ON GROWTH STAGES IN BRANCHIOSAURS

by D. M. S. WATSON

ABSTRACT. Lower Permian material from Niederhässlich, Friedrichroda, and Odernheim in the author's collection and in the British Museum (Natural History) is reviewed and described. A new species, *Branchiosaurus brachyrhynchus* sp. nov., is erected for specimens from Friedrichroda; *B. flagrifer* Whittard is redefined. New combinations are *Branchiosaurus* (*Micromelerpeton*) *credneri* (Bulman and Whittard) and *B.* (*Leptorophus*) *levis* (Bulman).

THE young amphibia of the Lowest Permian referred to the genus *Branchiosaurus* were exceedingly well described many years ago by Credner (1882, 1885, 1886) and placed by him in the order Phyllospondyli; he dealt with the abundant material from the middle Rotliegende of Niederhässlich, Plauen'sche Grund, Dresden. Since that time similar series of different stages of growth have been found at Odernheim, Rheinpfalz (in the highest part of the lower Rotliegende), and at Gottlob, Friedrichroda, Thuringia (Godlauterer Schichten; the highest part of the middle Rotliegende), though the material is less abundant. These do not provide so good a series as that set out by Credner, but so far as they go they agree in essence with it.

Since this time various authors have contributed to our general knowledge of branchiosaurs, including Bulman and Whittard (1926), Bulman (1928), Whittard (1930), and Steen (1938). Romer (1939) discussed them, and showed that the order Phyllospondyli was apparently founded on larval specimens of labyrinthodonts, the adults of which have presumably in some cases been described under other names. This interpretation seems to be essentially correct (I continued to use the term Phyllospondyli in 1940 only because I had not then seen Romer's paper), and naturally leads to a hunt for specimens of intermediate size connecting the branchiosaurs with the large labyrinthodonts into which they grew. In this paper Romer (1939, fig. 2) selects from Credner's figures a series of eight contemporary skulls to show that *Onchiodon* may have developed from '*Branchiosaurus*'; the smallest is 10 mm. long, the largest 120 mm., and the intermediates vary between 22 mm. and 56 mm., thus covering what is evidently a very long period of growth. Although there are some difficulties—for instance F seems to me quite clearly not a member of the series to which its neighbours E and G belong—the figure does suggest that the growth of labyrinthodonts involves changes in skull character which are reasonably represented in it.

Parrington's paper on the labyrinthodont middle ear (1959) is important, for it discusses in a most helpful way the change of position of the tympanic membrane, brought out by comparison of a small branchiosaur with a large labyrinthodont. He accepts Romer's figure 2 as a real growth series of the form *Onchiodon*, and points out that the tympanic membrane in the larva extends laterally to end above the attachment of the lower jaw, whilst in the adult, twelve times as long, the membrane lies high up, immediately lateral to the narrow skull roof in the occipital region, and does not reach the jaw articulation, but is nevertheless related to the same bones as it was in the larva.

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PRESERVATION AND PREPARATION OF MATERIAL

I have in my collection some beautifully preserved specimens of branchiosaurs from Niederhässlich, Friedrichroda, and Odernheim, covering a considerable range in size, and have been able to borrow others from the British Museum (Natural History). It seems, therefore, that it may be useful to figure a size range from each of these places in order to see what the differences are. Careful restored drawings of individuals, when arranged in order of size, could be expected to show not only whether they belonged to the same species or not, but also proportionate changes due to growth, and thus give an indication of the probable nature of the adult into which they should have grown.

The material used is as follows: From Niederhässlich, D.M.S.W., B. 91, 92, 97; B.M.N.H., R. 2011, 2711. From Friedrichrona, D.M.S.W., B. 36*a*, 37, 48–52; B.M.N.H., R. 5281–7, 5466 7, 5469. From Odernheim, D.M.S.W., B. 25–35, 39, 40, 44–47, 141; B.M.N.H., R. 5026, 5028, 6700. Several of the specimens show more than one individual. Some of them have already been figured by Bulman and Whittard (1926, 1928, 1930), but I have made new restorations of dorsal and some lateral aspects which differ slightly from theirs (at that time my collection had not been catalogued, and they gave to specimens temporary numbers which have since been replaced by permanent ones).

The material from the respective localities does not differ greatly in geological age. The matrix of both Niederhässlich and Odernheim specimens is an exceedingly hard, very calcareous rock, fine-bedded when seen in broken section, and at Niederhässlich grading into a very tough but less noticeably bedded limestone, whose colour on a clean fracture is light brownish-grey, weathering considerably lighter on a joint face. The Odernheim matrix is dark grey on a fresh surface, again weathering lighter. The Friedrichroda matrix is a fine-bedded, black shale which breaks flatly and a little uncertainly into thin slabs, looking very like some Coal Measure shales.

