STUDIES ON EARLY TETRAPODS
I. THE LOWER CARBONIFEROUS MICROSAURS

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[Plate 13]

CONTENTS

Redescriptions of *Adelogyrinus simnorhynchus* and *Dolichopareias disjectus* are given. The skulls of these forms are characterized by the very anteriorly placed small orbits and long post-orbital skull table. Further diagnostic characters are the exclusion of the 'post-orbital' from the orbit, the long straight suture between the squamosal and parietal and the absence of an otic notch. A parasternal process is present on the interclavicle.

A new genus and species *Palaeomolgophus scoticus* of early Carboniferous age is described. It is an aquatic form with branchial arches, yet the characters it displays are essentially reptiliomorph, quite unlike those of the labyrinthodonts and resembling more those of lower Permian reptiles. It has microsaur-type vertebrae in which the centrum is a pleurocentrum, winged ribs, a differentiated series of cervical ribs and an interclavicle with a posterior parasternal process. The limbs are small, but well developed, with ossified condylar surfaces.

Comparisons are made with *Microbrachis* from the Upper Carboniferous of Nyran, the type microsaur, which is represented mainly by larval forms, but the disappearance of the lateral line canals in larger skulls indicates a metamorphosis. *Microbrachis* is more primitive than *Palaeomolgophis* in that small pre-sacral as well as post-sacral intercentra are present.

Evidence is given which leaves little doubt that in microsaurs generally the vertebrae are of apsidospondylus type and the centrum is a pleurocentrum. They are not lepospondylous and the validity and usefulness of the term 'Lepospondyli' is questioned.

The evidence presented here supports the view that there was a deep and early split in tetrapods separating the labyrinthodonts (batrachomorphs) from the reptiliomorph types, (the Lower Carboniferous microsaurs, microbrachids, gymnarthrids, seymouriomorphs, etc.). All display more or less a series of structures never found in any labyrinthodont and which indicate either a very early divergence from the labyrinthodont stock or a separate origin from fishes.

The emergence of essentially reptilian characters in *Palaeomolgophis*, an apparently aquatic form of Lower Carboniferous age contradicts the assumption that these characters arose as adaptations to land life and indicates that the first move toward the reptilian condition was structural and that it was only at a later date that the life-history was modified and that terrestrial tetrapods, reptiles in the full sense, arose.

Introduction

Romer (1950, 1958, pp. 591–592) placed all Amphibia with an adelospondylous type of vertebral column (i.e. with a separate neural arch and centrum ossification and a persistent neurocentral suture) in the Order Microsauria and regarding the presence or absence of a neurocentral suture as unreliable for purposes of classification put the Microsauria with the Orders Nectridea and Aïstopoda in the Class Lepospondyli. He also proposed that the genus *Microbrachis* (from the U. Carboniferous of Nyran) should be regarded as the type microsaur and this has been accepted.

The oldest known amphibian fossils, with the exception of the ichthyostegids (which come from beds usually regarded as U. Devonian in age but which it is now said may be basal Carboniferous), are four specimens from the calciferous sandstone series of L. Carboniferous age in Scotland. They were named and described by Watson in 1929 as *Adelogyrinus simnorhynchus*, *Dolichopareias disjectus* (two specimens) and an undetermined lepospondyl (the type of *Palaeomolgophis scoticus* gen. et sp.nov. described in this paper). These four specimens represent all the known microsaur material of L. Carboniferous age from Scotland. An undescribed specimen from the Wardie shale beds in Harvard Museum was referred to by Baird in a recent paper (1964) as an Aïstopodan, family uncertain.

A small skull from U. Carboniferous beds in Scotland is that of an adelogyrinid and is being described by Dr Carroll under the name of *Adelospondylus watsoni* gen. et sp.nov.

The letters R.S.M. placed before the number of the specimen indicate that it belongs to the Royal Scottish Museum, Edinburgh; R. to the British Museum (Natural History) London.

The geological age of these specimens is as follows:

L. Carboniferous calciferous sandstone series	Upper oil shale group	4. Dunnet Shale, Pentland Oil group, R.S.M. 1889, 101.17. Type of *Adelogyrinus simnorhynchus* Watson.
		3. Burdiehouse limestone, Burdiehouse, R.S.M. 1950, 56.7. Type of *Dolichopareias disjectus* Watson.
	Lower oil shale group	2. Curley Shale, Pumperston, R.S.M. 1902, 100.1. Mentioned by Professor Watson 1929 but unnamed. Type of *Palaeomolgophis scoticus* gen. et. sp.nov.
		1. Wardie Shale. Harvard specimen.

Watson associated with the type of *Dolichopareias* a skull table (R.S.M. 1881, 43.37) which comes from Pitcorthie, Fifeshire. The beds from which it was obtained belong to the oil shale group but cannot be exactly correlated with the Lothian series. This specimen cannot therefore be precisely placed in the above table.

Adelogyrinus simnorhynchus Watson

Type and only known material. R.S.M. 1889, 101.17. (Watson 1929, pp. 245–247), Figures 1, 2, 3.

The type consists of an uncrushed skull with some sixteen vertebrae and remains of forelimb and scales. Romer (1950, text-fig. 1 *c*) suggested that Watson's figure of the skull was incomplete and incorrectly inserted a temporal bone lateral to the parietal.

The bones of the skull are for the most part represented by moulds of the internal surface but fragments of bone remain showing a coarse reticulate labyrinthodont ornament.

The skull for an amphibian is curious in shape and rather fish-like (figures 1, 2) with orbits lying near the front end of the skull and a long post-orbital skull table. This skull has been subjected to pressure during preservation and is pushed slightly sideways. The cheek has remained in contact throughout its length with the skull table. It could be assumed from this that the cheek is suturally united to the skull table, but the assumption

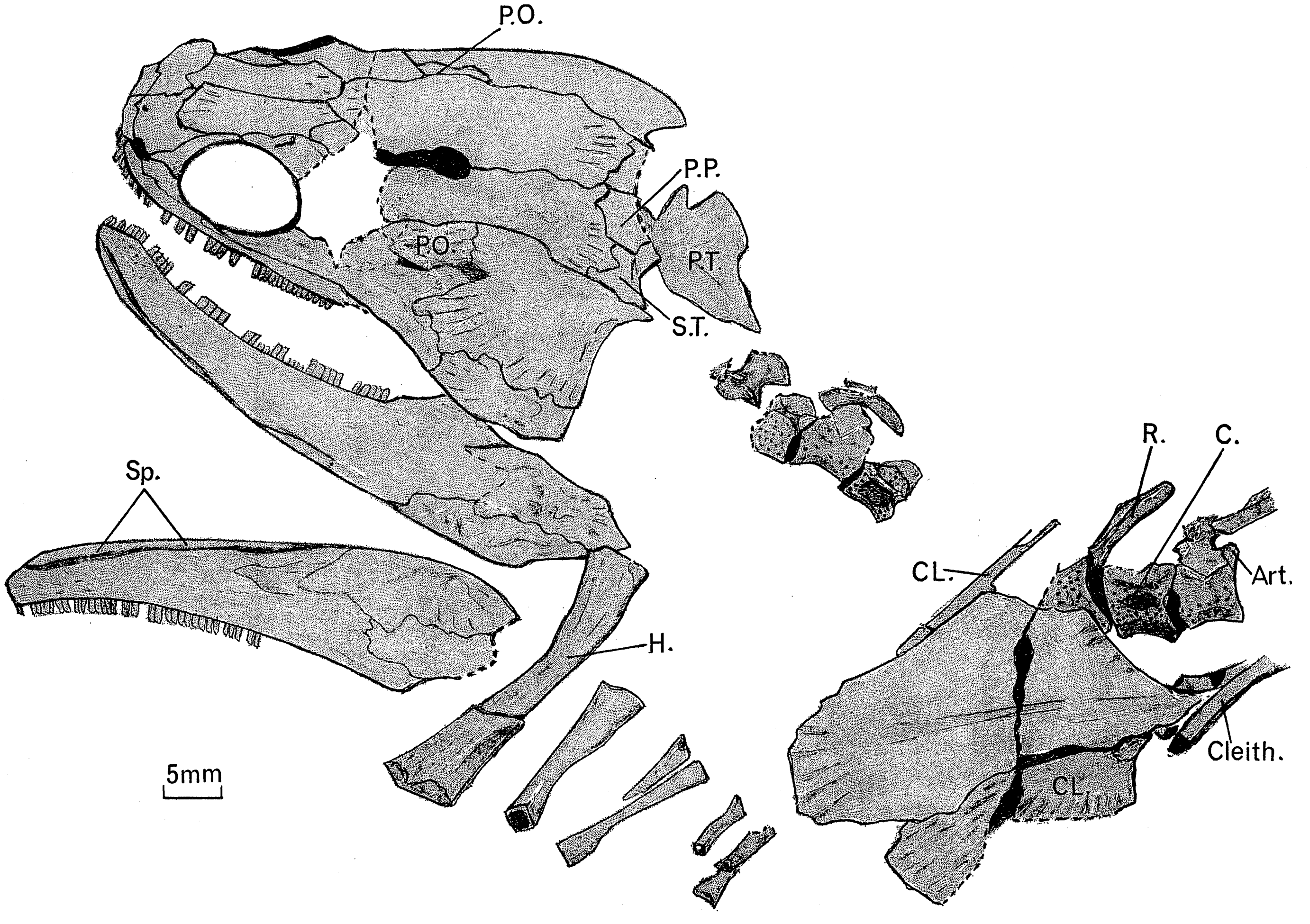


FIGURE 1. *Adelogyrinus simnorhynchus* Watson. Type R.S.M., 1889, 101.17. Skull and anterior part of skeleton, compare figure 15*a*, plate 13.

is possibly not correct. In *Microbrachis*, while the skull is often preserved in this way, there is a free articulation between the supratemporal and squamosal. No otic notch is present and the posterior margin of the squamosal is vertical and straight, from it a small process projects to lie alongside the supratemporal.

There is a long straight suture between the squamosal and parietal which is quite clearly shown on the right-hand side of the skull. The temporal row of bones is absent except for a single bone on the posterior corner of the skull table. This bone is designated as a supratemporal though its identity is not certain.

The posterior row of bones on the skull table consists of a pair of post-parietals and supratemporals. The supratemporals fit on to the posterior corners of the pareitals so that the post-parietals are in contact only with these two bones (a reptiliomorph pattern of skull table). The pineal foramen was called by Watson key-shaped. This extension of the pineal anteriorly is genuine, but it is likely that it only exists on the internal surface of the parietals which is the surface preserved here, and that the external pineal opening was more or less circular as in *Dolichopareias*.

