

CAPITOSAURID AMPHIBIANS FROM THE UPPER LUANGWA VALLEY, ZAMBIA

by

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ABSTRACT

The purpose of this paper is to describe two capitosaur skulls from the Luangwa valley, Zambia. A tentative decision is made assigning the material to *Parotosaurus pronus* (Howie, 1969).

The stratigraphy of the locality in which the material was found and that of the type species is discussed. A possible mechanism for opening the mouth of capitosaurids is put forward, with the qualification of its success depending on the animals being neutrally buoyant.

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INTRODUCTION

All the known members of the labyrinthodont family Capitosauridae were placed by Welles and Cosgriff (1965) in three genera: *Parotosaurus*, *Cyclotosaurus* and *Paracyclotosaurus*. Chronologically the genera occur as follows: *Parotosaurus* in the Bunter and early Muschelkalk; *Cyclotosaurus* in the Upper Muschelkalk and Lower Keuper; and *Paracyclotosaurus* in the Upper Keuper.

Watson (1962, p. 261) listed a number of evolutionary trends of the capitosaurids through the Triassic. Among these were the following: an increase in size of the skull; a disproportionate increase in the length of the nasal region; and a tendency to enclose the otic notch—this latter character dividing the family into the Lower Triassic parotosaurids with open otic notches and the Upper Triassic cyclotosaurids with closed otic notches. The third genus of capitosaurids, *Paracyclotosaurus* from the Upper Triassic of New South Wales, was considered to have a closed otic notch, and a deep skull.

Howie (1969) distinguished *Parotosaurus pronus* of the East African Triassic from ten other described species by the shape and position of its tabular horn, which is expanded laterally towards the squamosal, so that the otic notch is semi-closed.

In 1970, I recorded the presence of a large capitosaur from the Upper Luangwa Valley, Zambia (Chernin and Cruickshank, 1970), tentatively assigning it to *P. pronus*, on the basis of the similar tabular horn.

The purpose of this paper is to describe the above specimen and a second capitosaur found a few metres away. This latter material, although lacking the crucial tabular horns, displays proportions and other characters so similar to *P. pronus* that it has also been tentatively assigned to that species.

STRATIGRAPHY

The capitosaur material herein described was collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961.

The two skulls were found within a few feet of each other in Locality 15 (Drysdall and Kitching, 1963), which is situated south of the Sangu River 3½ miles west of Sitwe, in the Upper Luangwa Valley, Zambia.

The fossiliferous beds of Locality 15 consist of dark red soft mudstones with characteristic feldspathic grit bands, containing angular vein-quartz fragments. Towards the base of the beds, amphibians and molluscs are present. The molluscs have been identified as *Unio karooensis* (Drysdall and Kitching, 1963, p. 22). From the same locality, two cynodonts were also collected, the smaller perhaps belonging to the genus *Trirachodon* and the larger being a *Scalenodon*-like form resembling material described by Crompton (1955) from the Manda Beds of Tanganyika.

The type material of *Parotosaurus pronus* described and named by Howie (1969) was collected from Mkongoleko, Ruhuhu Valley, Tanzania, in the Manda Formation of East Africa, by F. R. Parrington.

The genus *Parotosaurus* is known to have lived during Lower to Lower-Middle Triassic times (Welles and Cosgriff, 1965; Chernin and Cruickshank, 1970).

Dixey (1937) correlated the N'tawere Formation with the Manda beds because of the common presence of *Unio karooensis*, which was an unreliable correlation because *Unio karooensis* is not a true zone fossil.

Crompton and Ellenberger (1957) described *Scalenodontoides macrodentes* from the Upper Molteno Beds of Basutoland, thus correlating not only the Manda and Molteno Beds of Basutoland, but also the N'tawere Formation and Red Marl of the Upper Luangwa Valley, but Turner (1972) believes that *Scalenodontoides macrodentes* comes from the Lower part of the Red Beds, in Lesotho, and not from the Molteno.

Dicynodont material described from the Manda Formation is remarkably primitive for correlation with the Molteno, comprising as it does *Kannemeyeria latifrons*, which animal is typical of the supposed Lower Triassic *Cynognathus* zone, and its suggested morphological antecedent *Tetragonias njalilus* (Cruickshank, 1967).

The rhynchosaur fauna from the Manda Formation is similar in many respects to that of the Middle Trias of Brazil.