In these very small animals little preparation can be done, and one is dependent on the facts shown by the original fracture revealing the specimen; sometimes they may be improved by the use of acid to dissolve the bone, for plasticene squeezes made from such moulds often show better surface detail than bones prepared out. The material has limitations: drawings can, as a rule, only be made of the dorsal aspect of the skull, whose roof pattern (so far as the number and general relationships of the individual bones are concerned) is uniform and modified only by changes in proportion in the bones involved. In very small specimens the lachrymal is usually badly preserved, so that its apparent shape may be determined by the borders of the surrounding bones, and has no independent validity. The palate is not often shown, and in many specimens the postcranial region is of no help in determining affinities for it is missing.

The practical difficulties of making the drawings were met by tracing from enlarged photographs of each skull on which the outline of bones (or their moulds) had been carefully inked in. The restorations were made by trial: it is assumed from the conditions found in adult labyrinthodonts, that the table between the otic notches is essentially flat, and that the parts lateral to it slope downwards at an angle, which cannot, of course, be determined directly by measurement, and is to that extent arbitrary. Into the area so marked out the pattern of the bones can be inserted, making allowance for the foreshortening of the orbit and of those bones which, like the squamosal, lie at an angle to the skull roof; each drawing was checked when possible by a projection on to the other plane. Lateral views can only be drawn when the squamosal, jugal, and maxilla are well preserved and their articulation evident.

The fundamental assumption of the names used in zoological nomenclature is that each such name should imply one particular kind of animal, at all stages of growth, even if it suffers a great metamorphosis in its life history, like a butterfly. The difficulty arising in the case of labyrinthodonts, whose growth stages may already have been referred to a variety of genera, raises the purely practical problem of what such individuals should now be called, when it may well be impossible to discover the name of the adult into which they grew. Large forms have been found at Niederhässlich, though they are very rare, but none are yet known in association with the branchiosaurs of Odernheim, or of Friedrichroda, though it is assumed by analogy that they also were large when adult; in the other case in which we have a long gradated series of individual amphibia, *Archegosaurus* (H. von Meyer, 1857, pls. 8*a*–23), which ranges from a skull less than 2 cm. in length to one (incomplete) at least 19 cm. long, it has never been doubted that the growth of a single species is represented. It should be evident that any name given to a branchiosaur is to be regarded, not as a normal specific name, but as a handle for convenience of reference, and on the whole it seems to me that the generic term *Branchiosaurus* may well stand for any labyrinthodont larva from Niederhässlich, Odernheim, or Friedrichroda whose adult has not yet been identified; and further, that those larval individuals which can be distinguished from the rest on features not related to growth may be given 'specific' rank in that genus.

MATERIAL FROM NIEDERHÄSSLICH

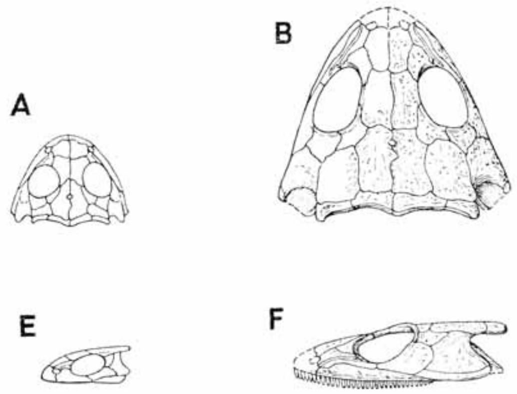
Credner completed his work on branchiosaurs by discussing the growth of the amphibian, the whole material being summarized in two magnificent plates (1886, pls. 16, 17), one reproducing a series of eleven skeletons, the other a series of sixteen skulls ranging from about 5 mm. to some 20 mm. in length, all drawn unrestored as they lie with the jaws spread out laterally. They are figured from the dorsal side only, but the drawings, like all Credner's work, are excellent, and show a gradual relative lengthening of the postorbital part of the skull, which becomes a little narrower proportionately: this is associated with the rapid growth of the brain.

Text-fig. 1 shows restorations of three individual skulls from Niederhässlich now before me, and of Credner's *Onchiodon* (*Sclerocephalus*) *labyrinthicus* (1893, pls. 30, 31). In this series A and B show the relative lengthening of the postorbital part of the skull, but in C the preorbital part has begun to grow disproportionately, in order to provide a mouth and jaws of sufficient size to meet the needs of an animal whose weight is increasing as a cube of a linear dimension. A significant feature is the meeting of pre- and post-frontals, excluding the frontal from the border of the orbit, which is evidently related to a reduction in the proportionate size of the eye; at the same time the jugal lengthens proportionately, and the quadratojugal, while retaining its old length, deepens. B and C show the nature of the lachrymal particularly well; in A it can scarcely be seen, as is the case in most of Credner's stages. In B this bone extends along the orbital margin, with a double opening for the duct, which is essentially surrounded by bone, and may not reach the nostril; in C the bone is beginning to be excluded from the orbit, and the duct is an open groove throughout its length, entering the nostril. It may be noted that the pineal foramen in A is on the level of the hinder border of the orbit, in B it lies entirely behind the orbit, in C it is relatively farther back. This depends on the fact that brain development takes place during the early stages of growth, and ceases quite soon, a point very well brought out in Credner's series.