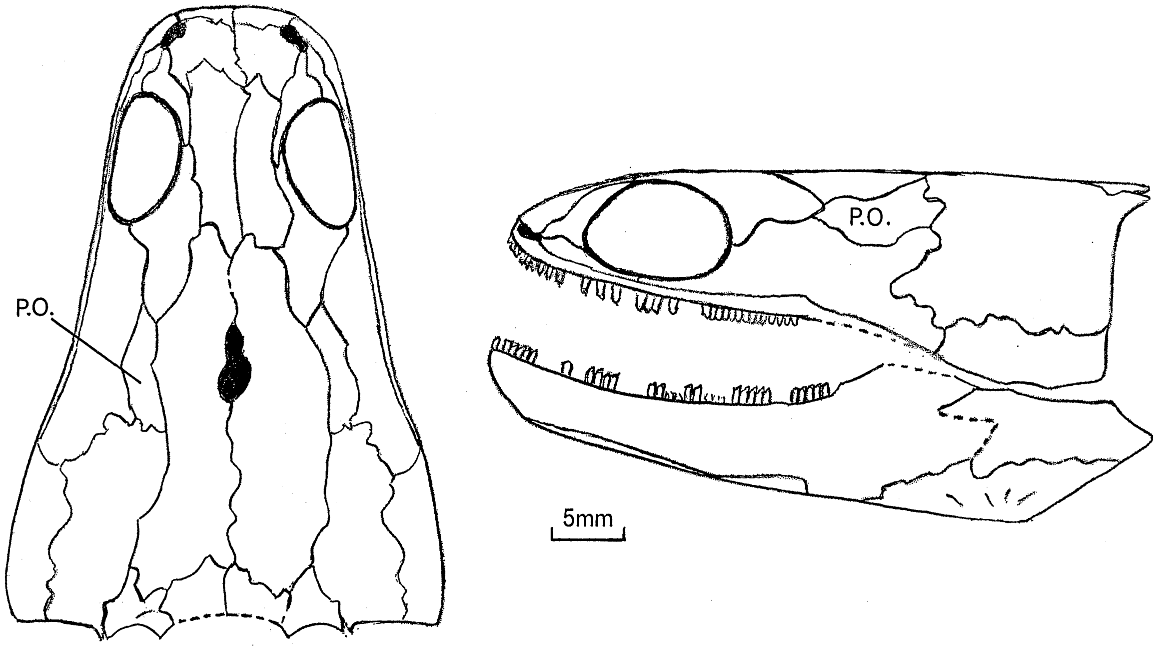


FIGURE 2. *Adelogyrinus simnorhynchus* Watson. Type R.S.M., 1889, 101.17. Reconstruction of the skull, 'post-orbital' restored from right-hand side of skull.

The bones immediately posterior to the orbit are damaged on the left-hand side of the skull but complete on the right-hand side. The posterior orbital margin is formed by the post-frontal and jugal. Lying behind these bones and excluded from the orbital margin and wedged in between them and the squamosal and parietal is a bone (figure 2) whose identity can only be guessed at, but which is called here 'post-orbital' (according to Watson post-orbital or supratemporal). In *Dolichopareias* there is a similarly placed bone which carries a lateral line canal. The pteriotic plate of the pterygoid is detached and exposed behind the skull.

The lower jaw, even when allowance is made for the curvature of the snout, appears to project a little behind the posterior margin of the squamosal (figure 2). Two splenials are present.

The series of small uniformly sized marginal teeth carried by the premaxilla, maxilla and dentary are very characteristic in form. They are parallel-sided columns and where preservation is good, the column is surmounted by a backwardly directed and sharply pointed apex.

Behind the skull follows a vertebral column, with gaps, in which sixteen vertebrae occur, some of which are shown in figure 1. This type of vertebra, which Watson called adelospondylous, consists of a separate neural arch and centrum ossification. The centra are amphicoelous, notochordal, as broad as long, and their surfaces markely pitted. The lateral and ventral centrum surfaces are depressed leaving intervening ridges. Where the centra are in contact with one another they fit tightly to the ventral margin and no spaces to accommodate intercentra occur. On the posterior margin of the centra at the level of the dorsolateral ridge a facet is developed to receive the rib capitulum.

The neural arches are all badly preserved except for three which lie towards the end of the slab and which were figured by Watson (1929, text-fig. 25). They have been refigured here to show the ribs associated with them (figure 3). The first arch is shown in anterior view, the second and third in lateral view; all are preserved as moulds of the external

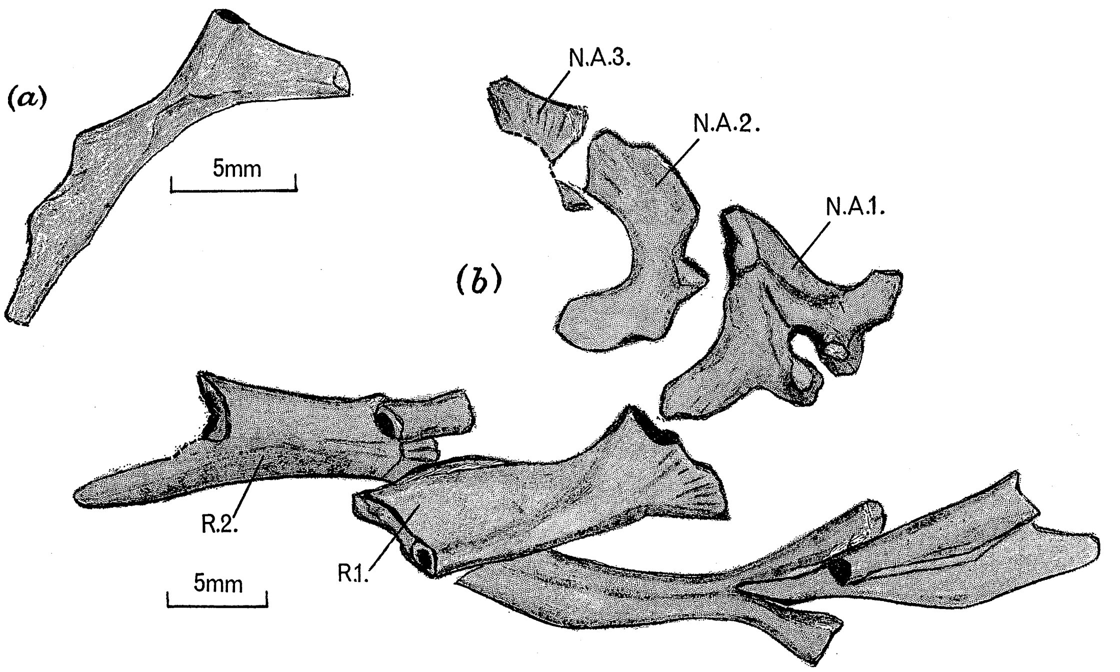


FIGURE 3. *Adelogyrinus simnorhynchus* Watson. Type R.S.M., 1889, 101.17. (*a*) isolated rib from behind the shoulder girdle; (*b*) three neural arches and their associated ribs.

surface so that the pedestal of the arch is not visible. The neural arches are single ossifications (a deep groove on the anterior face separates the two halves of the neural arch in *N.A.* 1), with low neural spines and broad transverse processes. Two ribs, that belonging to *N.A.* 1 and to the vertebra in front are complete except for their distal ends. A single complete detached rib lies alongside the vertebral column behind the shoulder girdle. All other ribs are very incomplete. The detached rib (figure 3*a*) has a wide head, the well developed tuberculum and capitulum connected by a web of bone, the shaft carries a posterior flange or wing which is not demarcated from the rib shaft. The ribs proximal to *N.A.* 1 and *N.A.* 2 are stouter than the rib which lies immediately in front of them, particularly in the development of the head and width of the rib wing. This suggests that *N.A.* 1 and *N.A.* 2 represent the sacral vertebrae.

The shoulder girdle is preserved as a mould of the internal surface of the interclavicle and two incomplete clavicles, one of which shows a coarse reticulate ornament similar to that of the skull (figure 1). The anterior plate of the interclavicle is very large, its parasternal process is overlaid by the shaft of a cleithrum and other bones so that its true length cannot be determined. This cleithrum shaft continues into a dorsal plate placed vertically in the specimen and for this reason not shown in figure 1. The cleithrum plate is normal in shape, and resembles that of *Palaeomolgophis*.

Between the lower jaws and the shoulder girdle lie a number of bones (figure 1) belonging to the forelimb. The humerus is long, without any condylar development on the free ends and broken across the shaft. That it is one bone is indicated by the surface striae which continue in alinement across the break. The radius and ulna are also long and slender and lack ossified condylar surfaces.

A few metacarpals are preserved. Small scales, disturbed and lying over one another are present from behind the shoulder girdle to the end of the slab. They are 2 to 3 mm long and 1 mm broad, with a thickened ridge running along one side of their length and show no well developed surface ornament.

Dolichopareias disjectus Watson

Type R.S.M. 1950, 56.7 (Watson 1929, pp. 247–249, text-fig. 26).

The type consists of an incomplete skull, seen from the right-hand side and with the actual bones preserved (figure 4*A*).

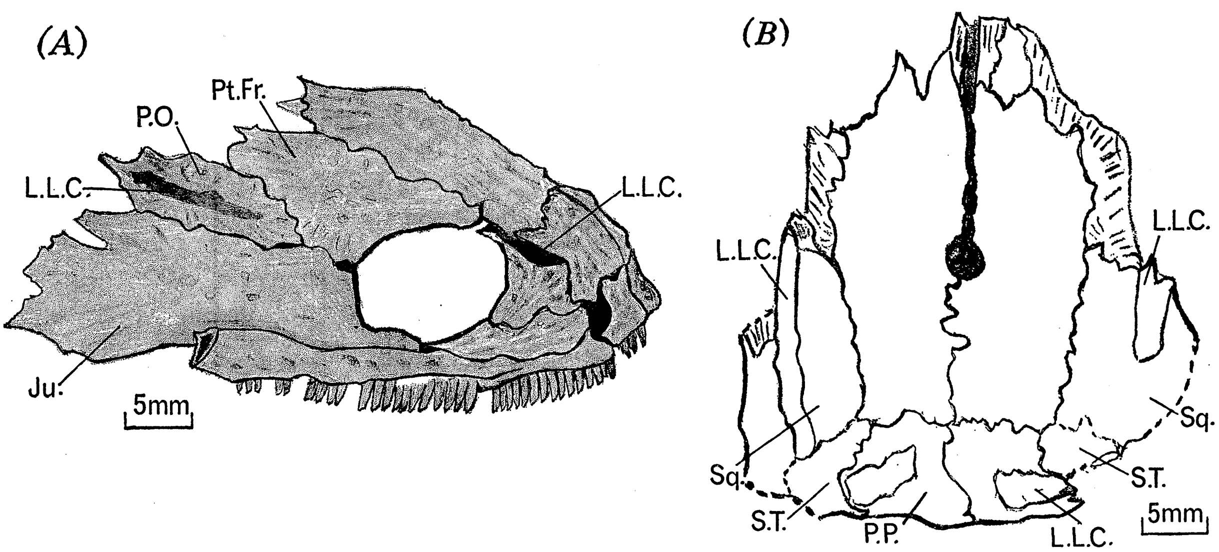


FIGURE 4. *Dolichopareias disjectus* Watson. (*A*) Type skull R.S.M., 1950, 56.7; (*B*) skull table R.S.M., 1881, 43.37.

