Microbrachis, The Type Microsaur

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STUDIES ON EARLY TETRAPODS
II. *MICROBRACHIS*, THE TYPE MICROSAUR

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[Plate 14]

CONTENTS

Microbrachis (*Limnerpeton*) *obtusatum* (Fritsch) is redescribed, and additions to our knowledge of the vertebrae and skull structure of *Microbrachis* have been made. The vertebrae of *Microbrachis* are apsidospondylous, the centrum is a pleurocentrum, the intercentra are small, caudal intercentra always being present with a varying number of pre-sacral intercentra.

In the *Microbrachis* skull there is a free attachment of the cheek and skull table the supratemporal resting on a shelf which projects inwards from the dorsal edge of the squamosal. In this *Microbrachis* resembles the pre-captorhinomorphs *Protorothyris* and M.C.Z. 1963 in which the relation of these two bones is similar. The occiput of *Microbrachis* has been described.

A statement of microsaur characters is given and the list of characters separating microsaurs from captorhinids given by Gregory is critically examined.

The conclusion is reached that microsaurs and captorhinomorphs are basically of similar structure and form part of a related group which separated from labyrinthodonts in pre-Carboniferous times, or had a separate origin from the rhipidistian fishes. The differences between microsaurs and captorhinomorphs lie not in basic structure but in evolutionary timing, the microsaurs, for example, being precocious in the structure of their vertebrae.

INTRODUCTION

Romer (1950) in an excellent survey of palaeozoic microsaurs makes the suggestion (already advanced by Westoll 1942) that *Microbrachis* should be regarded as the 'type' microsaur. If this very reasonable idea is followed it means that any additions to our knowledge of this form assumes a special importance and from materials at our disposal we have been able to present a new analysis of the skull and vertebral column of *Microbrachis pelikani* and *M. mollis* and to redescribe *M. obtusatum*.

The genus as at present defined contains the three species mentioned above, but a special comment must be made on *M. pelikani*. While *M. mollis* and *M. obtusatum* are represented by single specimens, *M. pelikani* is the commonest tetrapod in the Nyran fauna and many specimens are now in museums throughout the world.

The animals grouped together in this species prove to be highly variable in structure and could easily be broken down into a number of types which may merit specific rank. There are, however, unifying characters such as the very distinctive ornament of the skull bones, and while some of the varying characters will be described we think that no useful purpose would be served by the introduction of a series of new specific names. We prefer to regard *M. pelikani* as a variable species.

The original descriptions of *Microbrachis* were given by Fritsch (1883), Schwartz (1908) gave a good description of the vertebral column, Stehlik (1924) dealt briefly with these forms and Steen (1938) redescribed them dealing especially with the skull of *M. pelikani*.

The material described in this paper belongs to the Narodni Museum, Praha (Č.G.H.), the British Museum (Natural History), London (R.) and the Royal Scottish Museum, Edinburgh (R.S.M.). We are greatly indebted to the authorities of these institutions for allowing us to study their specimens which are identified by the above letters in the text.

***Microbrachis* (*Limnerpeton*) *obtusatum* (Fritsch)**

Type and only known material certainly belonging to this species: Č.G.H. Orig. 236 Fritsch 1883, pp. 154–5, Pl. 35, figs. 1–7, text-figs. 94–8.

Fritsch founded this species on a single specimen which now appears to be represented only by an electrotype. Stehlik (1924) referred five specimens to this species but figures only a hind foot. From his description it is impossible to be certain that his material has been correctly identified. *Limnerpeton obtusatum* is closely related to *Microbrachis pelikani* and its correct position is in this genus. It is therefore described as *M. obtusatum* (Fritsch).

Fritsch drew his plates from his type specimens and then, fearing their loss in many cases by pyritization, prepared a series of electrotypes from those he considered vulnerable. In this process the specimens were often altered and occasionally destroyed. The series of electrotypes may differ from one another, i.e. insecure areas of bones or parts of bones being removed in the process of producing an electrotype. The figures in this paper drawn from electrotype R 359 show discrepancies when compared with Fritsch's figures of the same specimen. In R 359 the cheek bones, clearly shown in Fritsch's plate, have disappeared to reveal part of the palate, the lower jaw and post-cranial vertebrae; while the ring of sclerotic plates, prominent in Fritsch's plate, is here only a faint impression.

M. obtusatum is a small animal similar in its general proportions to *M. pelikani* with a long body, a tapering slender tail not quite complete in the specimen, shorter than the body length and small limbs (figure 10, plate 14). The outer bones of the skull (figure 1) are known from an impression of their inner surfaces so that the dermal ornament is unknown. It presents all the characteristic features of the microbrachid skull, small orbits placed in the anterior half of the skull length, a large supratemporal* placed on the posterior corner of the skull table, and ending in the lappets diagnostic of the microbrachid skull and extension of the parietal to cover the position of an intertemporal. Supratemporals and post-parietals show a division into two areas, an exposure on the skull table passing posteriorly into occipital flanges which lie on the sloping occiput. The

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* This bone is generally regarded as a supratemporal. Gregory (1965, p. 278) points out that the *Cardiocephalus* supratemporal occupies much of the space of the *Captorhinus* squamosal and suggests that there is a possibility of some confusion in the nomenclature of these bones.