There seems no doubt that A, B, and C are part of a growth series, and in this connexion it is of interest that the snout of an individual almost the same size as C, showing an identical pattern of ornamented bones, and similar lachrymal ducts, lies close to R. 2011 (A) on the same slab. If, as has been suggested (Romer 1939) the final term of this series be *Onchiodon* it can then be seen how far further growth has altered the proportions of the cranial roof. D shows that the snout continues to elongate, the lachrymal in consequence losing its contact with the orbit, being separated from it by a short but quite definite suture between the prefrontal and jugal. The orbit lies relatively far back compared with C, and is proportionately smaller still; its lateral border is separated from the border of the skull by rather more than its own width, in other words the jugal is now extremely deep. The pineal foramen is relatively even farther back. The table, and therefore the braincase which lies beneath it, is now very narrow compared with the whole width of the skull at the same point. The squamosal and quadratojugal have greatly increased to form the characteristically deep cheek seen most typically in large skulls of *Eryops*.

Thus it seems evident that the large amphibian from Niederhässlich and the branchiosaurs found there are all members of the same growth series, and may be called *Onchiodon* (*Sclerocephalus*) *labyrinthicus* Geinitz, a procedure justified by the fact that Credner's work is confirmed by specimens not known to him, and a good intermediate stage has now been found between the small larva and the adult.

It is interesting (text-fig. 1) to compare the ornament of the dermal skull roof of C with that of D (remembering that the former was drawn from a squeeze of a mould, and the latter from the mould itself). In C the ornament consists almost entirely of a series of pits, with very rare ridges and grooves only recognizable in some bones, the jugal and quadratojugal, for instance. In D the areas covered with pits, the growing points, are very small in comparison with the surrounding radially arranged grooves and ridges, which represent the extension resulting from growth; in other words the ornament suggests the direction of growth. But there are nearly twice as many elements in the pattern of D (in the postorbital, for instance) as in the smaller form C, suggesting that the ornament is not enlarged commensurately with the bone, and that new elements are introduced into the pattern. It may be interesting to recall that in reptiles sutures in the skull have been known to close, presumably implying that the individual is old; in amphibia, so far as I know, the sutures never close, implying that growth remains possible even at extreme old age.



TEXT-FIG. 1 (*continued on opposite page*). *Onchiodon* (*Sclerocephalus*) *labyrinthicus* Geinitz. Reconstructions of four skulls from Niederhässlich.

A–C, Dorsal aspect; E–G, lateral aspect; $\times\frac{2}{3}$, surface ornament taken from squeezes and thus reproducing the bone, D, dorsal and H, lateral aspect $\times\frac{1}{3}$, the mould itself is drawn.

A, B.M.N.H., R. 2011, about the same size as Credner's no. 5 (1886, pl. 17), the smallest available skull from which a restoration could be made; mould of external surface of head. Fragmentary vertebral column and shoulder girdle present, and a pelvis and hind legs.

B, D.M.S.W., B. 92; isolated skull shown as a perfect impression of the external dorsal surface and right cheek. '*Branchiosaurus amblystomus*' (Watson 1940, fig. 22) was founded on it, but the new restoration modifies the nose (which is damaged) and orbit, and is confirmed by Credner's no. 15 (1886, pl. 17) and B.M.N.H., R. 2711, which are almost the same size.

C, D.M.S.W., B. 91; isolated skull shown as a sharp impression of the external dorsal surface and left cheek; new restoration of specimen figured as *Onchiodon* (Watson 1951, figs. 36, 37); nearly half as long again as Credner's largest (1886, pl. 17).

D, *Onchiodon* (*Sclerocephalus*) *labyrinthicus* reconstructed from Credner's best specimen (1893, pl. 30, fig. 1); anterior part of skull restored from two other specimens (pl. 30, fig. 2, and pl. 31, fig. 1). Note that this skull is five times as big as C.

E, B.M.N.H., R. 2011, teeth after Credner.

F, D.M.S.W., B. 92, left side restored from right. Teeth restored from short length of interlocking upper and lower ones, shown in three-dimensional detail; position of suture between jugal and lachrymal not certian.

G, D.M.S.W., B. 91, teeth restored from nearly complete series.

H, *Onchiodon* (*Sclerocephalus*) *labyrinthicus* reconstructed from Credner (1893, pl. 30, figs. 1–2, and pl. 31, figs. 1–2); lower jaw and shoulder girdle of same individual have been taken into consideration in determining height of skull.