In this skull, as in *Adelogyrinus*, the orbits are placed very anteriorly. The jugal and postfrontal form the posterior half of the orbital margin and wedged in between them posteriorly and excluded from the orbit is a 'post-orbital' bone. The ornament is heavy and deeply incised as in labyrinthodonts, and a lateral line canal is present on the 'postorbital' and on the prefrontal-nasal suture. The teeth form a uniform series, and like the teeth of *Adelogyrinus*, are columnar with small recurved acutely pointed apices; the outer tooth surface is smooth with no longitudinal grooves. The surface of the maxilla is broken away in this specimen, so that sections of the teeth are exposed. They are hollow cones and the base of the tooth is set vertically into the maxilla. The jugal is a long bone, suggesting an elongate cheek.

With the type, Watson associated a skull table, preserved as an impression of its external surface, R.S.M. 1881, 43.37 (figure 4*B*). This skull table fits remarkably accurately, as Watson pointed out, on to the back of the type skull, and although it came from another locality and possibly a different geological horizon, was used by Watson to form his reconstruction of the *Dolichopareias* skull. Prominent lateral line canals, wider than the lateral line canals of the type, are present on the post-parietals and squamosal and the ornament is coarser.

These two specimens, the type and the skull table associated with it by Watson show all the characteristic features of the *Adelogyrinus* skull. In the type, the anteriorly placed orbits, the presence of a 'post-orbital' bone excluded from the orbital margin and the characteristically shaped teeth. In the skull table, the long straight parietal-squamosal suture, the suppression of a normal temporal row and a supratemporal situated on the posterior corner of the skull table.

Palaeomolgophis scoticus **gen. et sp.nov.**

Type R.S.M. 1902, 100.1.

The type consists of a crushed skull with the greater part of the vertebral column (50 vertebrae are preserved but the end of the tail is missing), remains of shoulder girdle, and elements of fore- and hind limbs, figure 15 (*b*), plate 13. Watson (1929, text-fig. 23, pp. 244–245) referred to this specimen but did not describe it in detail.

The disrupted skull, figure 5, in which the actual bones are preserved, is exposed from the ventral side showing the palate overlaid by the cheek bones and lower jaw and exposing part of the inner surface of the skull table. A coarse reticulate ornament is present on the cheek and lower jaw bones, except for the dentary which is smooth as in *Adelogyrinus*.

The roofing bones of the skull displayed are a pair of frontals (in the left orbit) and the right supratemporal, post-parietal and part of the parietal. The cheek bones, turned over and superimposed on the skull table, consist of a jugal and squamosal below whose ventral margin the edge of the quadrato-jugal is visible. The squamosal, like that of *Adelogyrinus*, has a straight vertical posterior margin and a small posterior horn lying alongside the supratemporal. The ventral surface of the supratemporal shows that the cheek is not suturally attached to the skull table. No otic notch is present. The dorsal margin of the jugal is damaged so that it is not possible to determine if a 'post-orbital' is present. Both orbits are shown, sclerotic plates are present in the left orbit. Bounding the right orbit anteriorly are a prefrontal and a lachrymal of which the intact anterior margin indicates unusually large external nares. A maxilla and displaced premaxilla are present. The dis-association of the bones makes it difficult to restore the skull with accuracy but an attempt has been made in figure 6. It shows the resemblance of the squamosal to that of *Adelogyrinus*.

The palate has the same tantalizing incompleteness. Posteriorly a basioccipital and a pair of exoccipitals are present. The basioccipital seen in ventral view has an almost flat posterior margin. The exoccipitals have distinct condyles which when placed in correct position relative to the basioccipital face inwards. This agrees with the shape of the articulating facets on the 1st vertebra which slope outwards at about 45° (figure 5 *C*1).

The parasphenoid is a triangular plate-like bone, the processus cultriformis passing imperceptibly into the posterior plate and no basipterygoid processes projecting from the parasphenoid are present. A swelling on either side at the level of the displaced premaxilla represents the basisphenoid-basipterygoid processes. The surface of the parasphenoid is covered by a shagreen of small badly preserved denticles. The pterygoid is not exposed but the bones lying between the right maxilla and the two dentaries are the prevomers.

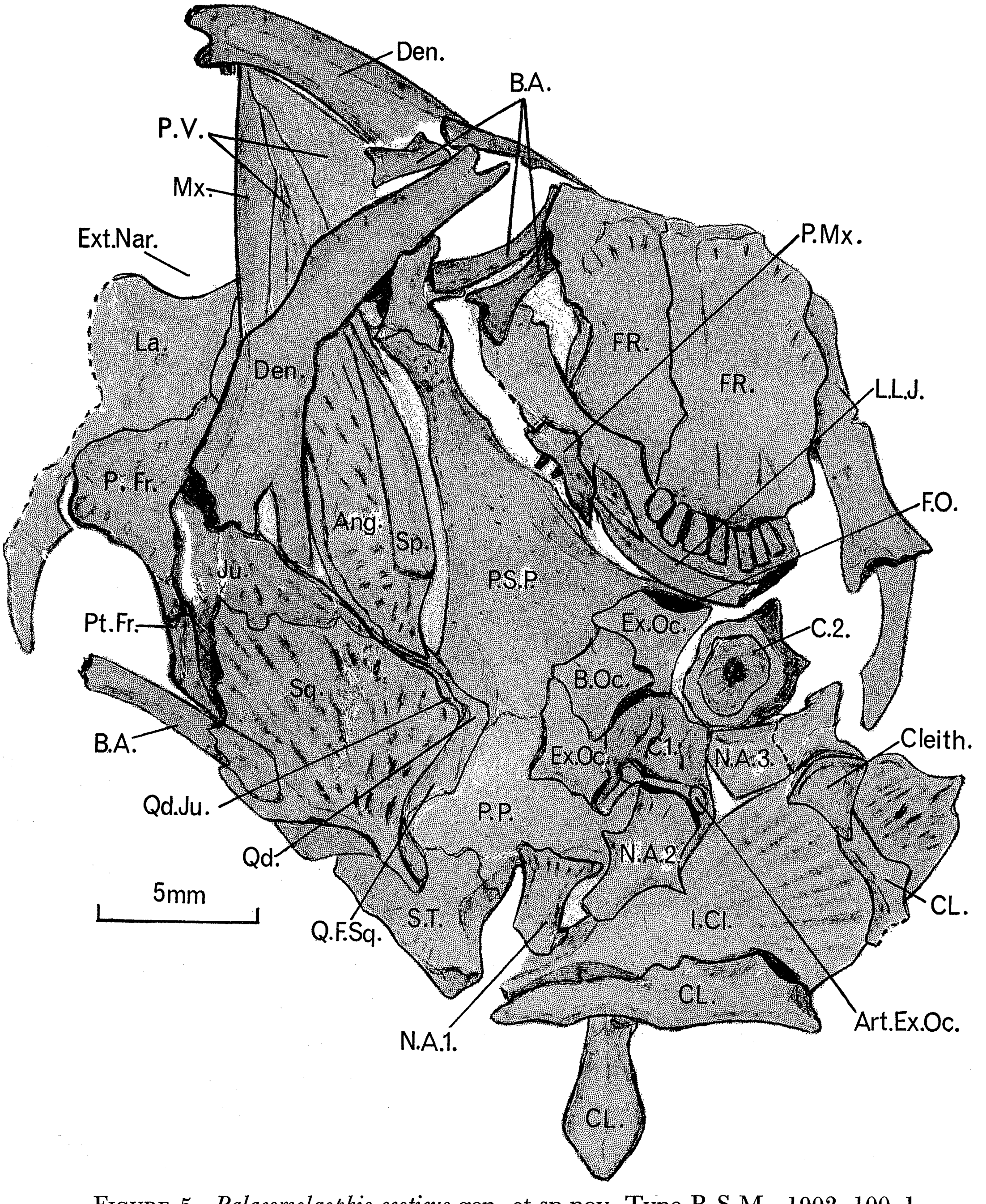


Figure 5. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Skull and post-cranial skeleton, compare figure 15 (*b*), plate 13.

Most of the bones of the lower jaw are present. The right lower jaw is represented by a dentary disassociated from an angular, part of a surangular and splenials. The left lower jaw by a detached dentary, the posterior end of which is exposed above the left orbit. A few small columnar teeth are present on the left dentary and premaxilla.

This leaves a number of bones not yet mentioned. These are a pair of rod-like waisted bones lying in front of the left orbit, a small bone lying in front of the anterior end of the right dentary and a similar isolated bones lying free from and in front of the skull, together with the bone overlapping the right squamosal. The isolated bone and that lying by the squamosal are longer than the ulna (preserved among the limb bones) and lack condyles such as are present in the forelimb bones. All these bones are therefore regarded as part of a well developed branchial arch skeleton.

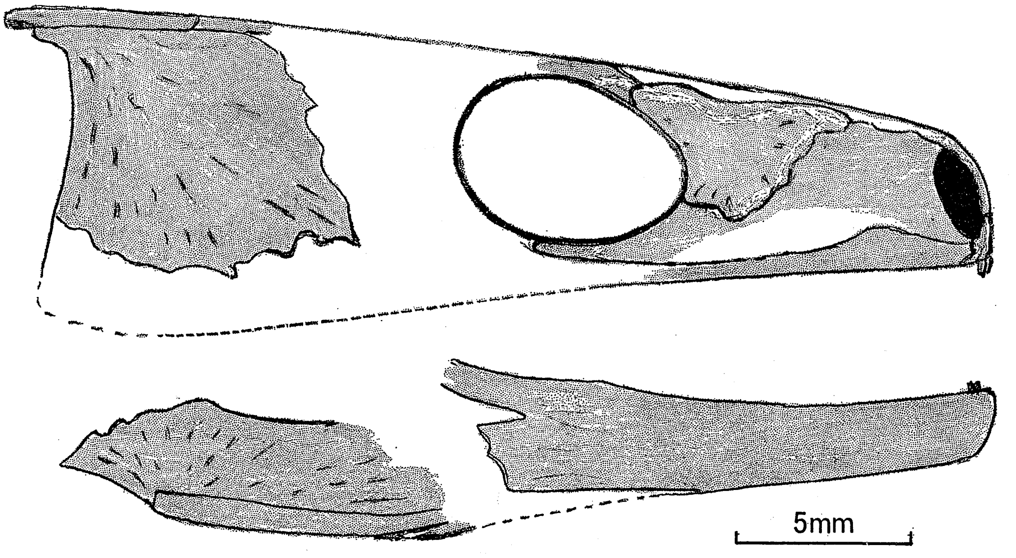


FIGURE 6. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Reconstruction of the skull.

The vertebral column consists of a series of some 50 vertebrae starting behind the skull and continuing into the caudal region; only the end of the tail is missing. They lie for the most part in natural articulation and are numbered in sequence for convenience in referring to the different regions though disturbance of the immediate post-cranial vertebrae and dislocation of the mid-dorsal regions means the numbering may not be quite exact (figures 7, 8, 9).