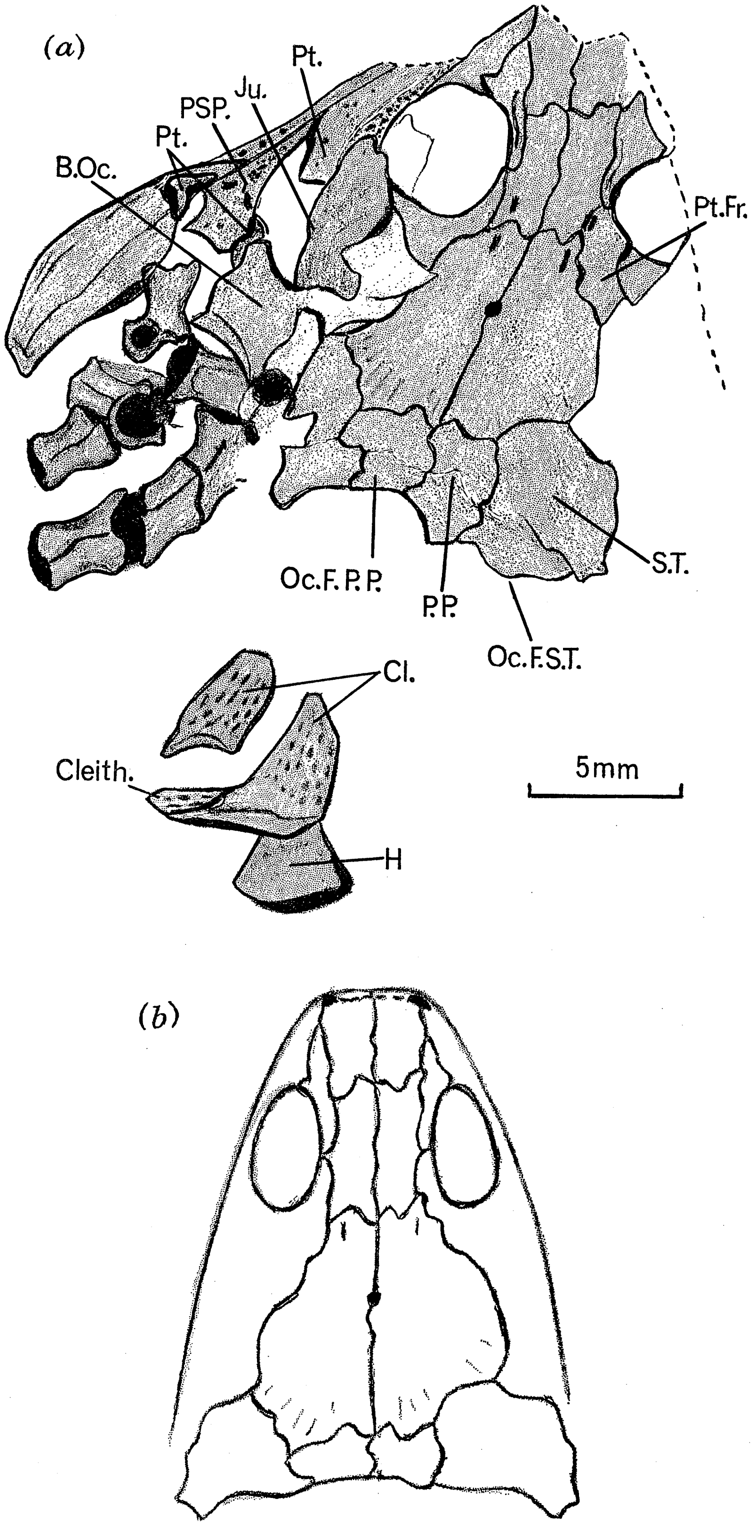

Figure 1. *Microbrachis obtusatum* (Fritsch). Electrotype R. 359. (*a*) Skull; (*b*) reconstruction of the skull, occipital flanges of supratemporals and post-parietals omitted.

occipital flanges are omitted in the reconstruction of the skull (figure 1*b*) so as to show the true posterior margin of the skull table. The exposures of the post-parietals on the skull table are much larger than in *M. pelikani*. A complete ring of sclerotic plates is present (Fritsch 1883, Pl. 35).

The cheek bones, absent in this electrotype, can be seen in Fritsch's figure (1883, Pl. 35) occupying the whole of the space between the margin of the skull table and the lower jaws. Their removal has exposed the palatal bones (figure 1*a*) which are dissociated from one another and turned outwards so that the denticulated palatal surface, i.e. the ventral view of the palate is exposed.

The parasphenoid, like that of *M. pelikani*, has a short posterior plate with well formed basipterygoid processes (at whose base lie canals and anterior foramina) which is continued anteriorly into a long narrow processus cultriformis. The anterior ramus of the right pterygoid lies below the left orbit and the buttressed processes which clasped the basipterygoid process of the parasphenoid are shown in position. Moderate sized interpterygoid vacuities were present as in *M. pelikani*.

Lying behind the parasphenoid and separated from it is a wider bone, the basioccipital.

The palate, though incomplete, indicates the breadth of the anterior half of the skull and suggests that the high cheek must have sloped steeply from the skull table (figure 1*b*) giving the skull a much narrower appearance than Fritsch's figure or the drawing in figure 1*a* suggests.

The remains of the shoulder girdle includes two clavicles with ornament, part of a cleithrum attached to the dorsal shaft of one clavicle and associated with it part of a humerus. The free end of the humerus is wide and without condylar surfaces. The forelimb and interclavicle are not preserved.

Stehlik (1924, p. 15) in the description of material which he designated as *Limnerpeton obtusatum* states that the interclavicle consists of an anterior circular plate and a 'flat quite broad' parasternal process. He gives no figures. In *M. pelikani* the parasternal process is very narrow and this raises a doubt as to whether his material really belongs to this genus.

The vertebral column (figure 10, plate 14) is imperfect in the mid-dorsal region and of the tail only sixteen caudal vertebrae are preserved. The posterior half of the specimen is exceptionally well preserved (figure 3) and in spite of the small size of the vertebrae (with a centrum length of 2·2 mm decreasing to 1 mm in the caudal vertebrae) their structure is very clearly shown.

The vertebra consists of a separate neural arch and centrum. The neural arches extend little above the level of the zygapophyses, and the pre- and post-zygapophyses are swollen and rounded. Both pre-zygapophyses and transverse processes lie above the arch pedestal from which the posterior zygapophyses sweep back free above the posterior half of the centrum. The centra are amphicoelous and notochordal (see Fritsch 1883, Pl. 35). The articulation for the neural arch occupies only the anterior half of the centrum and posterior to this articulation the centrum increases in height, the post-pedestal rise.

Above the pelvic girdle lie two vertebrae in which the neural arches and the transverse processes are larger than those of the adjacent vertebrae. These are the sacral vertebrae (their centra are not visible).

In this series of vertebrae extending from the posterior dorsal region into the tail, the ventral length of the centra is less than the dorsal length leaving small inverted Λ-shaped spaces between adjacent vertebrae (figures 2, 3). The small dorsal intercentra which occupied these spaces have for the most part dropped out but a few are preserved (figure 2, *I.C.*). From their size and the width of the centrum they could be small paired elements, but as pairs of intercentra are never seen they may well be single elements, or if paired could become single at a later growth stage.

In the caudal region, facets on the centra to articulate with caudal intercentra are exposed (figure 3 *F*), and the spaces which the caudal intercentra occupied clearly shown. They appear to drop out quite easily in microbrachid specimens.

No intercentra are present in the anterior body region. The vertebrae of the mid-dorsal region are disturbed so that we cannot tell exactly where the series of dorsal intercentra begins.

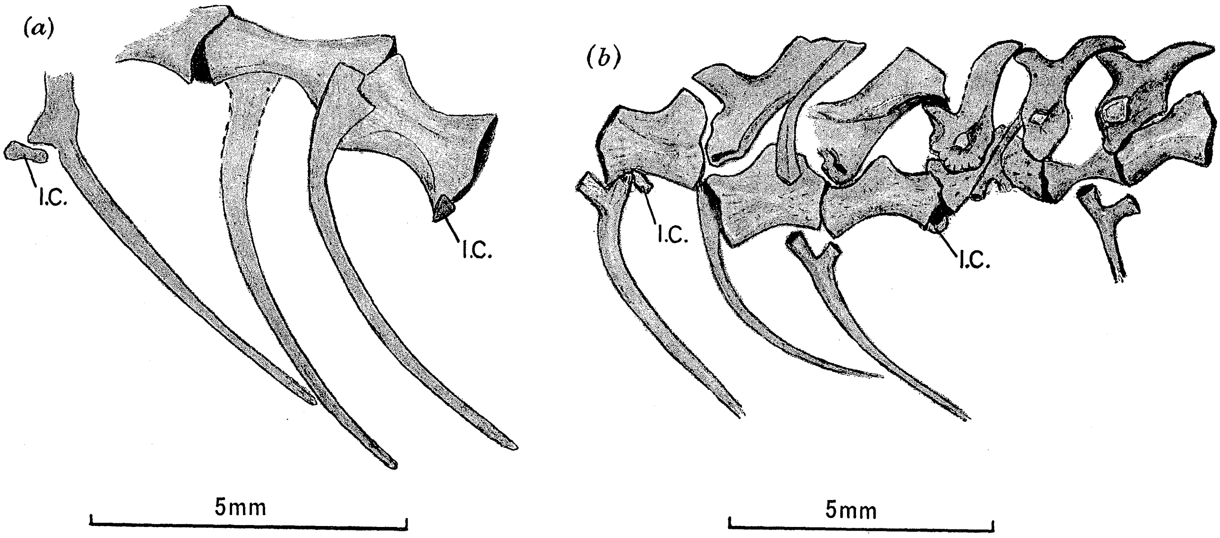

FIGURE 2. *Microbrachis obtusatum* (Fritsch). Electrotype R. 359. (*a*) Centra and ribs, neural arches omitted, anterior to series (*b*). (*b*) Presacral vertebrae and ribs.