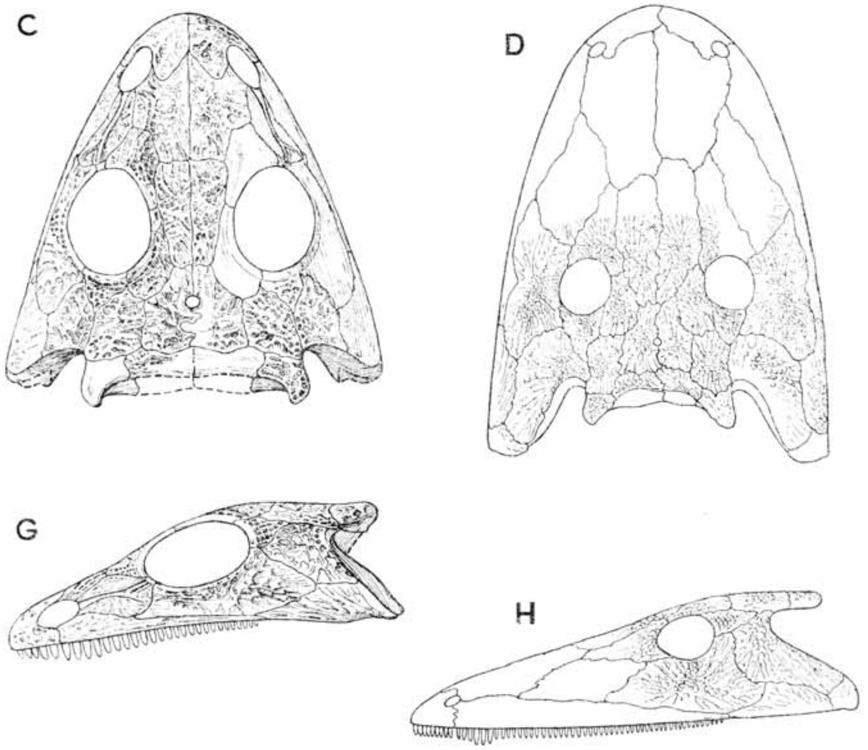
MATERIAL FROM FRIEDRICHRODA

Branchiosaurus flagrifer Whittard, 1930

Text-fig. 2A–C

Holotype. Specimen from D.M.S.W. Collection, now numbered B. 48.

Other specimen. D.M.S.W. Collection, B. 36*a*.



TEXT-FIG. 1. (*ctd.*)

Branchiosaurus brachyrhynchus sp. nov.

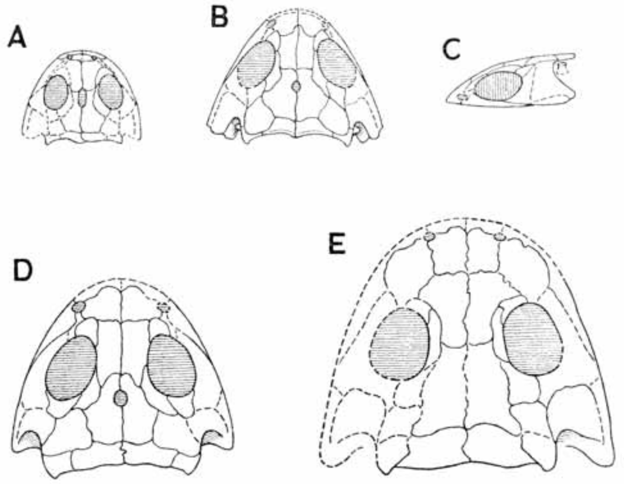
Text-fig. 2D, E

Holotype. B.M.N.H. specimen R. 5466/7.

Other specimen. B.M.N.H. specimen R. 5469.

Discussion of both species. The material from Friedrichroda, which was first found in the nineteen-twenties, contains a branchiosaur of which fifteen specimens were examined by Whittard (1930) and assigned to a new species, *Branchiosaurus flagrifer*. His drawings (figs. 1–3) represent the skull of my specimen B. 48 (the holotype) which has an incomplete vertebral column, and the vertebral column of B.M.N.H., R. 5466/7 which is a very complete individual retaining not only the head and body but also a very long tail, represented for the greater part of its length by a sharply defined, narrow skin impression. I have made a new restoration of the skull of B. 48 (text-fig. 2B, C) which differs somewhat from Whittard's, the differences arising, I think, from the fact that it is extremely difficult to draw such material consisting of a mould in which the relief is very shallow; colour differences hinder rather than help. I had the advantage of good photographs at a considerable magnification on which the outlines of the bones could be inked.

In text-fig. 2 this new restoration is compared with reconstructions of the smallest



TEXT-FIG. 2. Reconstructions of four skulls from Friedrichroda, A–D, $\times\frac{5}{3}$, E, $\times\frac{4}{3}$; each represents the external surface of the cranial roofing bones. The lachrymal is uncertain in A, B, and C; in D it occurs but its shape as shown depends on the borders of the surrounding bones.

A–C, *Branchiosaurus flagrifer*. A, D.M.S.W., B. 36*a*, the smallest specimen figured in the paper; note the large, elongated pineal foramen. Skull preserved as a mould, with no trace of ornament. Also present vertebral column complete from skull to traces of the pelvis, and part of a shoulder girdle and fore limb. B, New restoration of D.M.S.W., B. 48, holotype of Whittard (1930, fig. 1), from a very good mould of the cranial roof and lateral parts of the palate and lower jaw. A series of very small scattered projections on the supratemporal and parietals are of the nature of ornamentation; there are, perhaps, traces of the sclerotic ring. Vertebral column containing about twenty-six vertebrae, extending from skull to region of the pelvis, present in the specimen; also a set of ribs, a shoulder girdle, humerus, and femur in poor preservation. C, D.M.S.W., B. 48, restored lateral view.