The neural arch (single) and centrum are independent ossifications. The centra are notochordal (*C* 10) deeply amphicoelous (*C* 2, 46) and broader than long (4 mm broad, 3·5 mm long). With the exception of *C* 1 they are approximately of the same size into the tail up to the last vertebra preserved (*C* 50). In lateral view, they show pronounced dorsolateral and ventrolateral ridges between which the surface of the centrum is recessed. No pitting occurs on the surface of these centra such as is present in *Adelogyrinus* and to a less extent in *Lysorophus*. The ridges on the centra are as prominent in *Palaeomologphis* as in the much larger centra of *Megalomolgophis* (centrum length 15 mm), a L. Permian species with similar vertebrae which can be related to *Palaeomolgophis* (see p. 126). At the posterior rim of the centrum at the level of the dorsolateral ridge, a facet is developed for articulation with the rib capitulum. While this is generally true, in both *Palaeomolgophis* and *Megalomolgophis* in certain centra in which preservation appears to be perfect no facet can be observed and it is assumed that in these cases it is unossified. No facets occur on the anterior centrum rim except in the case of *C* 39. This vertebra and *C* 38 are slightly larger than the preceding vertebra and are assumed to be the sacral vertebrae.

The articulation for the neural arch lies on the anterior half of the centrum, posterior to which the centrum increases in height, the post-pedestal rise.

Centrum 1 (figure 5) lies immediately behind the basioccipital and is turned so that its ventral and anterior surfaces are exposed. It differs from all the other centra in that it is

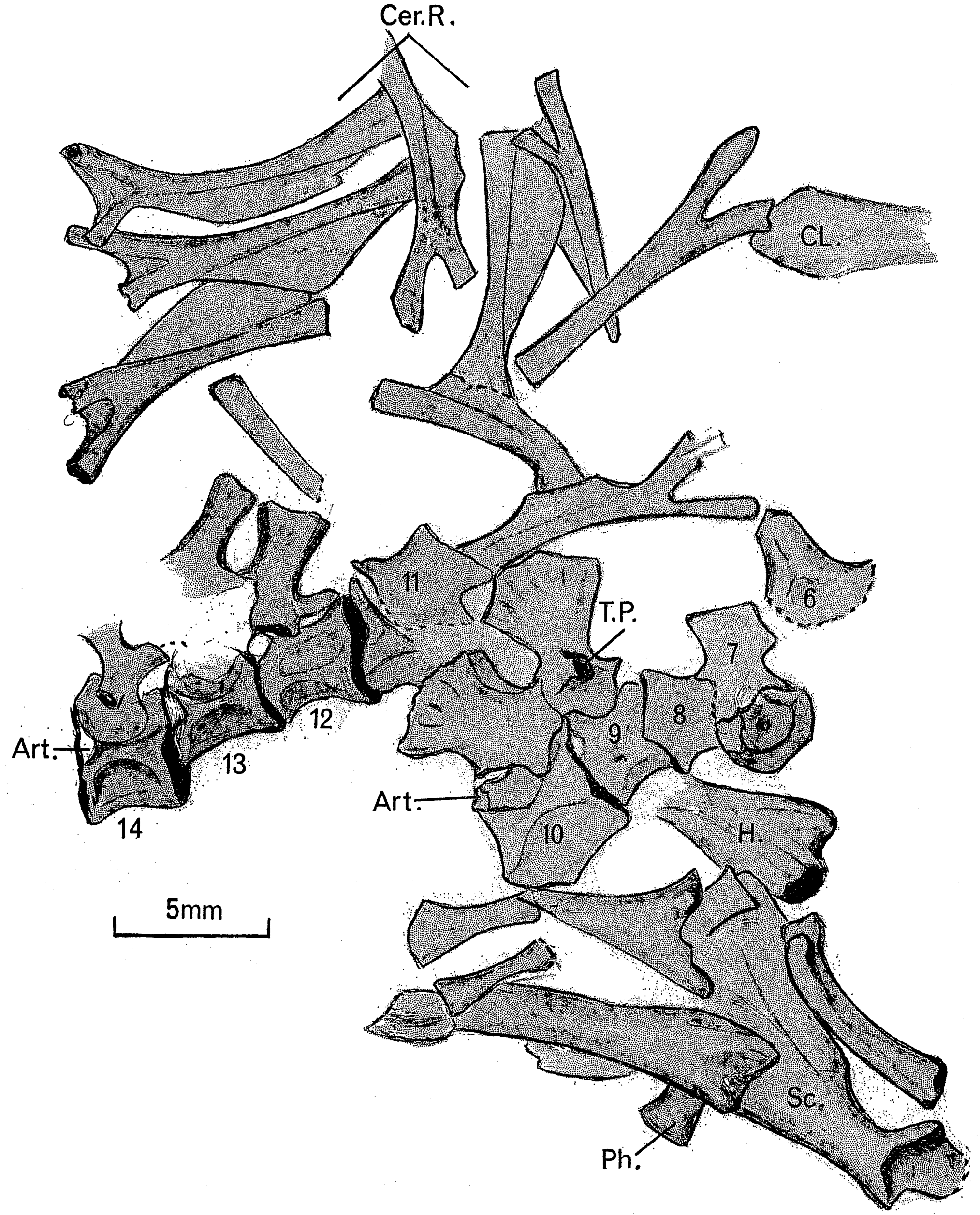


FIGURE 7. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Vertebrae 6 to 14, with associated ribs and remains of forelimb. This follows on figure 5 (see clavicle present in both figures).

U-shaped and not a complete ring. The ventral surface is slightly recessed and shows two slight ridges. In anterior view, the wide articular surface for the basioccipital is practically flat, and on either side of this basioccipital articulation, sloping backwards at an angle of 45°, are two well developed facets, oval in shape, and again almost flat, which articulate with the exoccipitals. That is, the exoccipital articulations on the skull (as in *Lysorophus*)

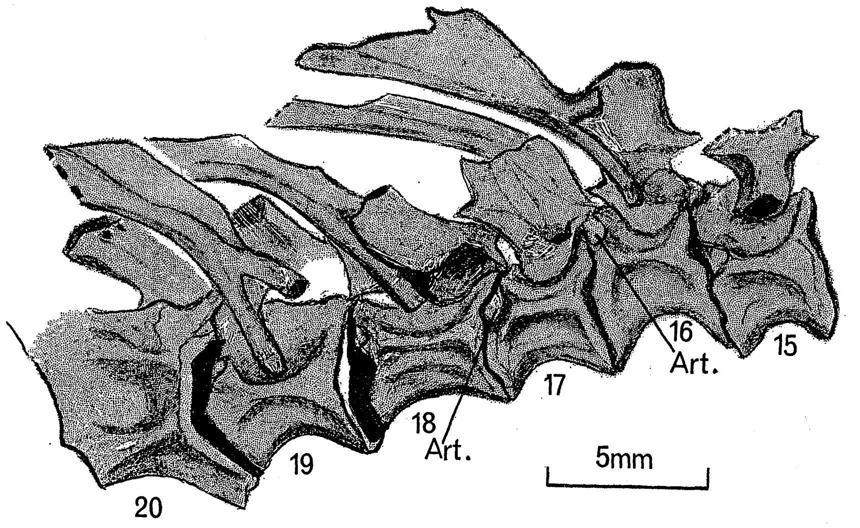


FIGURE 8. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Vertebrae 15 to 20.

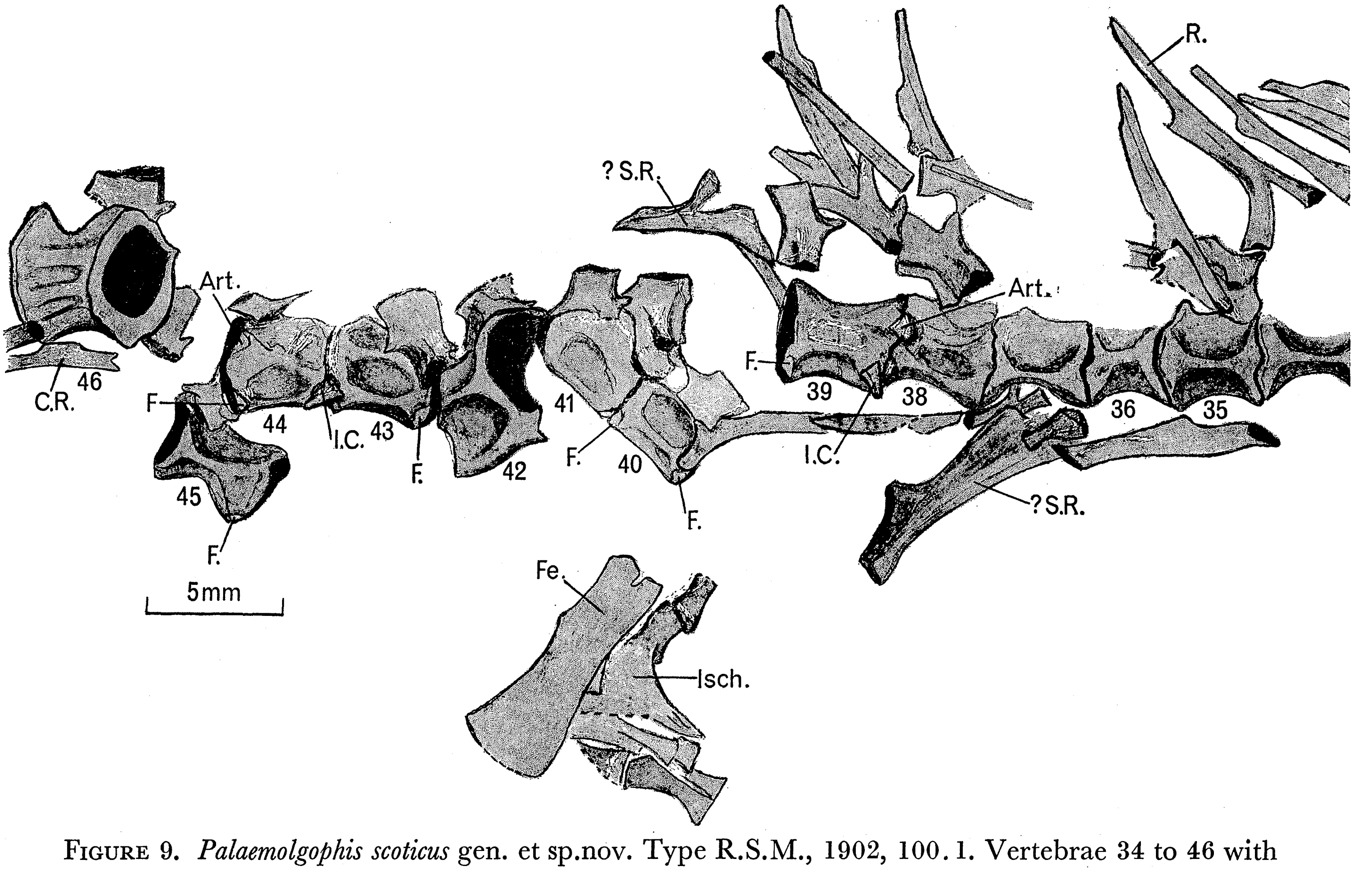


FIGURE 9. *Palaemolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Vertebrae 34 to 46 with remains of hind limb. Some neural arches and ribs omitted.

look inwards (unlike reptiles where they are directed outwards). The neural arch belonging to this centrum *N.A.* 1 is smaller than *N.A.* 2 and the pedestal is shorter.

Where the vertebrae are in natural articulation with one another, the centra fit tightly and no intercentra are present up to vertebra 38. Between vertebra 38 to 39 and 43 to 44 intercentra are preserved, and where they have been displaced or lost in the series of vertebrae 38 to 50, oblique facets on the posterior ventral margins and to a less extent on the anterior of the centra mark the position they occupied (figure 9). There is therefore a series of small caudal intercentra present starting at the sacral vertebrae, whether they are paired or single elements cannot be determined from this specimen.