The body ribs are double headed, long, their free ends tapering and obscured by scales. There is no obvious facet on the centrum for the articulation of the capitulum, but by fitting the tuberculum at the transverse process it becomes clear that the capitulum articulation must have been high up on the side of the centrum. Only one of the two sacral ribs is preserved and the first five post-sacral vertebrae carry ribs. The heads of the caudal ribs are progressively less ossified as are the transverse processes to which they are attached. The neural arches of the sacral vertebrae are also not completely ossified as is shown by their transverse processes which are not fully formed.

The one sacral rib preserved is long but not enlarged nor is the shaft widened. This is rather curious as there is a well developed pelvis and the sacral vertebrae are enlarged.

The pelvic girdle consists of a separately ossified ilium, pubis and ischium. The dorsal process of the ilium shows incipient anterior and posterior processes. The pubis is ossified in *M. pelikani*, Steen (1938) stated incorrectly that it was unossified.

The hind limb is represented by a femur, tibia and fibula and a foot with five digits. The limb bones are without ossified condylar ends.

The scales described and figured by Fritsch (1883, Pl. 35, figs. 5 to 7) are similar to those of *M. pelikani*.

The vertebrae of Microbrachis mollis *and* M. pelikani

The presence of small presacral dorsal intercentra in *M. obtusatum* led us to re-examine other specimens of *Microbrachis*.

M. mollis is known only by a single specimen from Nyran from which Fritsch prepared a series of electrotypes. The electrotype R. 371 (figures 4, 5) is a good one.

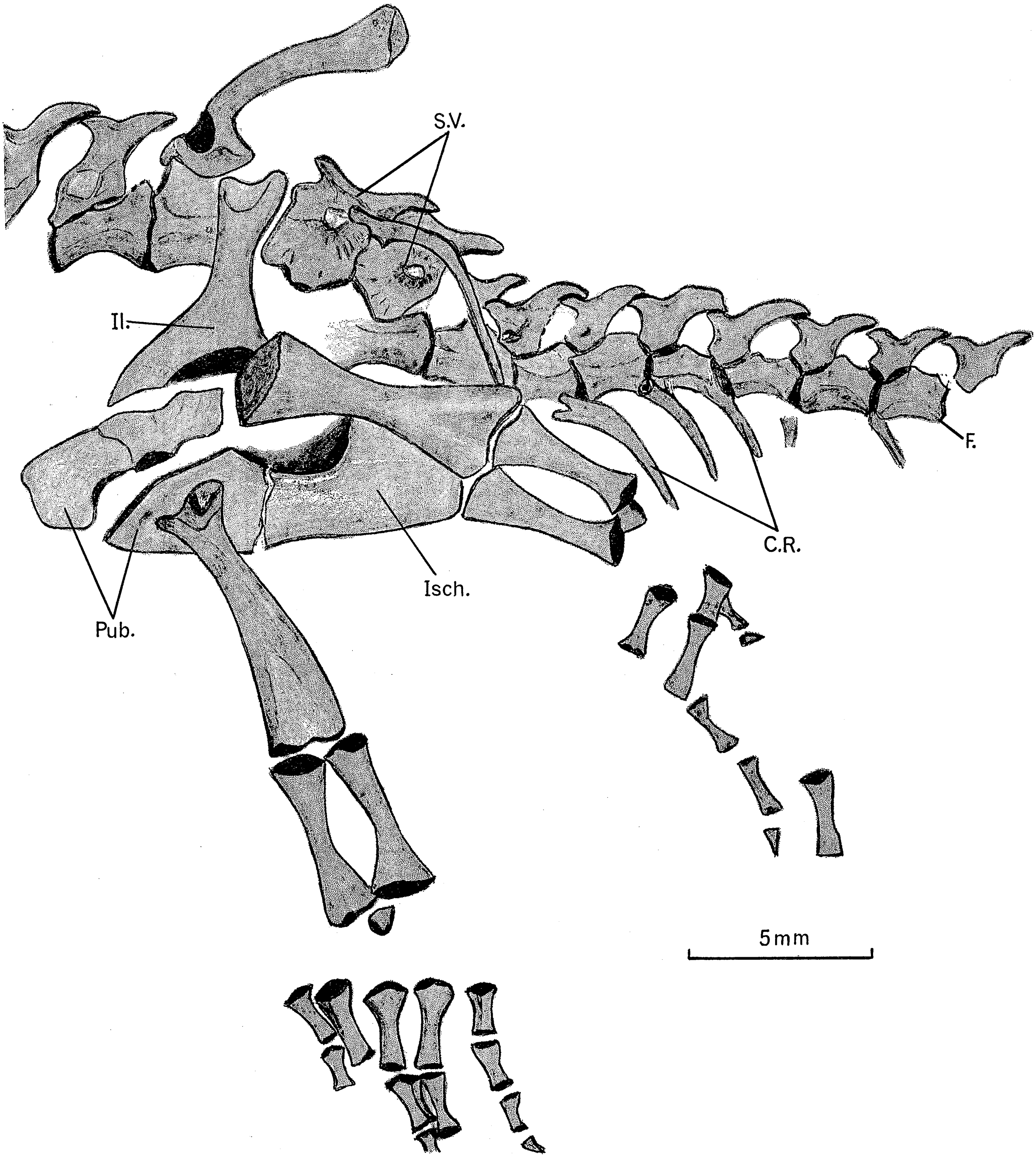

FIGURE 3. *Microbrachis obtusatum* (Fritsch) Electrotype R. 359
Sacral region and part of tail.

In *M. mollis* behind the skull there is a continuous series of thirty-five vertebrae extending almost to the sacral region. The vertebrae are similar in structure to those of *M. obtusatum* except that here the neural arches are paired. Dorsal intercentra are not present in the vertebrae of the anterior body region, but between vertebrae 20/21 and from here up to the 35th vertebra, small dorsal intercentra similar to those of *M. obtusatum* are present or where they have dropped out the bevelling of the ventral corners of the centra indicate the spaces they occupied.