The archosaurs in the Manda Formation are more advanced than those in the *Cynognathus* zone, in keeping with the progressive nature of the cynodonts.

Therefore, although the Manda Formation fauna in general is more advanced than that of the *Cynognathus* zone, it is not significantly so and must represent a stage following closely on it (Chernin and Cruickshank, 1970).

The N'tawere Formation contains two fossiliferous zones, the lower with *Diademodon rhodesiensis* among other *Cynognathus* zone-like forms, and an Upper (Red Marl) horizon which includes Locality 15. Locality 15 has yielded, so far, two specimens of *Parotosaurus pronus*, a gomphodont similar to the "advanced" Manda Formation genus *Scalenodon* and two genera of dicynodonts similar to the Middle Triassic Argentinian and Brazilian forms (Brink, 1963; Cox, 1969).

From these facts, it would seem that the "Red Marl" horizon of the N'tawere is largely equivalent to that of the Mkongoleko area of the Manda Formation and that both of these post-date the *Cynognathus* zone only slightly. The lower of the two N'tawere horizons may, in fact, be the same age as the *Cynognathus* zone, but much more information regarding its fossils is necessary before definite correlation is possible.

If the foregoing discussion is correct in its assumptions, and both the N'tawere Formation and the Manda Formation are of the Middle Trias, then they must be low in the Middle Trias, and the *Cynognathus* zone must be relatively high in the Lower Trias.

MATERIAL AND METHODS OF PREPARATION

The material studied was as follows:

Field No.	Museum No.	Identity	Remarks	Specimen
4221	*B.P.I. 424	<i>Parotosaurus pronus</i> , Howie	Broken skull + left lower jaw	A
4223	*B.P.I. 414	<i>Parotosaurus pronus</i> , Howie	Broken skull	B

* Bernard Price Institute for Palaeontological Research.

Both specimens A and B were collected from Locality 15 (Drysdall and Kitching, 1963) of the N'tawere Formation.

Specimen A is part of a skull with the associated left jaw ramus. This ramus has been almost perfectly preserved, with the exception of the teeth which have been broken off, their stumps remaining in most cases.

The skull was greatly fragmented and encased in N'tawere Green and Purple Marls (Dixey, 1937). The majority of the fragments have been joined with Glyptal. Sutures were made more evident by painting with a 2% solution of hydrochloric acid. Large gaps in the skull are still present (see Fig. 1).

Of the palate, only the vomerine plate and cultriform process of the parasphenoid are present. A fragmented brain-case which defied detailed preparation differed so greatly from right to left side that it seems possible that pathological deformation occurred on the right side.

Specimen B is part of a skull without the lower jaw. The skull was also greatly fragmented and encased in the N'tawere Green and Purple Marls.

Glyptal was used to join the majority of the fragments. However, large gaps are still present, as in the other.

The skulls were prepared using Vibro-tool and dental mallet.

In the case of Specimen B, the material permitted cleaning of the dorsal surface and the ventral surface of the condyles and pterygoids. The ventral surface of the skull roof was not prepared, many specimens of *Unio karoensis* being encased there in black manganese salts, which proved resistant against both Vibro-tool and a weak solution of acetic acid. A stronger solution of acid caused decomposition of the bone.

Specimen B has been greatly distorted (see Fig. 6), making a direct assessment of the outline impossible.

The sutures in both skulls are not apparent, or are only just visible, due to the high degree of fragmentation.

Because of the uncertainty of the outline in Specimen B and the considerable lack of distinct sutures in both skulls, I have used information from both Welles and Cosgriff (1965) and Howie (1969) to reconstruct the animals. The figures appearing in Tables 1, 2 and 3 were taken from direct measurements of my reconstructions, in order to obtain more direct comparisons with the other reconstructed parotosaurs. Also, my written descriptions rest entirely on my reconstructions.

In Figure 11 the illustrations of the lower jaw in Specimen A have been reversed left for right.

For key to abbreviations used in this paper, see pages 50—57.

It is possible that the much wider snouts in this material are due to growth changes, but I have discounted this here, because of the extreme distortion these skulls seem to have undergone.

It should also be emphasized that both skulls described herein are considerably larger than the type material and hence, for all these reasons, the identification of the material is given as *Parotosaurus* cf. *pronus*.