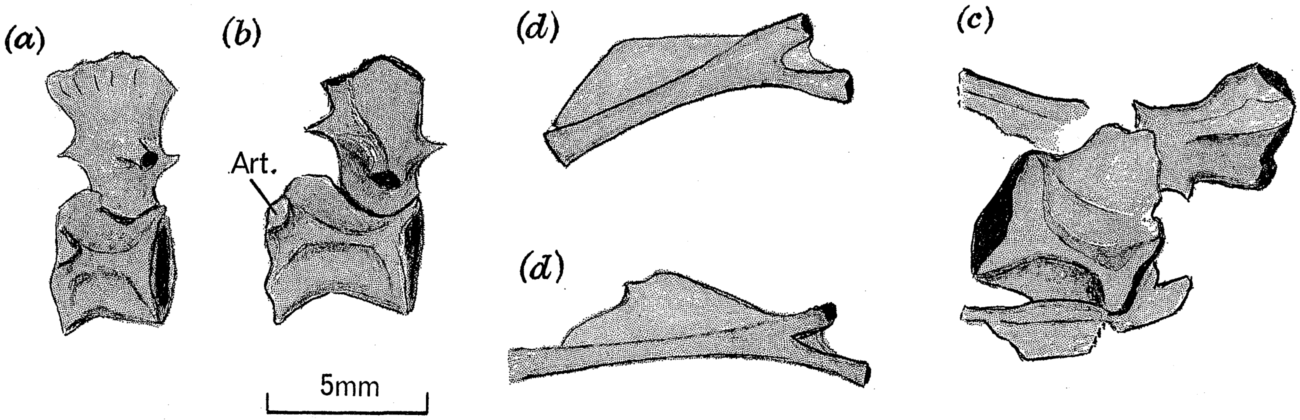


FIGURE 10. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M., 1902, 100.1. Reconstruction of vertebrae and ribs; (*a*) based on vertebra 9; (*b*) based on vertebrae 15–20; (*c*) vertebra 26 (see Watson 1929, text-fig. 23); (*d*) cervical and dorsal ribs.

The neural arches, in contrast to the centra, are badly preserved and in parts incompletely exposed. Nowhere do we see them in anterior or posterior view. In the disturbed post-cranial region the neural arches are represented by impressions except for *N.A.* 9 in which the anterior half of the neural arch with the prezygapophyses and transverse process is preserved in bone. The transverse process of *N.A.* 9 is directed anteriorly, its outer end being cupped. This is an unusual position but in *Lysorophus* (Sollas 1920, p. 519) the transverse processes of the dorsal neural arches are also directed anteriorly. The cervical neural arches contract slightly above the zygapophyses and then expand to a widened low spine which carries a few striae (figure 7).

Coming to the mid-dorsal region the neural arches show a recessed area (e.g. *N.A.* 17, 26, figures 8, 10). This recess is often covered by matrix when the neural arches appear narrow and parallel sided. The transverse process in these regions are directed downwards and outwards.

The cervical ribs (figure 7) are short, almost straight, double-headed, the capitulum and tuberculum connected by a web of bone. The shaft of the rib carries a triangular flange or wing which extends from the tuberculum to the end of the rib shaft. These ribs differ from the longer curved double-headed body ribs in which the rib wing is shallow and extends only part of the way along the rib shaft (figures 8, 9). *Megalomolgophis* has an additional anterior flange on the capitulum side of the rib shaft but this is not present in *Palaeomolgophis*. Many of the dorsal ribs are imperfect with the flanges usually broken.

The shoulder girdle is represented by a number of elements. There is a shield-like interclavicle, which is prolonged into a posterior stem (figure 5). One clavicle is broken, the ventral plate lying alongside the interclavicle, while the dorsal process with a small cleithrum still attached lies across the interclavicle shield; a second clavicle projects posteriorly.

Behind the shoulder girdle, and lying to one side of vertebrae 7 to 10 (figure 7), is a mass of bones, many broken and lying one on top of the other. In this a few phalanges, a scapulocoracoid with the glenoid surface exposed, and a number of limb bones with well defined condylar surfaces, can be seen. The glenoid on the scapulocoracoid is a deep socket, sharply delineated and strongly buttressed dorsally: in correlation with this the ends of the humeri have well developed condyles. The presence of such a well ossified anterior limb, in such an ancient and apparently aquatic form, is only one of the unexpected characters of *Palaeomolgophis* and will be referred to later.

Below the 37th and 38th vertebrae lies a bone (figure 9, ? *S.R.*) covered by a thin film of matrix whose identity is uncertain. It is wider and more massive than the ribs which lie around it and was first thought to be an ilium. The slope of the exposed end and the marked flange on the shaft suggests that it is a rib. *Adelogyrinus* (figure 3*b*) has solid enlarged sacral ribs and it is therefore tentatively suggested that this bone in *Palaeomolgophis* represents an enlarged sacral rib. If this identification is correct then *Palaeomolgophis* like *Adelogyrinus* has enlarged stout sacral ribs of normal length.

Impressions of a femur, part of an ischium and some phalanges lie below the 40th to 42nd vertebrae (figure 9).

Patches of scales, covered by a thin film of matrix are exposed between the ribs and vertebrae which are superimposed on them. They resemble the oat-shaped *Adelogyrinus* scales.

The photograph of *Palaeomolgophis*, figure 15 (*b*), plate 13, shows much of the structure reproduced in the text figures but areas where the bone is lost do not appear on the plate, e.g. the femur. A comparison of the reconstruction of the whole animal (figure 11) with the plate shows a longer body than the plate suggests, as in the actual specimen the post-cranial vertebrae are displaced and lie transversely across the back of the skull.

The transverse process in the 9th vertebrae, preserved in bone, is directed anteriorly. The short cervical ribs must therefore stand out almost horizontally from the vertebral column, a position not very successfully represented in figure 11. The body ribs, a curious feature, do not shorten markedly in length towards the sacral region as one would expect. Caudal ribs are present up to the 48th vertebra, i.e. there are at least nine pairs of caudal ribs.

The marked dorsolateral and ventrolateral ridges on the centra give the vertebrae of *Palaeomolgophis* a very distinctive appearance. The vertebrae of *Pleuroptyx* and *Megalomolgophis* (whose centra are about $4\frac{1}{2}$ times the size of those of *Palaeomolgophis*) show similar prominent ridging. Although such ridges are only a developmental stage in other microsaur type vertebrae, their retention in the large and therefore adult vertebrae of *Megalomolgophis*, etc., suggest that these genera are related to one another (this is borne out by other structures in *Megalomolgophis*) and can be placed together in a single family, the Molgophidae (see p. 126) for which the structure of the vertebrae is a valid character.

The general characters of *Palaeomolgophis* can now be summarized. It is a long bodied form with 37 dorsal vertebrae and a stout and long tail. Dorsal intercentra are not present, but there is a series of small free intercentra present throughout the tail region. The ribs are winged and there is a differentiated series of cervical ribs. The body ribs are not shortened to any extent until they approach the sacral region. At least nine pairs of caudal ribs are present.

The interclavicle has a parasternal process. The scapulocoracoid has a well defined glenoid cavity the dorsal margin of which is thickened. The forelimb bones have well formed condylar surfaces, the limb bones and phalanges in fore- and hind limbs are well developed and the forelimb is larger than the hind limb.

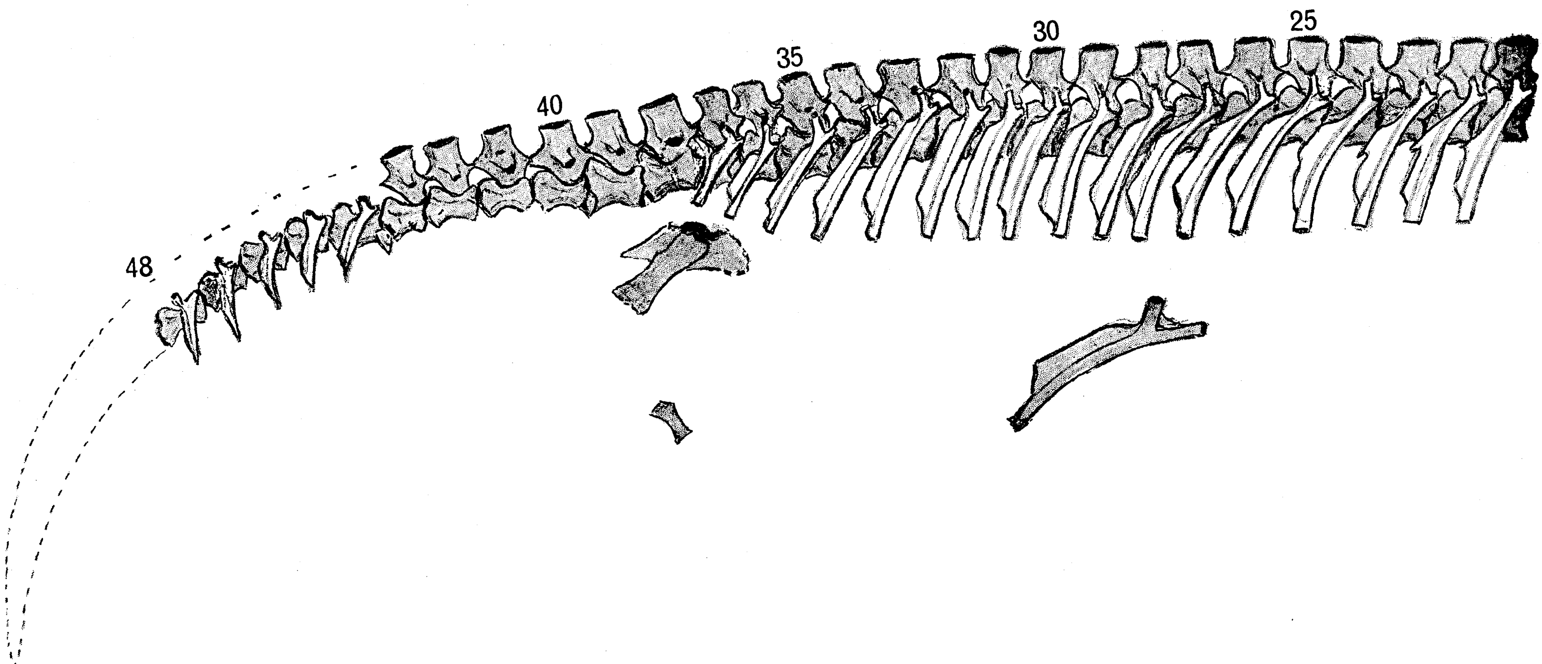


FIGURE 11. *Palaeomolgophis scoticus* gen. et sp.nov. Type R.S.M. 1902, 100.1. The caudal ribs have been omitted from the 38th to the 43rd vertebrae to show the caudal intercentra which have