D–E, *Branchiosaurus brachyrhynchus*, sp. nov. D, B.M.N.H., R. 5466/7, holotype. Skull of specimen on which restoration of postcranial region of the type of *B. flagrifer* was founded (1930, fig. 3). The part and counterpart show the specimen split through longitudinally, the mould of the skull roof suggests that a very shallow ornamentation exists. R. 5467 shows traces of a sclerotic ring in both eyes. E, B.M.N.H., R. 5469. A particularly difficult skull to interpret as the surface is not well preserved and the sutures are obscure; they have been determined by the meeting of radial striation of the bones, which have traces of ornament. The specimen has a vertebral column in articulation from the skull to the pelvis, damaged in one place; a set of ribs is present, fragments of tail, a shoulder girdle, and nearly complete fore and hind limbs.

suitable Friedrichroda skull I could find (B. 36*a*), R. 5466/7, which is larger, and the largest available one (B.M.N.H., R. 5469) which is not founded on such good evidence as the others, but the extreme width across the snout—with an enormous lachrymal and small external nostril—and the position of orbits and otic notches is clear, though the pineal foramen cannot be seen with certainty. These skulls agree in general structure, and it will be seen that in B. 36, B. 48, and R. 5469 the pre- and post-frontals exclude the frontal from the border of the orbit, whilst in R. 5466 this bone enters quite largely into the orbital margin; R. 5466 also differs from B. 48 in that the tabular appears not to meet the squamosal, and the postorbital is widely separated from the parietal, which suggests that this skull is different from it. Moreover, comparison of the postcranial region of B. 48 with that of R. 5466 confirms the difference in the specimens, for in B. 48 the vertebrae from skull to pelvis number about twenty-six and are short antero-posteriorly and closely packed, and the ribs immediately behind the shoulder girdle are long and slightly curved, and then shorten to half-length at about the ninth vertebra; while in R. 5466 the comparable number of vertebrae is about twenty, and they lengthen behind the pectoral region so that the interval between successive ribs is long, and the ribs are all short and straight. This leads to the unfortunate conclusion that the type skull is united in a drawing with a body belonging to a different species.

Examination of the postcranial regions shows that B. 36 appears to have close-packed vertebrae like the type (though its ribs are straight), and R. 5469 has about twenty vertebrae (also with straight ribs) like R. 5466/7. None of the differences between the columns could readily be accounted for by changes due to growth, therefore as indicated formally above at least two different species occur. B.M.N.H., R. 5466/7 may be taken as the type of *Branchiosaurus brachyrhynchus* sp. nov.; I also place R. 5469 into this species on the grounds that its vertebral column matches, and that so much of its skull as can be seen conforms to what might be expected as a result of further growth.

The logical step would then be to investigate the sixteen other individuals from this locality to see if they could be put into one or other of these species. This would involve an elaborate procedure of interpreting enlarged photographs, which I do not propose to enter on, but preliminary inspection of the materials seems to show that the two sorts of vertebral column and skull do occur.

The ornament on the dermal skull roof of B. 48 is not well shown, but B.M.N.H., R. 5286, which is nearly the same size, and probably the same species, shows definite ornament in this region. It is not like that of a normal large labyrinthodont, but is shallow. The central pitted region is surrounded by poorly developed radial striae, and the units of the pattern are large compared with the size of the bone, both features depending on the youth of the individual.

MATERIAL FROM ODERNHEIM

Branchiosaurus credneri (Bulman and Whittard) comb. nov.

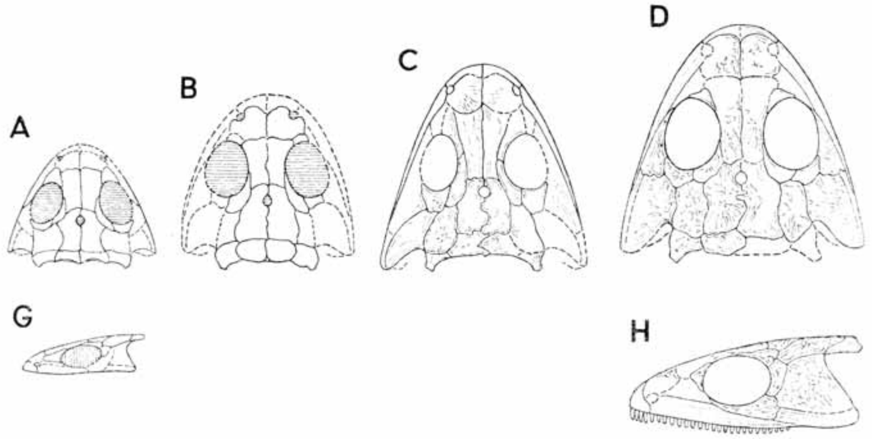
Text-fig. 3A, B, D, F

Lectotype (here chosen). D.M.S.W. Collection, B. 40 (text-fig. 3F).

Branchiosaurus levis (Bulman) comb. nov.

Text-fig. 3C, E

Holotype. D.M.S.W. Collection, B. 44/45 (text-fig. 3C).