DESCRIPTION OF MATERIAL

Diagnosis of Specimen A

Skull broad posteriorly (B : L approximately 81), (ratios from Welles and Cosgriff 1965) but tapers anteriorly (S : L approximately 40); skull deep posteriorly (H : B approximately 17,2); external nares elongate, lateral, long axes parallel to skull border; orbits close together, well posterior, oval, long axes parallel to midline.

Pineal foramen rectangular, just posterior to hind border of orbits; posterior skull border concave (K : C approximately 32); frontal and jugal enter orbital margin; supratemporal excluded from otic notch.

Exoccipitals barely exposed on palate; pterygoid with facet for jaw articulation.

Processus lamellosus of exoccipital present.

Lower jaw with large prearticular process.

Description of skull roof

Unless otherwise stated, the left side of the skull is discussed.

The superficial sculpture of the bones is characteristic of all capitosaurs. The centre of ossification of each bone displays an area of irregular pentagonal pits. From this central area, ridges and grooves radiate outwards. These longitudinal grooves are probably the regions of intense growth (Bystrow, 1935). Where growth is slow, transverse ridges are able to develop so that such bones consist mostly of pits (Welles and Cosgriff, 1965). The postorbital bones are exclusively pitted, while the preorbital bones have elongated ridges (see Fig. 1).



Fig. 1. Dorsal view of Specimen A, showing superficial sculpture.

KEY TO LINE DIAGRAMS

Solid line	—Visible outline or suture in estimated correct position.
Broken line	—Reconstructed outline or suture.
Double line of hooks	—Visible lateral line canal in estimated correct position.
Single line of hooks	—Reconstructed lateral line canal.
Heavy regular stipple	—Vacuity of foramen.
Light regular stipple	—Hollow or depression.
Parallel lines	—Worn broken surface.

For list of abbreviations used in text pages see pp. 54—55.

The preservation of a comparatively undamaged left maxilla shows that the skull was probably triangular with a rounded snout. The estimated length of the skull is 64,4 cm.

The superficial bones of the skull are seen in Figs. 1 and 2.

It should be noted that the supratemporal is excluded from the otic notch and that the frontal and jugal enter the orbital margin. Both of these characters are diagnostic (see Table 3).

Openings in the skull roof

No premaxillary foramen is seen, as the anterior tip of the skull is not preserved. For the same reason, no external nares are seen, except for a small region of hind border on the left hand side of the skull.

The orbits are probably oval. Only the posterior border of each orbit is smoothly rounded; the rest of the border has been shattered. The orbits are situated 10 cm apart in the posterior one-third of the skull. The long axes are probably parallel. The