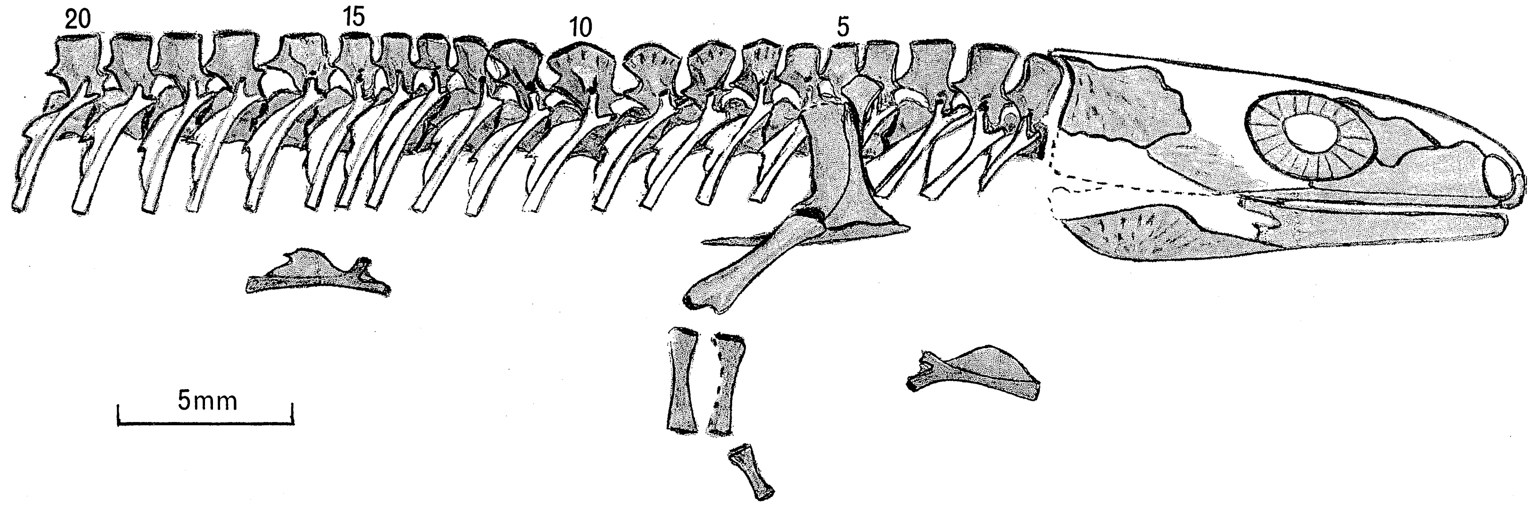
In the skull an otic notch is not present, the posterior border of the squamosal being vertical and straight, a large supratemporal is present on the posterior corner of the skull table. Unfortunately the post-orbital region of the skull is not exposed so that one does not know if a post-orbital excluded from the orbital margin (a diagnostic character of the *Adelogyrinus* and *Dolichopareias* skull) is present. The palate has a triangular plate-like parasphenoid without basipterygoid processes and small slit-like interpterygoid vacuities. Two exoccipital condyles facing inwards (like *Lysorophus*) are present. Other minor characters also present in *Adelogyrinus* and *Dolichopareias* are the close-set columnar teeth with recurved chisel-like apices, the smooth external surface of the dentary and the fact that it becomes easily detached from the posterior bones of the lower jaw, and the nature of the scales.

Lysorophus sp.

R. 3445, figure 12. These vertebrae of *Lysorophus*, with a centrum length of 4·5 mm, are only a little larger than those of *Palaeomolgophis* (3·5 mm) and have been figured for this reason so that a direct comparison can be made.

Professor Watson (1929, p. 245) pointed out the resemblance of *Lysorophus* vertebrae to those of *Adelogyrinus*. They are typical microsaur vertebrae with a separate neural arch and centrum ossification, the pedestal of the neural arch articulating only with the anterior half of the centrum. They differ from the vertebrae of *Palaeomolgophis* and *Adelogyrinus* in that the dorsolateral and ventrolateral ridges are less marked. No facet is developed here on the centrum for the articulation of the rib capitulum. Slight pitting is present on the centrum surface. The ribs are without well developed wings or flanges such as are present in *Adelogyrinus* and *Palaeomolgophis*.

Dorsal intercentra are unknown and Willeston asserts that caudal intercentra are not



been preserved and the space between the pleurocentra to accommodate intercentra which have dropped out. The branchial arch skeleton is omitted.

present. Dr Olson tells us that elements in one of his specimens may represent caudal intercentra.

The parasphenoid is plate-like but not triangular as in *Palaeomolgophis* and the dermal bones of the skull reduced. Nevertheless, it seems to be of reptiliomorph pattern.

Discussion

Microsaur vertebrae and the status of the Lepospondyli

The microsaur type vertebrae of *Adelogyrinus*, *Palaeomolgophis*, *Lysorophus*, and the genera which can be associated with them, are seen to consist of a separate neural arch and centrum ossification, with a neurocentral suture. This suture can disappear with age in microsaur type vertebrae but it is not known to do so in any Lower Carboniferous microsaur.

The centra are amphicoelous, notochordal and with the facet for the neural arch confined approximately to the anterior half of the centrum. There is an increase in height of the centrum posterior to this articulation, the post-pedestal rise.

The neural arch has rounded, slightly swollen zygapophyses, and the transverse process and prezygapophyses lie close together and almost directly above the pedestal of the arch from which the posterior zygapophyses sweep back free over the posterior half of the centrum.

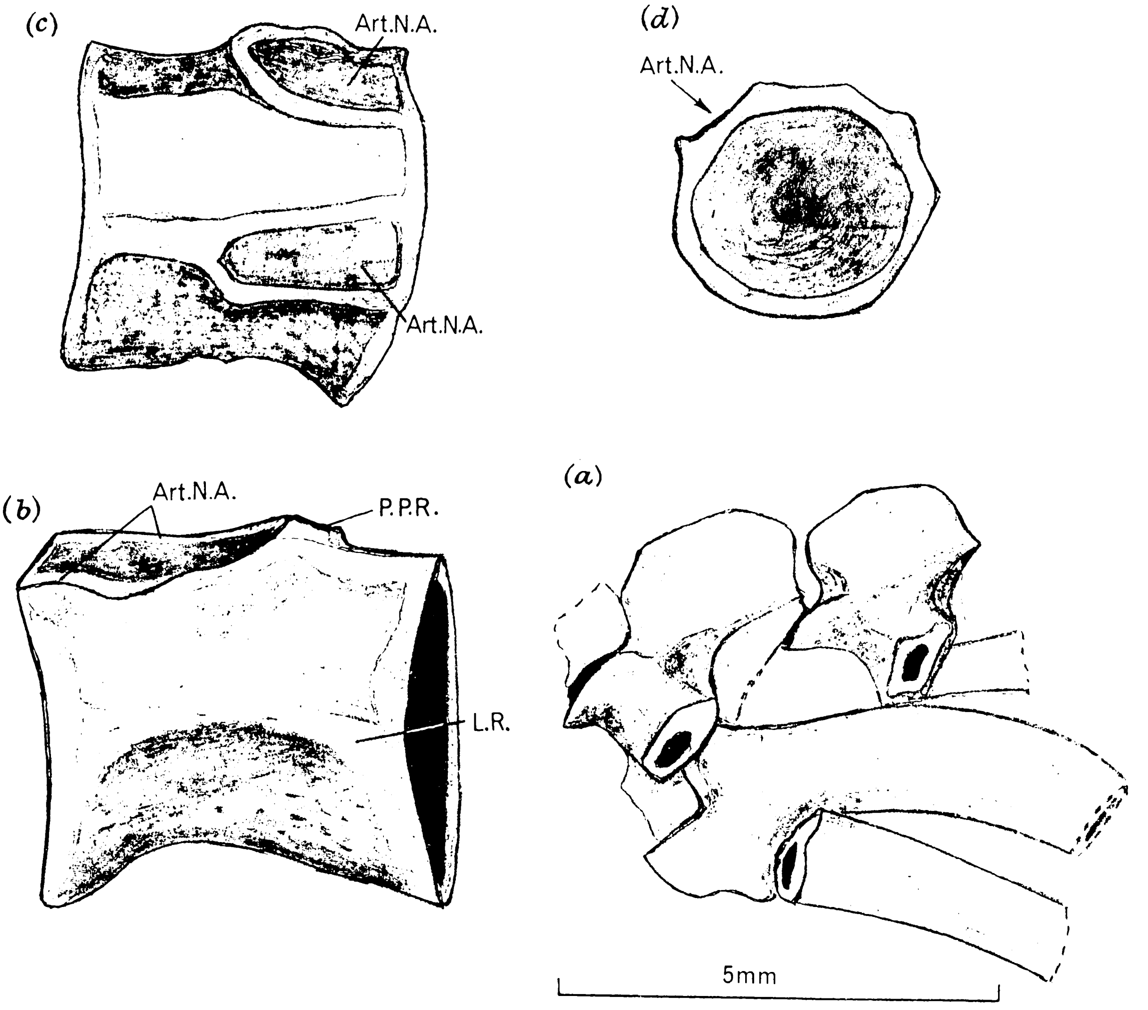


FIGURE 12. *Lysorophus* sp. R. 3445. (*a*) Neural arches and ribs. (*b* to *d*). Three isolated centra: (*b*) lateral view, (*c*) dorsal view, (*d*) end view.

No dorsal intercentra occur, neither is there any trace of a suture across the postero-ventral corner of the centrum nor a projection which would suggest that an intercentrum element is included in the centrum ossification. Where the caudal region is known, small free intercentra are present, and when the caudal vertebrae are placed in natural articulation small Λ-shaped gaps indicate their presence when they have been lost, which often occurs in the process of fossilization.

In the microsaurs from the Lower Carboniferous the centra are as broad or broader than long. This gives them a superficial resemblance to fish centra which has been commented on in various papers. The prominence of the dorsolateral and ventrolateral ridges and the amount of pitting on the centrum surface varies. Sollas (1920, p. 518) has pointed out that *Cryptobranchus* centra are covered with a dense layer of bone perforated by small pores such as occur here.

*Microbrachis pelikani** the type microsaur from the U. Carboniferous of Nyran is a small animal. Complete specimens vary from 7 to 13 cm in length, including the tail, which is $\frac{1}{2}$ to $\frac{2}{3}$ of the body length. Skulls vary from 11 to 23 mm in mid-dorsal length, though one larger skull of 28 mm with no post-cranial remains attached is known. In this series of skulls (Steen 1938, text-fig. 16) one can see the development of the diagnostic deeply incised dichotomous ornament on the skull bones and the development of the lateral line pits and canals. In the 28 mm skull, the lateral line has completely disappeared. This would indicate that *Microbrachis* is known to us mainly by larval aquatic forms and that there is a metamorphosis when the lateral line canals disappear.