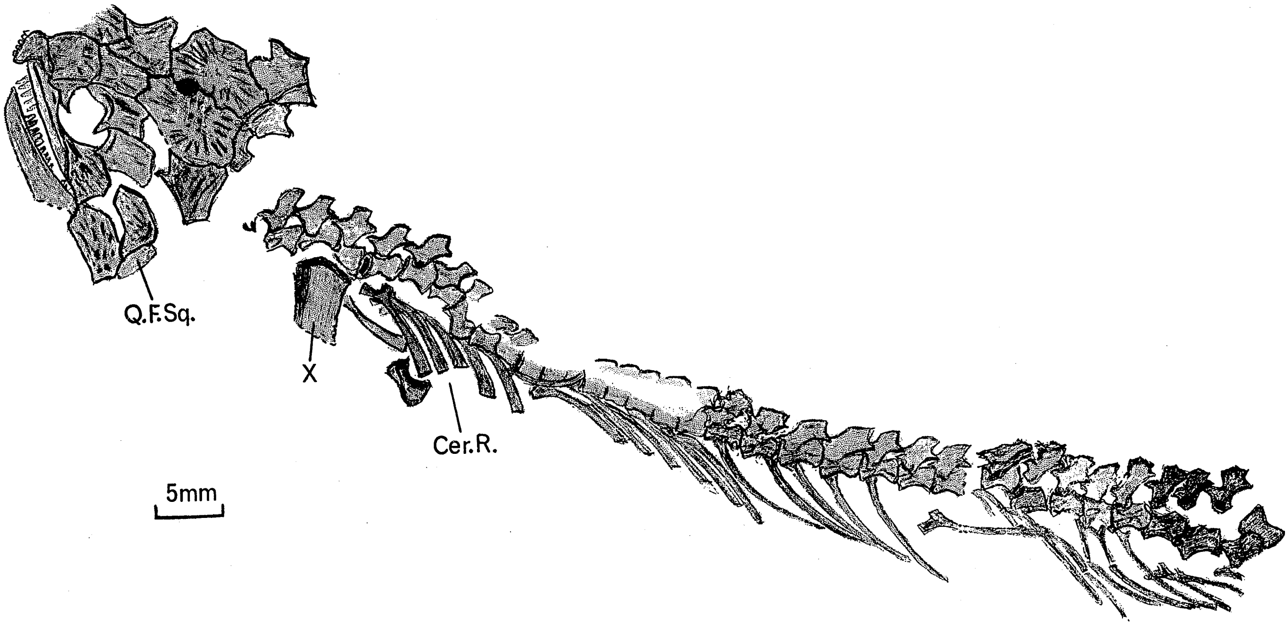

FIGURE 4. *Microbrachis mollis* Fritsch Electrotype R. 371, See Fritsch 1883, Pl. 45, fig. 1. *X*. This is largely a defect in the electrotype.

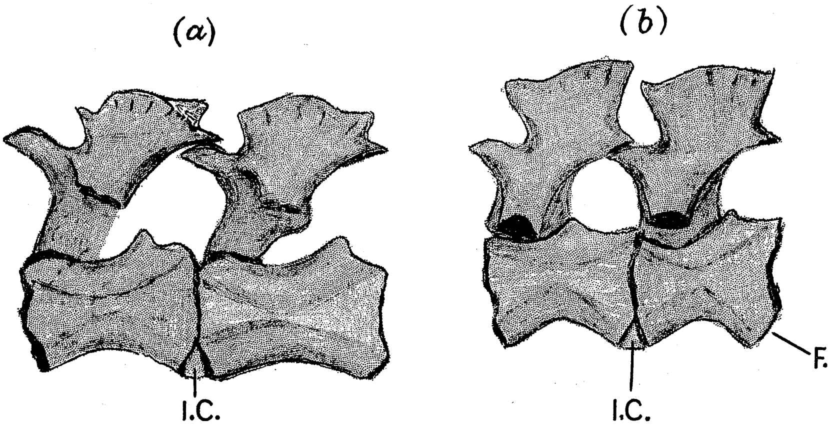

FIGURE 5. *Microbrachis mollis* Fritsch. Electrotype R. 371. Reconstruction of: (*a*) Vertebrae 20/21. (*b*) Vertebrae 29 to 30 to show intercentra, and facets on centra for their reception.

The body ribs are long, tapering and curved. There is a series of cervical ribs which are shorter, only slightly curved and square ended (figure 4).

Complete specimens of *M. pelikani* in which both body and tail are preserved are rare. They are from 7 to 13 cm in length including the tail, which is from one-half to three-fifths of the body length. The specimen of *M. pelikani* R. 2814 (Steen 1938, Pl. 1, fig. 2) is complete, the vertebrae undisturbed except unfortunately in the presacral region. The series of twenty-five vertebrae behind the skull are seen in lateral view and as a deep mould so that part of the ventral surface of these vertebrae is shown. Their centra fit very tightly together right down to their ventral margins so that as in *M. obtusatum* no intercentra are present in the anterior body region. There is also no projection from the centrum or suture which would suggest that an intercentrum had been incorporated. It follows therefore that intercentra are not present at least as far as the 25th vertebra. The succeeding vertebrae up to and including the sacrum are poorly preserved and difficult to interpret. In the tail, however, the caudal vertebrae are in natural articulation, and the ventral spaces between the centra clearly indicate that a complete series of caudal intercentra were present, although they have not been preserved. Schwartz (1908, p. 48) and Steen (1938, p. 231) record ossified caudal intercentra in *M. pelikani*.

It is clear that intercentra are present in the vertebral column of *Microbrachis*. Where material is available well enough preserved to show details of structure they are seen not only in the caudal but also in the pre-sacral region. It follows from this that these vertebrae are apsidospondylous in nature and the centrum is a pleurocentrum. There is no longer any warrant for calling them lepospondyls.

The occiput of the microbrachid skull

The small specimen of *Microbrachis* (R.S.M. 1899, 32.5 figures 6, 7) consists of a very complete skull, 19 mm in mid-dorsal length, followed by a length of vertebral column in two disconnected parts. It has the occipital region preserved in bone which is much easier to interpret than an impression and for this reason has been described.

This specimen is included provisionally and with some hesitation in the species *pelikani*. The skull shows the very typical *M. pelikani* ornament but differs from it in the following respects. There is a larger exposure of the ornamented part of the post-parietal on the skull table, and the skull is wider and flatter. This specimen since lateral line canals are not present is assumed to be post-larval, yet in a 23 mm skull of *M. pelikani* lateral line canals are present.

The posterior margin of the skull table (figure 7*a*) is shown by a marked ridge which separates the ornamental exposures of the post parietals and supratemporals from their smooth occipital flanges. The ornament is only indicated in the figures. The left supratemporal is complete with the shape so characteristic of *Microbrachis*. The posterior part of the right supratemporal is broken away to expose a smooth solid shelf from the squamosal extending inwards. Thus the connexion between the skull table and the cheek is not sutural, the supratemporal resting on the squamosal shelf.

In many specimens of *M. pelikani* the cheek is preserved in close contact with the skull table throughout its length, and the assumption was therefore made that the connexion was a sutural one. This specimen shows clearly that it was not so.

The squamosal shows the quadrate flange. The quadrate, as shown in the lectotype (Steen 1938, text-fig. 16) is large and visible only in a ventral view of the skull and is therefore not exposed in this specimen. Further experience of microbrachid material suggests that in the restoration of the *M. pelikani* skull (Steen 1938, text-fig. 15) the cheek has been placed at too wide an angle with respect to the skull table. The restorations now given of *M. obtusatum* and of this skull are more accurate in this respect.