TEXT-FIG. 3 (*continued on opposite page*). *Branchiosaurus credneri* (Bulman and Whittard) comb. nov., and *B. levis* (Bulman) comb. nov. Dorsal and some lateral reconstructions of the series of branchiosaur skulls from Odernheim, all ×2. A and B drawn from the under surface of the cranial roofing bones; C, D, E, and F from the upper surface.

A, D.M.S.W., B. 27, *B. credneri*. New reconstruction of specimen figured as *B. amblystomus* Credner by Bulman and Whittard (1926, fig. 1, I). Their 'lachrymal' is probably a prefrontal, the strip of bone at the upper border of the orbit being part of the frontal; there may be a lachrymal in the specimen, but if so it cannot be seen. The specimen has seven vertebrae in articulation with the skull, also a fore limb.

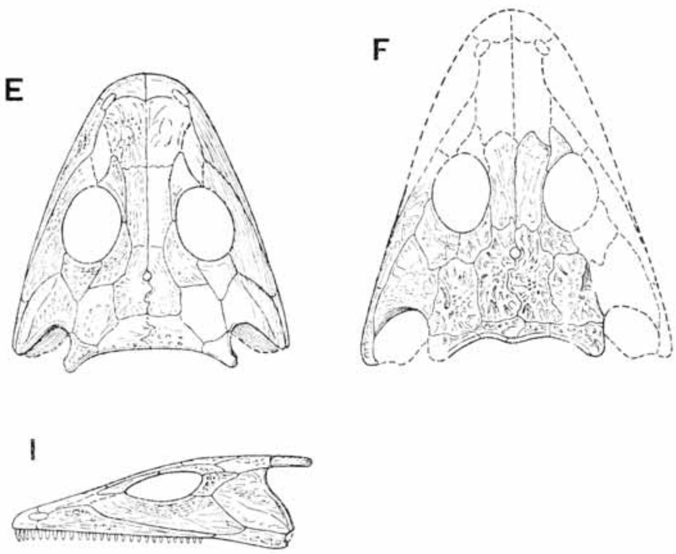
B, D.M.S.W., B. 39, *B. credneri*. Reconstruction of skull on which (with B. 40) *Micromelerpeton credneri* Bulman and Whittard (1926, figs. 11–13 and pl. 4*a*) was founded. Much of the palate can be seen, also both rami of lower jaw, and anterior part of body including shoulder girdle, but not the fore limb.

C, D.M.S.W., B. 44/45 (part and counterpart), *B. levis*. New reconstruction of the type specimen of *Leptorophus levis* Bulman (1928, figs. 2–4). Traces of ornament of the skull table are shown in very low relief, which is probably genuine, and not due to poor preservation. Specimen shows an indistinct shoulder girdle, and a well-defined area of ventral scutes in chevron-shaped rows. An oval area with a definite margin in the centre of the right orbit of B. 45 is presumably a trace of the crystalline lens.

D, D.M.S.W., B. 46, *B. credneri*. Reconstruction of specimen on which (together with B. 47*a*, and B.M.N.H., R. 5026) the drawing of *Pelosaurus laticeps* Credner (Bulman and Whittard 1926, fig. 14) was founded. Most of the bone has survived and shows well-preserved ornament. A lachrymal is present, though its shape is uncertain, but no sclerotic plates are to be seen. There are no intelligible postcranial parts.

E, D.M.S.W., B. 47*a*, *B. levis* one of the specimens on which *Pelosaurus laticeps* Credner (Bulman and Whittard 1926, fig. 14) was founded. Skull represented by a mould in which the table is slightly disarticulated, but its relation to the rest of the dorsal surface is evident. Ornament well preserved on some bones, such as the postorbital and tabular, but incomplete in the rest of the skull. There are about a dozen vertebrae in articulation with it, but no girdles or limbs.

F, D.M.S.W., B. 40, *B. credneri*, Lectotype. Reconstruction of skull on which (with B. 39) *Micromelerpeton credneri* Bulman and Whittard (1926, figs. 11–13 and pl. 4*a*) was founded; the table now lies about in the middle of the vertebral column, having been separated from the frontals before burial. The skull, drawn from a squeeze, is represented by a beautifully preserved mould, which shows the ornament exceedingly well; the presence of lateral-line grooves on the supratemporals suggests that the individual was still aquatic. A column of thirty presacral vertebrae is in articulation with it; a complete series of ribs and both limb girdles are present, with a nearly complete fore limb, and partial hind limb, but little of the tail remains.



G. D.M.S.W., B. 27, *B. credneri*, lateral view. Teeth are present, but are only represented by sections of crowns and are not reconstructed.

H. D.M.S.W., B. 46, *B. credneri*, lateral view. The tooth row is conventionalized, but in number and size the teeth are essentially correct; the premaxillary teeth are taller and perhaps more massive than those of the rest of the series.

I. D.M.S.W., B. 47*a*, *B. levis*, lateral view. The teeth are restored from an incomplete row, the premaxillary teeth being longer, and of larger diameter, than the bigger ones at the anterior end of the maxilla.