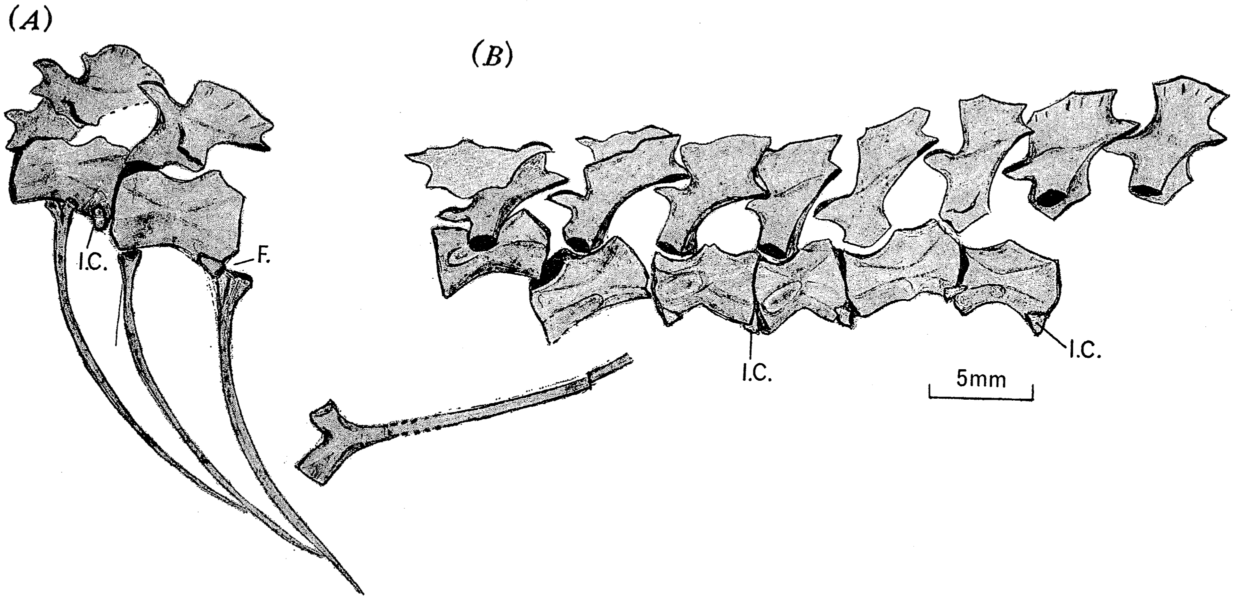


FIGURE 13. *Microbrachis mollis* Fritsch. Electrotype R. 371. (*A*) Vertebrae 20 to 21; (*B*) vertebrae 27 to 34 to show intercentra, ribs omitted.

The direct and early ossification of the post-cranial skeleton of *Microbrachis* is illustrated in the smallest vertebrae where, at a centrum length of 1 mm, the zygapophyses are already rounded and slightly swollen and the transverse process is already being delimited from the neural arch surface. The range in size is usually 1 to 2+ mm in centrum length though some of 3 mm are known. Thus, they are smaller than the vertebrae of the L. Carboniferous microsaurs. They are almost identical in structure with these vertebrae, but differ from them in having no ossification of a facet on the centrum for the capitulum of the rib and other slight differences, e.g. paired neural arches which are due to the larval nature of the microbrachid material and are early growth stages. *Microbrachis* like *Palaeomolgophis* has a long back with 38 to 40 dorsal vertebrae (Schwartz 1908, p. 91). Variation in the number of dorsal vertebrae is also found in living amphibia such as the salamanders.

In *Microbrachis* there is a complete series of small free caudal intercentra (Schwartz 1908, p. 93; Steen 1938, p. 231) and these coexist with five pairs of ossified caudal ribs. Dorsal intercentra are present, but only in the immediate presacral region, the number varying from one species of *Microbrachis* to another. In the anterior body region intercentra are

* Fuller details of vertebral structure are given in the following paper.

absent, nor is there a suture or projection from the centrum which would suggest that they are incorporated in the centrum.

It follows from this that dorsal intercentra are in process of disappearing in *Microbrachis* (they have already disappeared in the L. Carboniferous *Palaeomolgophis*) and that the centrum in microsaurs is a pleurocentrum and a pleurocentrum only. Further, that *Microbrachis* represents the most primitive known microsaur vertebra.

In *Microbrachis* growth stages in the centra can be observed. The smallest centra are double cone shaped the surface smooth and the neural arches paired. At a later stage, dorsolateral and ventrolateral ridges appear on the surface of the centrum and the neural arches are single elements. Growth stages in the vertebrae of the primitive seymouriamorph *Gephryostegus* (like *Microbrachis* from the U. Carboniferous of Nyran; centrum length 3 to 13 mm), show that with increase of size both ridges and depressions disappear, the vertebra filling out as it becomes more heavily ossified (figure 14),

The swollen convex zygapophyses with firm horizontal overlapping of the zygopophysis and low neural spines are said in seymouriamorphs to be adaptations to land life, but they occur not only in the vertebrae of larval microbrachids but also in the probably aquatic L. Carboniferous microsaurs. In the L. Carboniferous microsaurs the centra are the predominant element in the vertebra, in *Seymouria* the neural arches the dominant element.

The articulation of the rib capitulum consequent on the reduction in size or loss of the dorsal intercentrum in microsaur-type vertebrae is of some interest. In L. Carboniferous microsaurs the rib capitulum articulates with an ossified facet (this fails to ossify in individual vertebrae) high up on the posterior rim of the centrum. In *Microbrachis* and *Lysorophus*, the width of the rib head suggests that it articulates in a similar position, but no facet is observable in the specimens figured.

In the seymouriamorphs whose vertebrae are basically of the same type as the microsaurs, the rib capitulum retains the primitive position attached to the small dorsal intercentra in *Seymouria* and *Kotlassia*, but in *Gephryostegus* it articulates adjacent and anterior to the transverse process (Broili 1924, Plate 1).

With the loss of the dorsal intercentra, the rib capitulum articulation with the centrum varies, and its position is not a reliable guide in the interpretation of vertebrae structure. Whatever its position, in all forms it moves towards the transverse process in the sacral vertebrae.

The orders Aïstopoda and Nectridea are placed with the microsaurs in the Class Lepospondyli (Baird 1965). These two orders differ from the microsaurs in that even at the earliest growth stage (centrum length less than $\frac{1}{2}$ mm) no neurocentral suture is present. In both orders also the neural arch pedestal extends the whole of the centrum length unlike microsaurs where it is confined to the anterior half of the centrum.

The haemal arches in Nectridea, where they arise from the middle of the centrum, and in Aïstopoda in which they are said to be *de novo* outgrowths from the centrum surface (Baird 1964) on either side of the haemal canal, are quite different in their relation to the body of the centrum from that of any other amphibian order. A possible explanation of this would seem to be that the intercentrum ossification remained large in both these orders and became incorporated in the single vertebra rather than that new structures, as assumed in the Aïstopoda, should be formed. An unique character of the Aïstopoda vertebra is the

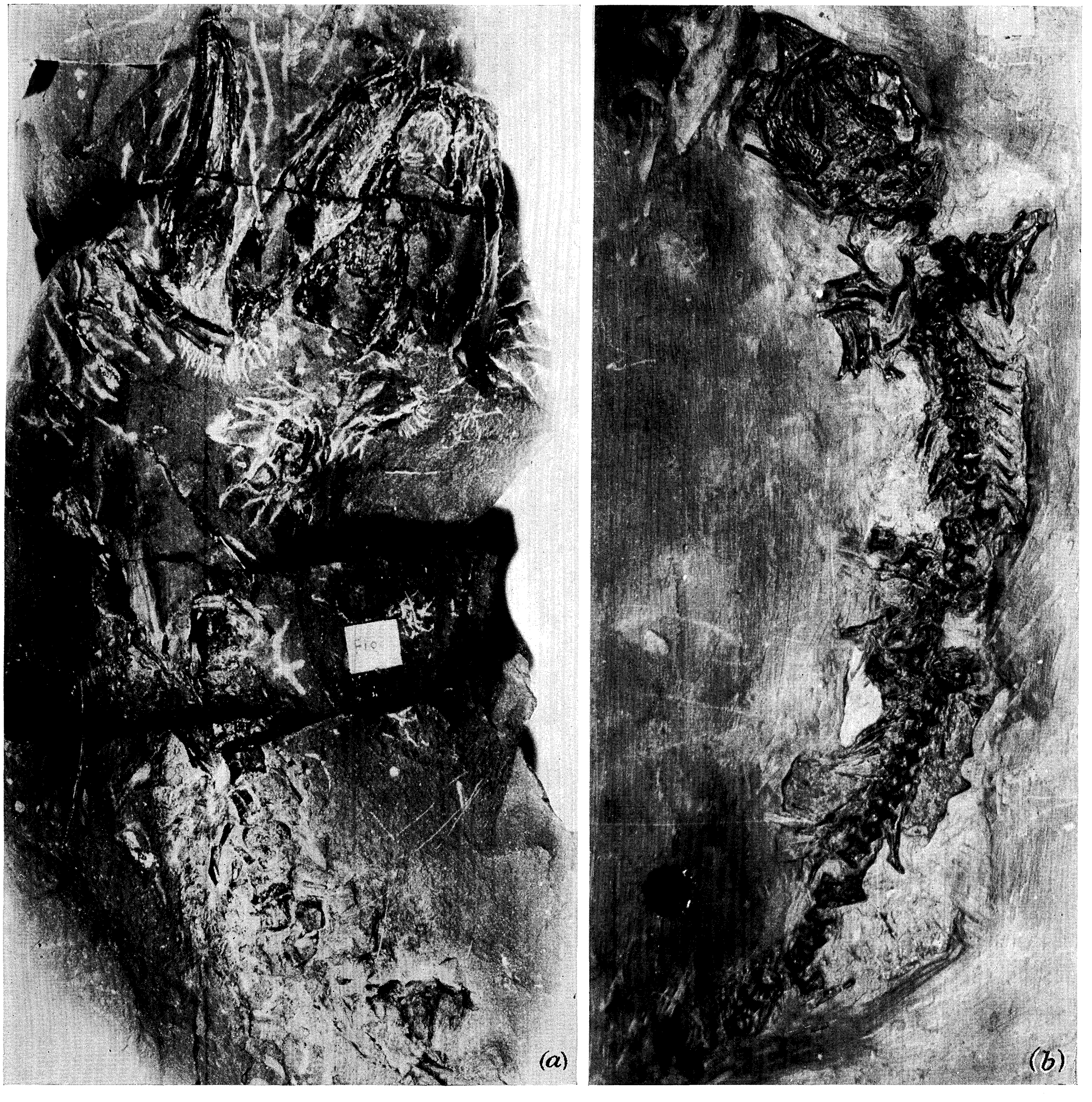


FIGURE 15 (*a*) *Adelogyrinus simnorhynchus* Watson, R.S.M. 1889, 101.17. (Magn. × 1 approx.)
(*b*) Type *Palaeomolgophis scoticus* gen. et sp.nov. R.S.M. 1902, 100.1 type. (Magn. × 1 approx.)

(*Facing p.* 124)

inclusion of the spinal foramen in the neural arch. This condition could easily be derived from that of the microsaur by the extension of the neural arch ossification along the whole length of the centrum.