In the occiput, the basioccipital, two opisthotics* and one stapes are preserved: the exoccipitals are missing and the supraoccipital not known. The basioccipital has the median part preserved in bone showing a slightly concave posterior margin and on the dorsal surface on either side a pair of foramina. Extending laterally on either side of this central plate are thin wing-like flanges incompletely ossified at their outer margins.

In the smaller skull of *M. obtusatum* (figure 1) the basioccipital is independent of the parasphenoid and no lateral wings are present. With increase in size the parasphenoid and basioccipital unite and lateral wings develop as in this specimen and the isolated basioccipital-parasphenoids figured by Fritsch.

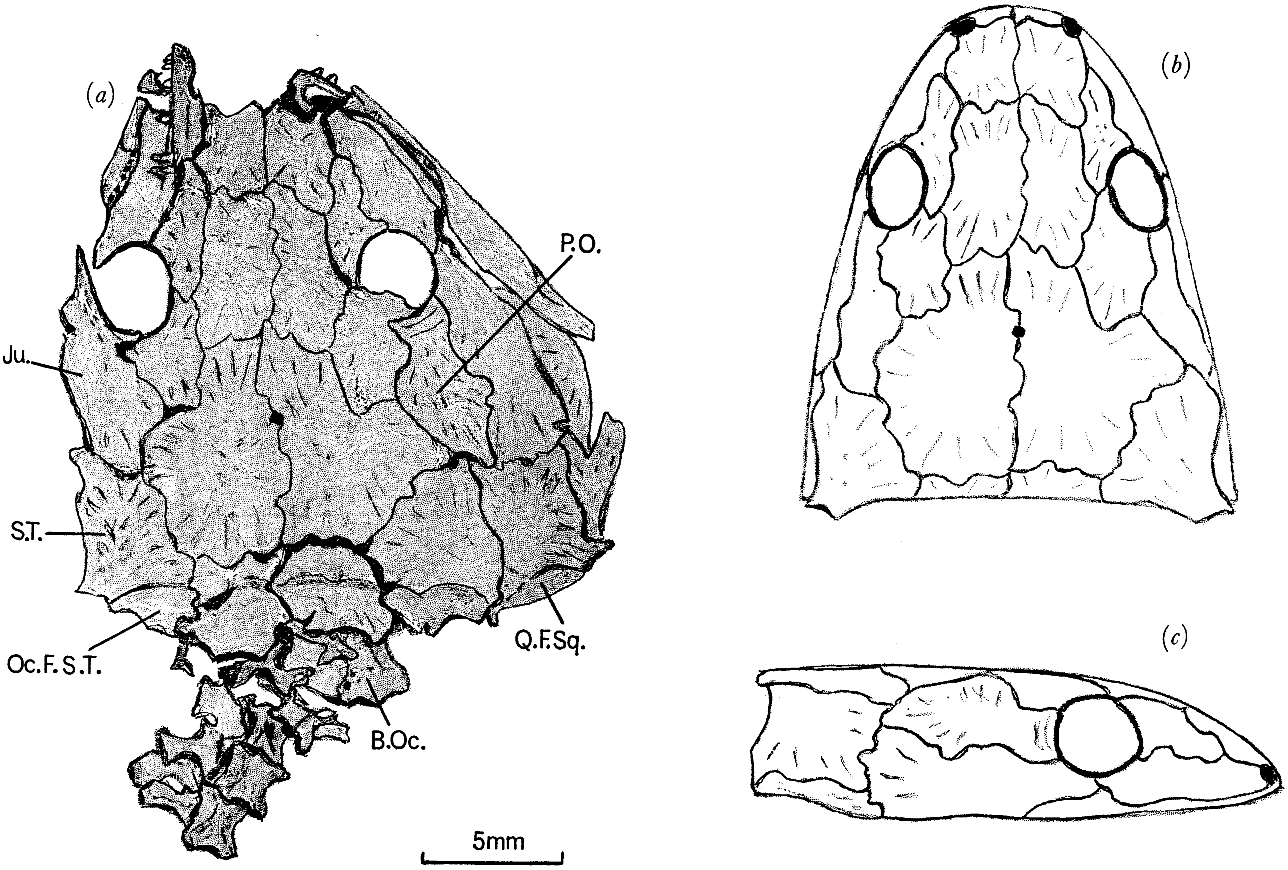

FIGURE 6. *Microbrachis pelikani* Fritsch R.S.M. 1899, 32.5. (*a*) Skull and post-cranial vertebrae. The skull ornament is only indicated. (*b*), (*c*) Reconstruction of dorsal and lateral view of the skull.

The left opisthotic has a ventral limb and a long paroccipital process. To the left of the paroccipital process is a stapes with an expanded foot plate, no stapedial foramen and only part of the columella exposed.

The restoration of the occiput (figure 7*b*) shows a low wide skull. An attempt has been made (figure 7*c*) to place the basioccipital, opisthotics and stapes in relation to one another but their position is not certain. One would expect the basioccipital to be situated above the line forming the ventral margins of the quadrato-jugals and if this is so the occipital

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* These bones are named as opisthotics rather than exocipitals as there is no condylar foramen present and the distal end of the ventral limb is unossified. The strong lateral process (Par. Occ. Pr. figure 7*b*) in which they resemble the opisthotic process of *Captorhinus* also suggest that this identification is correct.

ossifications would be almost covered by the large occipital flanges of the post-parietals and supratemporals. For this reason the occipital bones in figure 7*c* have been presented separately from the view of the occipital surface of the skull.

The contrast between the complete ossification of the dermal bones and the incomplete