Discussion of both species. The six skulls in text-fig. 3 were certainly found in the same quarry, in rock of exactly the same character. It cannot be shown that they lie in the same bedding plane, but there is no reason to suppose that there was much variation in time between them, in fact they must represent a fauna of a quite small lake. C, D, E, and F show the upper surface of the skull roof, A and B are from its under surface, the only part exposed; few specimens show the palate, and only one (F) has adequate postcranial elements, in this specimen there are thirty presacral vertebrae, which is a very large number. In contrast to the original figures of Bulman and Whittard, which often included facts drawn from several individuals not necessarily the same size, each drawing in this figure represents one individual only.

There are points of general similarity between the members of this series, for instance the tabular horns of C (*Leptorophus levis* of Bulman), D, and E have much in common, and Bulman (1928, p. 255) says '*Leptorophus levis* may thus occupy an intermediate position between the *Micromelerpeton–Pelosaurus* type and the geologically younger species *L. tener*', but only C and E can be said to differ from the rest in significant ways; in C and E the pre- and post-frontals meet in suture above the orbit, and the suture between the dermosupraoccipital and the parietal meets the admedian border of the supratemporal nearly at its mid point, making the parietals relatively shorter, whereas in A, B, D, and F the pre- and post-frontals are widely separated, and the anterior sutures of the dermosupraoccipitals and tabulars are very nearly continuous, the parietals being relatively long compared with their width. It should be pointed out that in C all the bones of the skull roof are extremely thin, whilst in E they are of normal thickness, although this could well depend on some accident of preservation. Also B as drawn differs from A, D, and F in that the postorbital does not meet the anterior end of the supratemporal at all, whereas in the other individuals it does; but in this specimen (B) the supratemporal is shown only as an impression of its lower surface, and is somewhat confused by being pressed down on the pterygoid, itself shown merely as a mould.

It may be noted that the pineal foramen (which is not accurately circular) in the younger stages of these two species is in an anterior position, but in the two later stages, E and F, it is relatively farther back, implying that in these animals, as in vertebrates in general, the brain is early developing, so that in later stages its growth is greatly exceeded by that of its surroundings. And in F the quadrate is far back showing the general trend of change of shape with age found in nearly all labyrinthodont skulls.

Thus it appears, as indicated formally above, that at least two species of labyrinthodonts were present in the pool in which the rocks were laid down.

COMPARISON OF MATERIAL

When a comparison is made between skulls from these three localities one difference seems clear: in the Friedrichroda series the eyes are relatively farther forward, and the noses wider and blunter, than in those from the two other places. In the Friedrichroda series also the meeting of pre- and post-frontals above the orbit has taken place in a skull only 5·6 mm. in length; in the Niederhässlich series this event occurs in a skull measuring between 20·0 mm. and 36·0 mm. in length; and in the Odernheim series one of the two species has achieved it in a skull measuring 15·6 mm., while the other has not yet done so in a skull about the same size as the largest Friedrichroda one. There is also, perhaps, a difference in the posterior part of the skull table in the older and more characteristic members of each series; in those from Niederhässlich the tabular horns tend to turn inwards, in the Odernheim forms they tend to turn outwards, and the Friedrichroda skulls differ from both.

Enough has been said about the differences between individual skulls of one locality, and those of one locality compared with another, to suggest that the group of labyrinthodonts of this age was more elaborate than has yet been recognized, and that larvae can be determined as well as adults.

SURVIVAL OF BRANCHIAL ARCHES

The Odernheim series used in this paper covers the point of growth at which gills are lost, thus presumably representing the transition from a larval to an adult life. The following table shows these specimens arranged in order of skull length, with the nature of the gill apparatus of each individual indicated. It appears that those with a length of 11·2 mm. or less have internal gills, implied by the presence of gill rakers, and also (in some cases) external gills shown as a carbonaceous film; at 11·75 mm. and above no indication of gills can be found, though a ventral remnant may be present in one individual measuring 12·7 mm. Only a single individual with a skull length of 15·6 mm. (and possibly one other) shows the presence of ventral armour in the form of rows of scales in a chevron pattern, perhaps a sign of the approach of maturity.

