Platyrhinops* is apparently related to *Stegops* (Steen, 1931, p. 867) and hence is presumably rhachitomous. *Mytaras* is of more uncertain position; its elongate skull shape suggests that, despite its small size, it is an adult; it may well be a rhachitomous form.

Eugyrinus (Watson, 1921) from the upper Carboniferous of Europe shows the skull construction of typical members of the Rhachitomi. Since members of that group are now known from the Pennsylvanian, the genus is reasonably interpretable as a labyrinthodont.

It was suggested by the writer (1933, p. 437) that the ichthyostegids might be phyllospondyls, for they exhibit several features of the skull roof comparable to those seen in the colosteids. But since the latter forms appear to be labyrinthodonts, this tentative allocation need not be considered further. Of various other forms which have been placed in the Phyllospondyli by one author or another, many are imperfectly known and obscure in nature. Very probably a majority are larval labyrinthodonts. Some, however (as *Dawsonia*), are probably lepospondyls, in a broad use of that term. Miss Steen has in recent years made valuable contributions to our knowledge of the smaller Paleozoic Amphibia. Much more, however, must be accomplished before a definite position can be established for many of these poorly known types.

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Museum of Comparative Zoölogy,
Harvard University,
Cambridge, Mass.