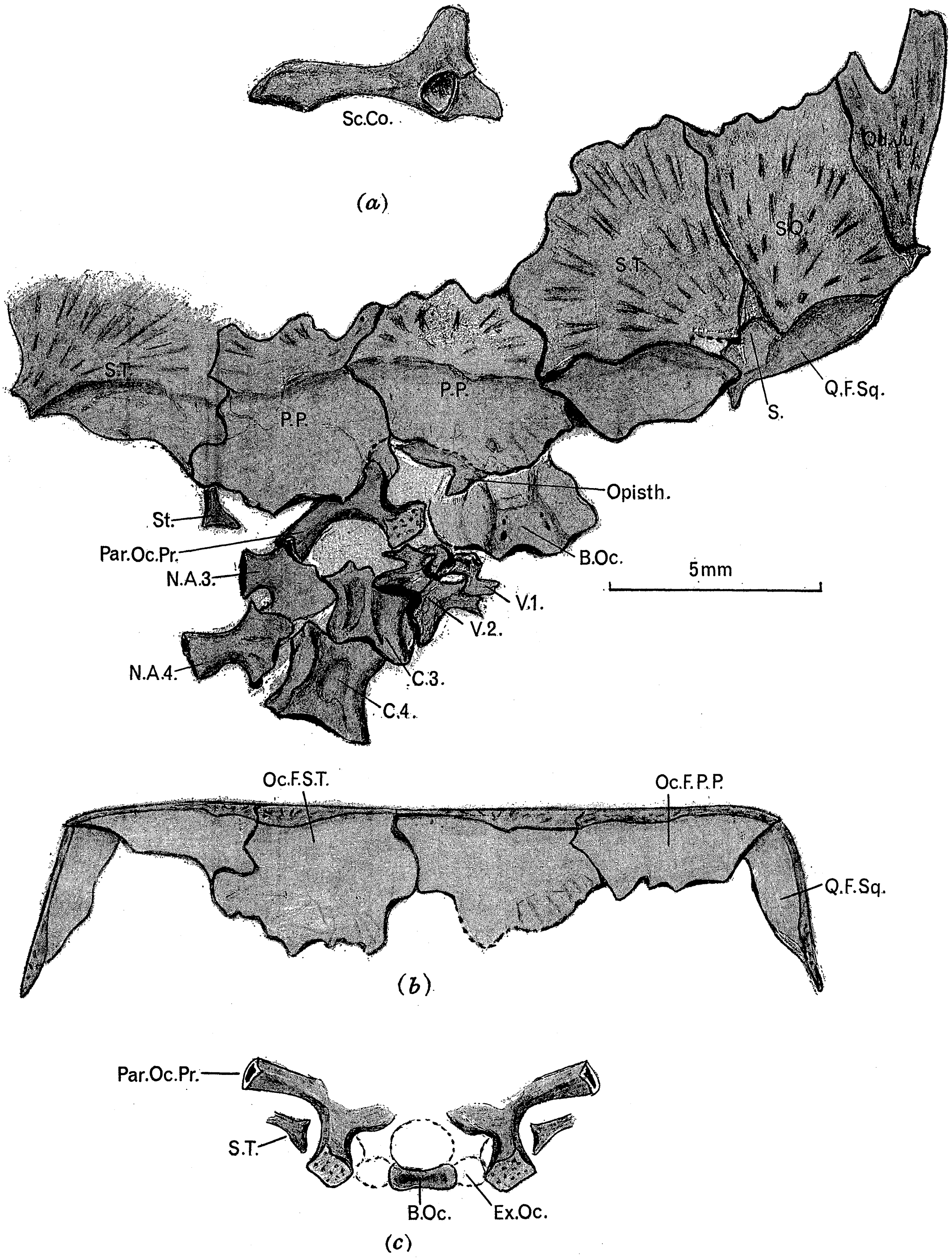


FIGURE 7. *Microbrachis pelikani* Fritsch R.S.M. 1899, 32.5. (*a*) Enlarged view of occiput; (*b*), (*c*) reconstruction of occiput.

ossification of the neural cranium is very marked and raises problems as to the support of the head on such a poorly developed vertebral-occipital articulation. The problem here is partly solved by the highly developed occipital flanges of the post-parietals and supratemporals which provide a large surface for the attachment of cervical muscles to take the weight of the head.

The post-cranial vertebrae, of which the first four have been figured (figure 7*a*), lie in natural sequence behind the skull. In vertebrae 3 and 4, the centra (1·8 mm in length)

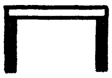
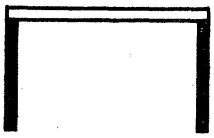
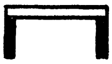
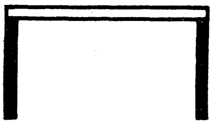
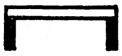
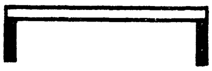
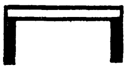
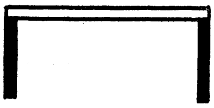
	mid-dorsal length of skull (mm)	ratio table width/cheek height	outline of posterior view of skull: natural size	skulls magnified to same width of skull table
1. *Microbrachis obtusatum* (Fritsch.) inner surface of skull (figure 1)	16	1·8		
2. *Microbrachis mollis* Fritsch. little ornament, no lateral line (figure 4)	19	2		
3. *Microbrachis pelikani* Fritsch. ornament, no lateral line (figure 6)	19	4		
4. *Microbrachis pelikani* Fritsch. Lectotype Ornament, lateral line	23	2·6		

FIGURE 8. Microbrachid skulls to show the variation in skull height. The cheek has been placed at right angles to the skull table to facilitate comparison.

show dorsolateral and ventrolateral ridges developing; their neural arches are not fully ossified, the 3rd neural arch lacking a transverse process while in the 4th neural arch it is being developed.

The 1st and 2nd vertebrae are very small (the 2nd about 0·5 mm in centrum length). Their neural arches are represented by the wing-like processes on either side (they are too broad to be cervical ribs) but they cannot be delimited from the centra to which they belong.

The primary shoulder girdle in this specimen has a well defined glenoid lying above the ventral margin of the bone. It is therefore a scapulocoracoid.

Discussion

Before dealing with microsaur relationships it is necessary to state the salient characters of microsaurs and to consider the evolutionary trends which affected members of this group.

The Microsauria include the Lower Carboniferous species recently described, Brough & Brough 1967*a*, Microbrachidae, Gymnarthridae and many of the small species included by Romer (1950) in this group.

Microsaurs display the following characters:

1. *Life history*. Microsaurs, with the exception of the Lower Permian Gymnarthridae are either fully aquatic forms with branchial arches or lateral line canals on the skull, or have an aquatic stage in their life history.

2. *Vertebrae*. The vertebrae are apsidospondylous with large pleurocentra and small intercentra. Dorsal intercentra are restricted to the posterior body region or absent altogether, caudal intercentra are always present.

The number of dorsal vertebrae varies. *Palaeomolgophis* has 37, and *Microbrachis* 38 to 40, '*Hylonomus*' *fritschi* 19, '*Hylonomous*' *geinitzi* 26.

Two sacral vertebrae are present in *Microbrachis* one in the two species of '*Hylonomous*'.*

3. *Ribs*. A differentiated series of cervical ribs is present. The ribs of the sacral region where known are of normal length except in the two species of '*Hylonomus*' where a single shortened and widened sacral rib is present.

4. *Interclavicle*. This has an expanded anterior plate and a parasternal process.

5. *Limbs*. It has been assumed that the typical microsaur forelimb is like that of *Microbrachis* where the humerus is smaller than the femur and the number of digits in it reduced to three.

In '*Hylonomus*' the humerus is as large and in *Palaeomolgophis* larger than the femur. Such metacarpals and phalanges as are present in both forms are well developed. This suggests that these microsaurs may well have had a pentadactyl forelimb.

6. *Scales*. Ornamented and very characteristic scales are present in most microsaurs (*Microbrachis*, *Asaphestera*, '*Hylonomus*' *geinitzi* etc.), but unornamented oat-shaped scales occur in the Lower Carboniferous forms.

7. *Skull*. An otic notch is never present. The cheek in most forms appears to be in free articulation with the skull table, the supratemporal rests on a shelf projecting inwards from the dorsal border of the squamosal in *Microbrachis*. In some forms the mode of preservation of the skull may falsely suggest that this articulation has become sutural but in some late forms it may indeed be sutural (e.g. the Lower Permian gymnarthrids).

The supratemporal is relatively small in *Adelogyrinus* and *Dolichopareias* but in all later microsaurs it is generally large and accepted as a diagnostic character.

8. *Palate*. In Lower Carboniferous microsaurs the parasphenoid where known is a triangular plate without basipterygoid processes and slit-like interpterygoid vacuities are present. All later microsaurs have a narrow, shaped parasphenoid with small but well formed basipterygoid processes and interpterygoid vacuities which are small or moderate in size.

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* '*Hylonomus*' *geinitzi* Credner and '*Hylonomus*' *fritschi* Credner from the Lower Permian of Niederhässleich are true microsaurs with presacral and caudal intercentra, cervical ribs, ornamented scales, an interclavicle with a parasternal process, moderate interpterygoid vacuities and in '*H*' *fritschi* lateral line pits on the skull.