Branchiosaurs from Odernheim

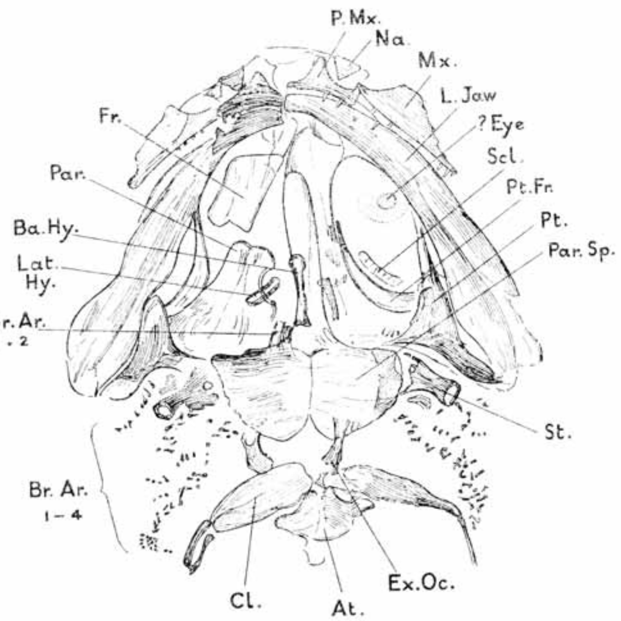
Registered number	*Species*	*Skull length in mm.*	*Total length to pelvis in mm.*	*Presence of gills*	*Ventral armour*
R. 6700	undetermined	6·1	. .	?	none
B. 34	,,	8·1	28·0	internal	,,
B. 27	*B. credneri*	8·2	. .	,,	,,
B. 26	undetermined	9·0	38·5	? internal, and external	,,
B. 30	,,	9·1	41·0	internal	,,
B. 32	,,	9·1	41·0	,,	,,
B. 35	,,	9·5	46·0	? external	,,
B. 33	,,	9·5	47·0	?	,,
R. 5028/9	,,	11·0	49·0	internal	traces
B. 25	,,	11·2	. .	internal and external	none
B. 29	,,	11·2	45·0	internal	,,
B. 28	,,	11·75	. .	none	,,
B. 31	,,	12·7	51·0	? ventral remnant	,,
B. 39	*B. credneri*	13·0	. .	none	,,
B. 44/45	*B. levis*	15·6	. .	,,	present
B. 46	*B. credneri*	18·0	. .	,,	. .
B. 47a	*B. levis*	23·8	. .	,,	? none
R. 5026	undetermined	24·0	84·0	,,	none
B. 40	*B. credneri*	28·5	102·5	,,	,,
B. 141	undetermined	28·5	103·0	,,	,,

My Niederhässlich material is too scanty to allow of a comparison, but Credner (1886, p. 586) gives a table showing that in his individuals gills are found in those with a skull length of 14·0 mm. and under, above which size they are never seen; but those larvae which have gills lack ventral armour which is found in all the larger individuals.

The Friedrichroda specimens range from 5·2 mm. to 29·0 mm. in skull length, and of these only four (B. 50 and B 51, B.M.N.H., R. 5285A, B) show the branchial arches, and none shows any sign of ventral armour.

DETAIL OF BRANCHIAL SKELETON

The specimen B.M.N.H., R. 5285 (individual A), from Friedrichroda, shows the branchial arches exceptionally well. They lie in position undisturbed, extending back almost as far as the shoulder girdle, each with a paired row of gill rakers. The structure of the anterior part of the hyoid arch is, however, better shown in one of my Odernheim specimens (B. 30) than in any other known to me (text-fig. 4). This skull, 9·1 mm. in length, is seen from below. Both rami of the lower jaw are present as impressions. The premaxillae have been crushed down so that their posterior points, which should have articulated with the nasals, now lie directed forward and the impression of their outer surfaces is seen. The parasphenoid is shown as bone on the lateral parts of its widened hinder end, and by the impression of its processus cultriformis, superimposed on the impression of



TEXT-FIG. 4. D.M.S.W., B. 30, a branchiosaur from Odernheim, × 6. Skull and shoulder girdle seen from below, drawn unrestored. Specimen almost complete to the fourth caudal vertebra.

Reference letters: *At.*, atlas; *Ba.Hy.*, basihyoid; *Br.Ar. 1 & 2*, ventral elements of branchial arches 1 and 2 attached to the basihyoid; *Br.Ar. 1–4*, series of gill rakers attached to the upper ends of branchial arches 1–4; *Cl.*, clavicle; *Ex.Oc.*, exoccipital; *Fr.*, frontal; *Lat.Hy.*, laterohyoid; *L.Jaw*, lower jaw; *Mx.*, maxilla; *Na.*, nasal; *P.Mx.*, premaxilla; *Par.*, parietal; *Par.Sp.*, parasphenoid; *Pt.*, pterygoid; *Pt.Fr.*, postfrontal; *Scl.*, sclerotic plates; *St.*, stapes.

the visceral surface of the skull roof. The stapes—pierced by a foramen—is present on each side, and the exoccipitals, pressed down into the general plane of the palate, are small, rather featureless bones widely separated dorsally. The anterior part of the hyoid apparatus—a basihyoid and laterohyoids—is seen in the region of the parasphenoid, followed by two pairs of shreds of bone which are the ventral attachments of the first and second branchial arches. Behind the stapes lie the dorsal ends of the branchial arches, now perished and indicated only by the rows of attached gill rakers, which open outwards lateral to the dorsal ends of the clavicles. The left orbit has impressions of sclerotic plates, and also a grey area which appears to be some part of the eye itself. (B.M.N.H., R. 6700, skull length 6·1 mm., also shows in both orbits carbonaceous impressions of the eye.) The vertebral column, complete as far back as about the fourth caudal vertebra, is in articulation with the skull. Both fore limbs are present, but not the hands. The two femora are shown, and the right tibia and fibula in a somewhat fragmentary condition.

In this specimen the gill rakers suggest that open gill slits of very considerable length existed, and that something of the nature of internal gills must have occurred. Since the branchial skeleton was so well developed it presumably carried out functional movements.

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D. M. S. WATSON
Department of Zoology,
University College, London

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