It would seem then that the 'Lepospondyli' is little more than a term of convenience

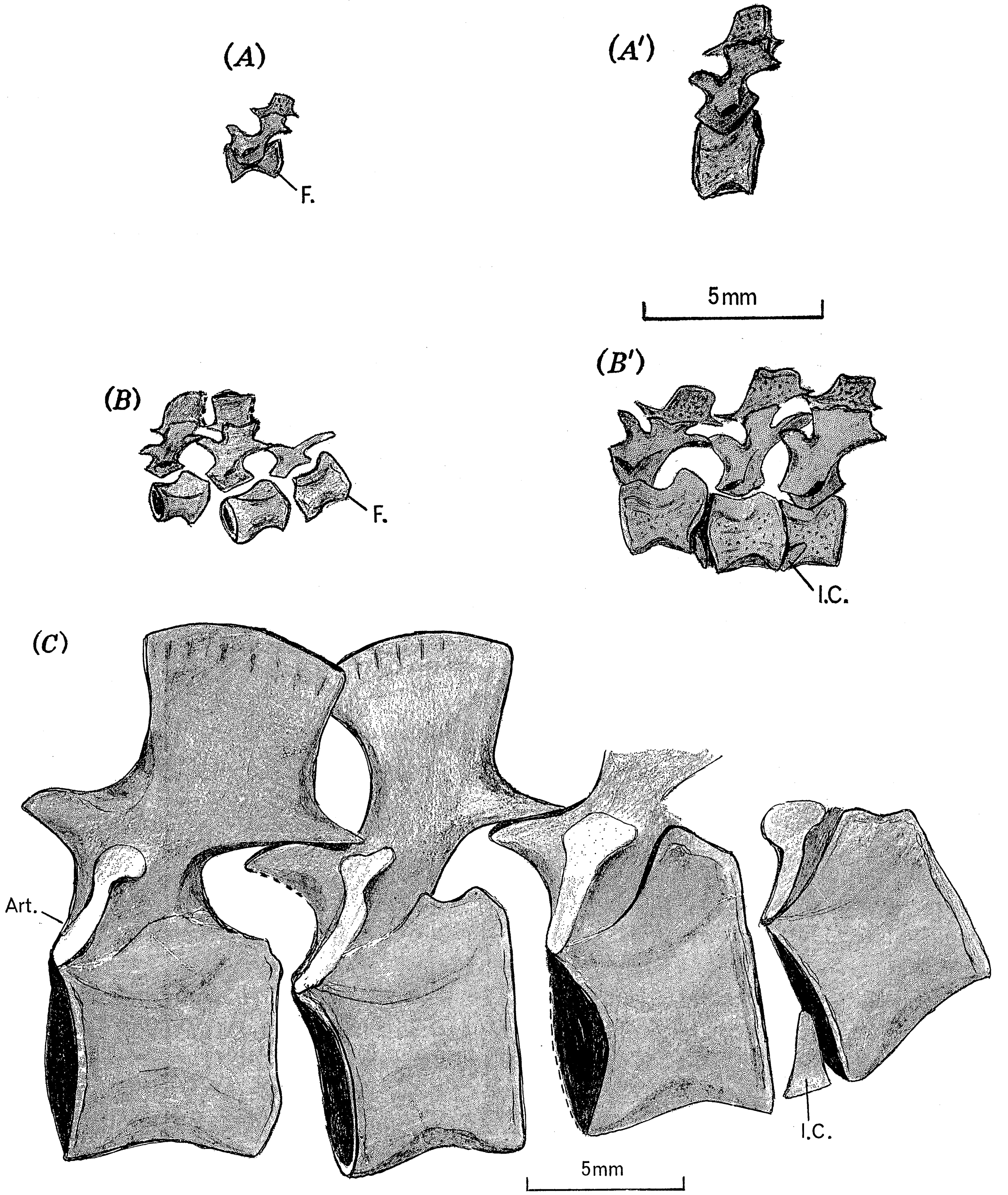


FIGURE 14. *Gephyrostegus bohemicus* Jaekel. Growth stages of the vertebrae. Specimen I. (*A*) 15th vertebra; (*B*) 21st to 23rd vertebrae, Specimen II. (*A′*) 15th vertebra. (*B′*) 21st to 23rd vertebrae. (*C*) after Broili 1924, Pl. 1.

to include orders in which direct and early ossification of the vertebrae occurs and has no real validity. The microsaur vertebra as has been demonstrated above is clearly of apsidospondylus type and the centrum is a pleurocentrum. The fact that some of the earliest known forms as *Palaeomolgophis* show a relatively advanced condition does not invalidate the general view, and is explained by the now widely held opinion that such an evolution can proceed at different speeds in independently evolving though related groups. The composition of the nectridian and aïstopodan centra is a more difficult problem and remains unresolved, but in our opinion there is some evidence which at least hints at an apsidospondylous origin for these as well.

Classification and relationships of the Lower Carboniferous microsaurs

Certain U. Carboniferous and L. Permian genera can be associated with the L. Carboniferous forms described in this paper. The suggested classification for all these genera is as follows:

1. Family Adelogyrinidae
   Adelogyrinus (L. Carboniferous), *Dolichopareias* (L. Carboniferous)
2. Family Molgophidae
   Molgophis (U. Carboniferous), *Palaeomolgophis* (L. Carboniferous)
   Pleuroptyx (U. Carboniferous), *Megalomolgophis* (L. Permian)
3. Family Lyrosophidae
   Cocytinus (U. Carboniferous) *Lysorophus* (L. Permian)

These three families have the following characters in common:

1. All the evidence indicates that they are fully aquatic forms with lateral line or branchial arch skeleton.

2. Microsaur vertebrae with pleurocentra as broad or broader than long with dorso- and venterolateral ridges, the centrum surface recessed between them. No dorsal intercentra, free caudal intercentra present where the tail region is known.

3. Ribs double headed, the capitulum articulating with a facet high up on the posterior rim of the pleurocentrum. This facet fails to ossify in individual vertebrae (*Palaeomolgophis*, *Megalomolgophis* Romer 1952) or remains unossified (as in the specimens of *Lysorophus* figure 12).

4. The interclavicle has a large anterior plate and posterior parasternal process.

5. No otic notch in the skull.

6. Palate, where known, solid with slit-like interpterygoid vacuities, parasphenoid plate-like.

There is thus a considerable community of structure in these three families which seem to form a natural group and probably merits subordinal status.

The characters of the three families are as follows:

1. Family. Adelogyrinidae. Skull; orbits anterior in position, long straight suture between parietal and squamosal, post-orbital excluded from the orbital margin (diagnostic of this family), squamosal with posterior margin vertical and straight and small horn, marginal teeth close set, columnar with recurved chisel-like apices, outer surface of dentary smooth in contrast to the posterior bones of the lower jaws. Ribs winged, double-headed, two enlarged sacral ribs. Centrum surface with close set pitting.

2. Family. Molgophidae. Skull; orbit in anterior half of skull length but placed towards the middle of the skull, squamosal with posterior margin vertical and straight and small horn, parasphenoid a triangular plate without basipterygoid processes, outer surface of dentary smooth. Ribs winged, double-headed, cervical ribs present. Pleurocentra with marked dorsolateral and ventrolateral ridges, the centrum surface recessed between them, centrum surface unpitted.

3. Family. Lysorophidae. Skull; dermal bones reduced in number, parasphenoid plate-like without basipterygoid processes, marginal teeth simple sharply pointed cones. Ribs without wings, double-headed. Pleurocentrum surface with dispersed pits.

It becomes quite clear then that although related and of earlier geological age the Lower Carboniferous microsaurs cannot be considered as ancestral to the microbrachids. The presence of dorsal intercentra in the latter would alone exclude this possibility and the Lower Carboniferous forms seem to constitute as Baird suggests (1965, p. 292), an early divergent group.

Finally, this investigation of these very early tetrapod fossils may throw some light on the wider questions of the origin of terrestrial vertebrates. It has been widely assumed that the structural characters associated with reptiles arose in relation to land life. There is increasing evidence that this is not so. The L. Carboniferous microsaurs, the U. Carboniferous microbrachids, gymnarthrids, forms such as *Hylonomus lyelli* (Carroll 1963) and the seymouriamorphs all show, more or less, characters in the post-cranial skeleton which are accepted as reptilian. These are briefly the nature of the vertebral column, the presence of cervical ribs, and a stalked interclavicle. It is emphasized that these characters can be observed in demonstrably aquatic forms such as *Palaeomolgophis* and larval microbrachids.

These structures are not characteristic of batrachomorphs, and the facts set down here relating as they do to early Carboniferous forms lend strong support to the view first advanced by Säve-Söderberg (1935) that there is a deep fission almost from the beginning in tetrapod structure dividing it into two groups, batrachomorphs and reptiliomorphs. Whether this is an early dichotomy or represents a polyphyletic origin for tetrapods is a matter for further investigation.

It has been generally assumed in connexion with the origin of reptiles that structural evolution went hand in hand with the evolution of life-history, the change to a cleidoic egg and fully land life. This we believe is a misconception and that in fact the structural changes toward the reptilian condition were initiated at an early date when the creatures displaying them may not only have possessed an amphibian type of larva but may have been aquatic throughout life. We hope to expand this thesis in a later paper.

We would like to thank Professor J. G. C. Anderson for information on the Lower Carboniferous succession in Scotland, Dr E. C. Olson for information on *Lysorophus*, Mr W. O'Grady for much technical help including the taking of photographs, and the authorities of the British Museum, London and the Royal Scottish Museum, Edinburgh for the loan of the specimens described in this paper.

Abbreviations used in the figures

Ang.	angular	*La.*	lachrymal
Art.	articulation for capitulum of rib	*Mx.*	maxilla
Art.N.A.	articulation for neural arch	*N.A.*	neural arch
Art.Ex.Oc.	articulation on *C*, for exoccipitals	*P.Fr.*	prefrontal
B.A.	branchial arches	*P.Mx.*	premaxilla
B.Oc.	basioccipital	*P.O.*	'post-orbital'
C.	centrum (= pleurocentrum)	*P.P.*	post-parietal
C.R.	caudal ribs	*P.P.R.*	post-pedestal rise
Cer.R.	cervical ribs	*P.S.P.*	parasphenoid
CL.	clavicle	*P.V.*	prevomer
Cleith.	cleithrum	*Ph.*	phalanges
Den.	dentary	*Pt.*	pterygoid
Ex.Oc.	exoccipital	*Pt.Fr.*	post-frontal
Ext.Nar.	external nares	*Pub.*	pubis
F.	facet for intercentrum	*Q.F.Sq.*	quadrate flange of squamosal
F.O.	foramen ovale	*Qd.*	quadrate
Fe.	femur	*Qd.Ju.*	quadrato-jugal
FR.	frontal	*R.*	rib
H.	humerus	*S.Ang.*	surangular
I.C.	intercentrum	*S.R.*	sacral rib
I.Cl.	interclavicle	*S.T.*	supratemporal
Isch.	ischium	*S.V.*	sacral vertebra
Ju.	jugal	*Sc.*	scapula or scapulo-coracoid
L.L.C.	lateral line canals	*Sp.*	splenial
L.L.J.	left lower jaw	*Sq.*	squamosal

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FIGURE 15 (*a*) *Adelogyrinus simnorhynchus* Watson, R.S.M. 1889, 101.17. (Magn. × 1 approx.)
(*b*) Type *Palaeomolgophis scoticus* gen. et sp.nov. R.S.M. 1902, 100.1 type. (Magn. × 1 approx.)