9. *Stapes*. The stapes (known only in *Microbrachis*, *Lysorophus* and the gymnarthrids) has a footplate, no stapedial foramen and a short columella without a dorsal process. It is directed towards the quadrate without impinging on it. This is a primitive condition directly comparable to that of rhipidistian fishes.

10. *Occiput*. This region is not well known, but in *Lysorophus* and the gymnarthrids two small exoccipital bones lie on either side of an ossified basioccipital.

The relationships of microsaurs and captorhinomorphs

Leaving aside for the moment the question of evolutionary relationships, it might be profitable to see how close a structural resemblance there is between microsaurs and captorhinomorphs. Some authors (Watson, Gregory, Romer) in denying any close relationship between these two groups have perhaps over-emphasized the distinctions between them. Gregory (1965) for example summarizes the position and sets down a list of distinguishing characters and it is proposed to re-examine these in the light of the facts we have presented.

1. *The exposure of the post-parietals on the skull table*

As Gregory (1965) points out this is variable in both captorhinomorphs and microsaurs and is not particularly significant. In both, the post-parietal is moving from a position on the skull table to the occipital surface.

2. *The supratemporal*

In microsaurs such as *Adelogyrinus* and *Dolichopareias* the supratemporal is relatively small and separated from the post-orbital, the parietal and squamosal meeting in a long suture, i.e. the post-orbital region of the skull is long. In *Microbrachis*, the gymnarthrids and ?*Palaeomolgophis* the supratemporal is large (a diagnostic feature) and meets the post orbital (*Microbrachis*) or the post-orbital and post-frontal (*Cardiocephalus*) so that the parietal and squamosal do not touch.

In *Captorhinus*, the supratemporal is small and there is a parietal-squamosal suture as in *Adelogyrinus*, but in *Limnoscelis* the supratemporal is large and meets the post-orbital so that the parietal and squamosal do not touch. It is thus apparent that similar patterns occur in both groups (figure 9).

3. *Articulation between cheek and skull table*

In microsaurs a free articulation occurs in *Palaeomolgophis*, *Microbrachis*, *Asaphestera*, a sutural union in the gymnarthrids. As shown in this paper this free articulation in which the supratemporal rests on a dorsal shelf from the squamosal is identical with that of the pre-captorhinomorphs *Protorothyris* and M.C.Z. 1963 as described by Watson (1954) and similar to that of an anthracosaur such as *Palaeogyrinus*. A sutural connexion is established in *Captorhinus*.

4. *Palate*

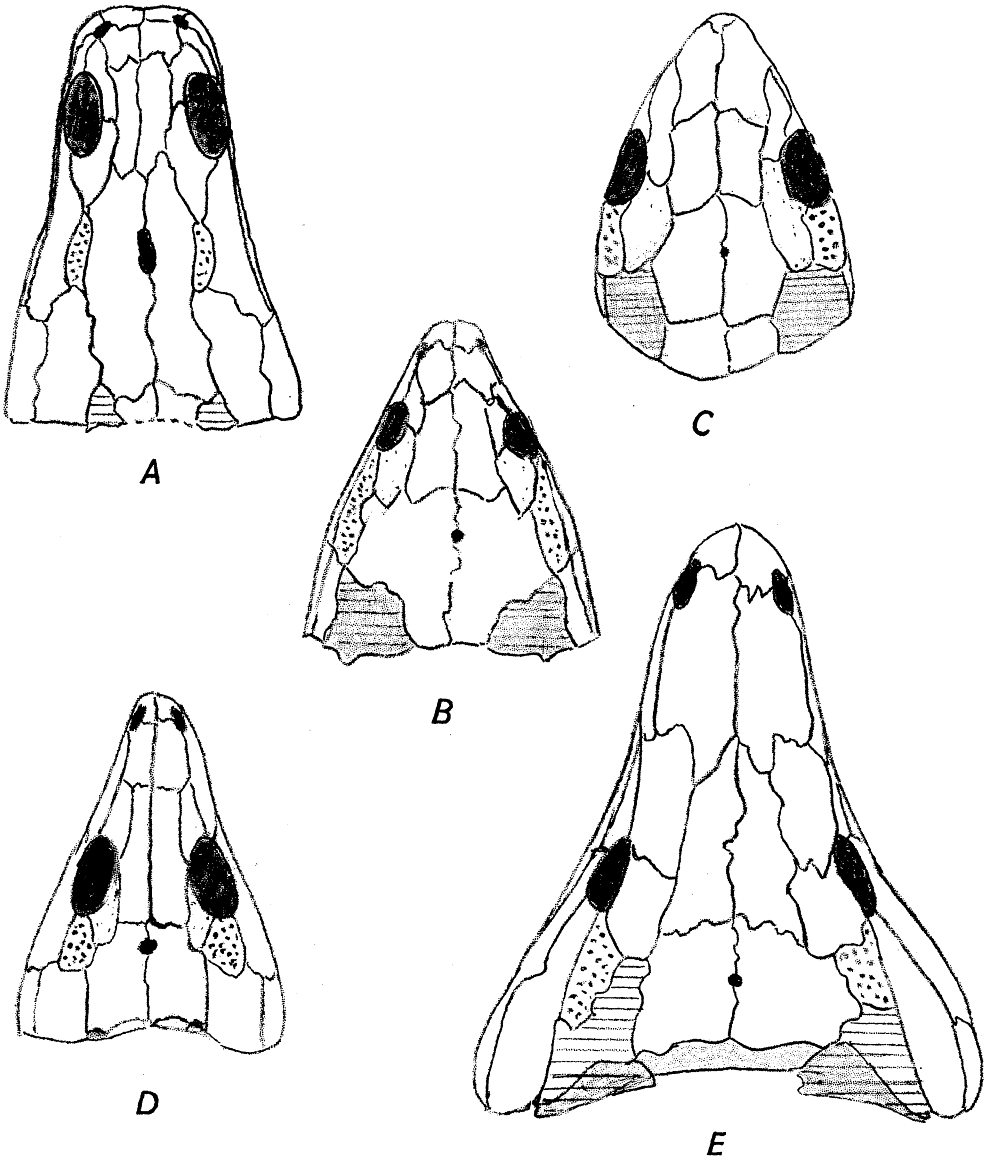
It is not easy to make a direct comparison between the palates of microsaurs and *Captorhinus* because in the former the condition is variable. If the palates of *Captorhinus* and *Microbrachis* are compared differences are clearly apparent. The moderate sized interpterygoid vacuities as compared with the solid palate and slit-like vacuities of *Captorhinus*.

It should be pointed out, however, that in forms such as *Palaeomolgophis* and in some of the Permian species interpterygoid vacuities are small and slit-like.

Much has been made of the presence of a transverse flange on the pterygoid of *Captorhinus* which is regarded as a reptilian feature never found in microsaurs. Its significance may have been over-rated, since it could have been derived from the microsaur condition mainly by a forward extension of the subtemporal fossa in association with muscle changes.

5. *Basioccipital*

Gregory makes a sharp distinction here in stating that in contrast to the basioccipital with condylar surface seen in *Captorhinus* 'Microsaurs on the other hand lack an ossified basioccipital and have paired condyles at the side of the foramen magnum on the



Post-orbital line dotted. Supratemporal lined.

FIGURE 9. Pattern of skull table in microsaurs and captorhinomorphs. Microsaurs: *A*, *Adelogyrinus*; *B*, *Microbrachis*; *C*, *Cardiocephalus* (after Gregory). Captorhinomorphs: *D*. *Captorhinus* (after Romer), *E*. *Limnoscelis* (after Romer).

FIGURE 10. *Microbrachis obtusatum* (Fritsch). Type from the electrotype R. 359. (Magn. × 1 approx.)

exoccipitals'. While exoccipitals are present with articular surfaces, an ossified basioccipital has been recognized in a number of microsaurs (*Palaeomolgophis*, *Microbrachis*, *Lysorophus and the gymnarthrids*). In *Palaeomolgophis* and *Lysorophus* the condition appears to be primitive with basioccipital as well as exoccipitals being in close contact with the first vertebra.

6. *Stapes*

Microsaur stapes have a footplate, no stapedial foramen and a short columella with no dorsal process which reaches towards but does not extend to impinge on the quadrate. In *Captorhinus* the footplate is large, a stapedial foramen is present and the heavily ossified columella impinges on the quadrate and has a small dorsal process near the stapedial footplate.

7. *Vertebral column*

The facts set out in this and in the preceding paper (Brough & Brough 1967*a*) show clearly that there is no basic dissimilarity in the vertebral column of microsaurs and captorhinids. The presence of pre-sacral as well as caudal intercentra in the former has been demonstrated and it becomes clear that although evolution has been precocious and uneven in the microsaurs we are essentially dealing with the same structure in both groups.

The above analysis while leaving distinctions between captorhinomorphs and microsaurs shows that the differences may be not so fundamental after all. Taking the animals as a whole there are many real resemblances both in the skull and post-cranial skeleton. This is particularly striking in the latter where in each case the centrum is a pleurocentrum, cervical ribs are present and the interclavicle is stalked; while the skull is of similar general pattern, lacks an otic notch and with the stapes occupying a similar and primitive position in both.

It would seem that there is a real community of structure between these two groups. It is not difficult to imagine them both coming from the same starting point, and the differences being accounted for largely by different speeds of evolution affecting different organ systems with the microsaurs being precocious in certain respects, particularly in the vertebral column. Indeed *Captorhinus* is more primitive than any microsaur in the structure of the vertebral column and, with the exception of *Palaeomolgophis*, in the palate.

It is interesting that the pattern of the bones in the skull table of *Captorhinus* resembles that of *Adelogyrinus* and *Dolichopareias* (with a suture between the parietal and squamosal) while that of *Limnoscelis* resembles the pattern in *Microbrachis*, *Asaphestera* and the gymnarthrids.

Romer in separating microsaurs from reptiles was much influenced by the fact that the typical microsaur scale was a highly ornamented structure unlike the oat-shaped or rod-like scales, the forerunners of abdominal ribs, which are seen in early reptiles. This distinction is not entirely valid as oat-shaped scales occur in the Lower Carboniferous microsaurs.

It is quite certain that no known microsaur gave rise to captorhinomorphs for all known forms are too specialized in the vertebral column. But it is easy to imagine a simplified version of some of the earliest microsaurs which might have done so.

It is suggested therefore that captorhinomorphs and microsaurs had a common origin. Whether they diverged from the labyrinthodonts in pre-Carboniferous time as Säve-Söderbergh (1935, p. 198–199) suggested or had a separate origin in the rhipidistean fishes is a matter for further discussion.

Abbreviations used in the figures

B.Oc.	basioccipital	*Oc.F.S.T.*	occipital flange of supratemporal
C.	centrum	*Opisth.*	opisthotic
Cl.	clavicle	*P.O.*	post-orbital
Cleith.	cleithrum	*P.P.*	post-parietal
C.R.	caudal ribs	*Par.Oc.Pr.*	paroccipital process
Cer.R.	cervical ribs	*Pt.Fr.*	post-frontal
Ex.Oc.	exoccipital	*Pub.*	pubis
F.	facet on centrum for intercentrum	*Q.F.Sq.*	quadrate flange of squamosal
H.	humerus	*Qd.Ju.*	quadrato-jugal
Il.	ilium	*S.*	shelf from dorsal border of squamosal
Isch.	ischium	*S.T.*	supratemporal
I.C.	intercentrum	*S.V.*	sacral vertebra
Ju.	jugal	*Sc.Co.*	scapulocoracoid
N.A.	neural arch	*St.*	stapes
Oc.F.P.P.	occipital flange of post-parietal	*V.*	vertebra

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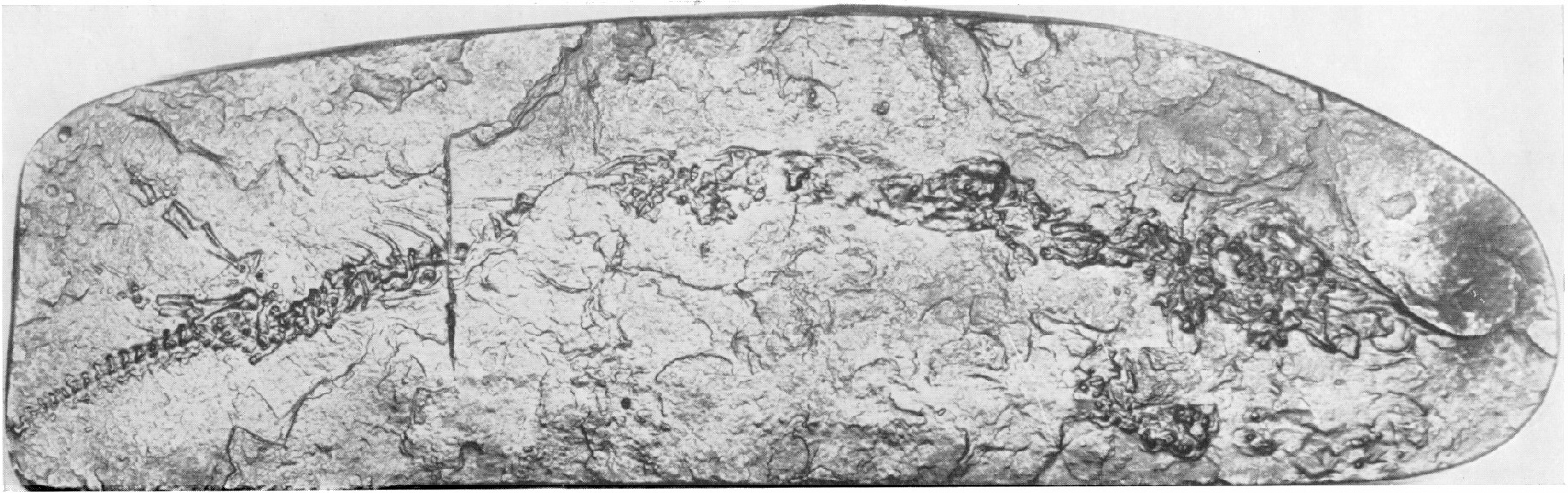

FIGURE 10. *Microbrachis obtusatum* (Fritsch). Type from the electrotype R. 359. (Magn. × 1 approx.)