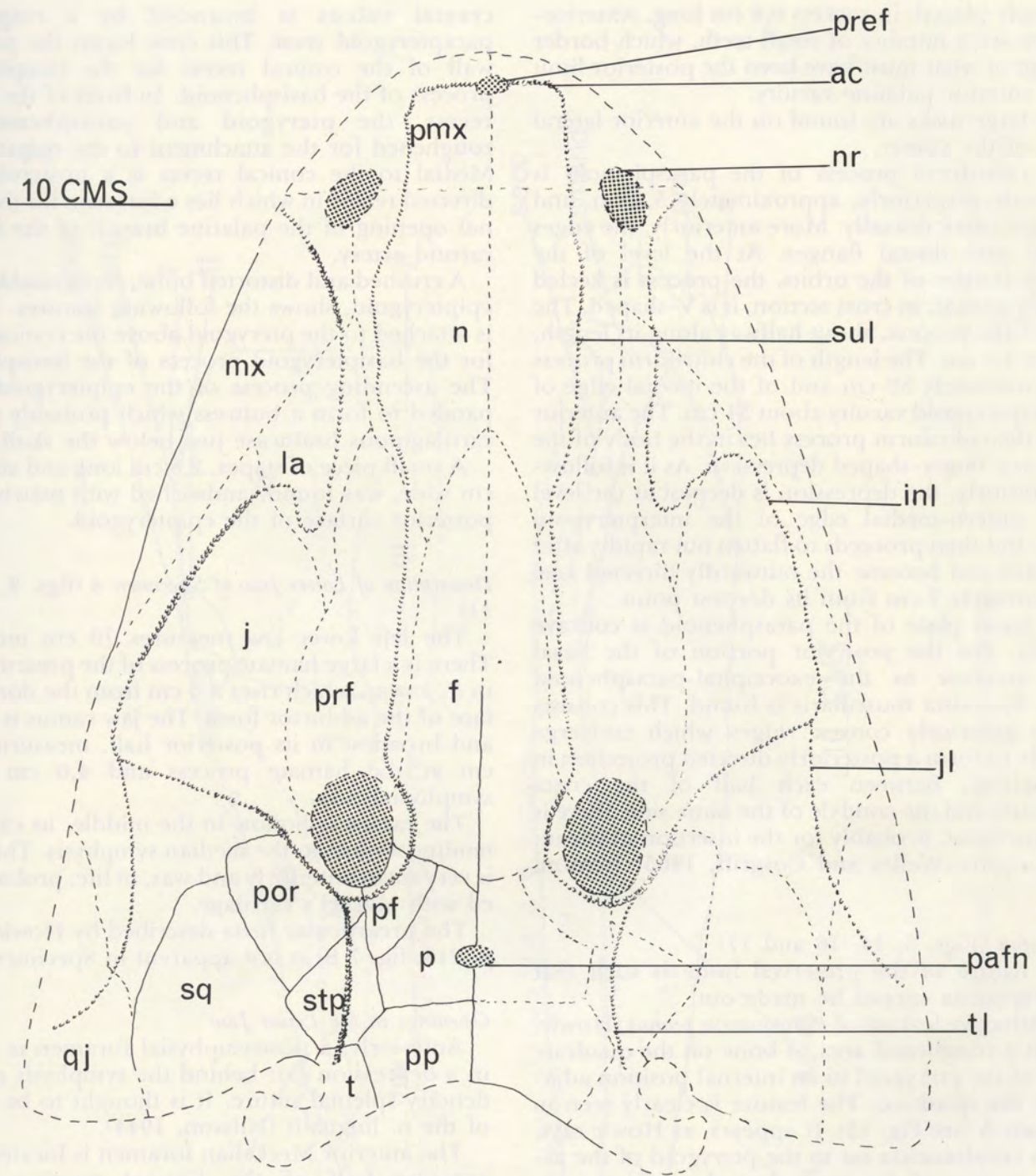


Fig. 2. Reconstruction and analysis of the dorsal view of Specimen A.

rim of the left orbit is raised slightly above the level of the skull so that a shallow groove between the orbits may have existed.

Where the parietal foramen probably existed, mostly a gaping hole now remains. A very small smooth edge is present, to show the approximate position of the foramen, but no shape can be made out.

The otic notch is clearly open, but the diagnostic tabular bone is missing. The skull is badly distorted in this area.

Lateral line system (Figs. 1 and 2)

It is possible to make out the 4 sets of canals on the skull roof. As the snout is missing, no anterior commissure can be determined.

The Palate (Figs. 4 and 12)

The vomerine plate forms a square flat platform about 11 cm long and 11 cm wide. Antero-laterally, this platform has a small smooth edge which probably is the antero-medial border of the choana. Internal to this edge are some small teeth,

alternately placed, in sockets 0,8 cm long. Anteriorly, there are a number of small teeth, which border the edge of what must have been the posterior limit of the anterior palatine vacuity.

Two large tusks are found on the anterior lateral corner of the vomer.

The cultriform process of the parasphenoid is quite wide posteriorly, approximately 5,2 cm, and the edges curve dorsally. More anteriorly, the edges develop into dorsal flanges. At the level of the anterior border of the orbits, the process is keeled ventrally so that, in cross section, it is V-shaped. The width of the process, about halfway along its length, is about 3,5 cm. The length of the cultriform process is approximately 39 cm and of the medial edge of the interpterygoid vacuity about 34 cm. The anterior end of the cultriform process lies in the body of the vomer as a finger-shaped depression. As it is followed posteriorly, the depression is deepest at the level of the antero-medial edge of the interpterygoid vacuity and then proceeds to flatten out rapidly after this point and become the outwardly directed keel approximately 7 cm from its deepest point.

The basal plate of the parasphenoid is concave ventrally. On the posterior portion of the basal plate, anterior to the exoccipital-parasphenoid suture, the crista muscularis is found. This consists of two anteriorly convex ridges which converge medially to form a posteriorly directed projection in the midline. Between each half of the crista muscularis and the condyle of the same side, there is a shallow fossa, probably for the insertion of the m. rectus capitis (Welles and Cosgriff, 1965; Watson, 1962).

The occiput (Figs. 5, 14, 16 and 17)

The nature of the preserved bone is such that small foramina cannot be made out.

A distinctive feature of *Parotosaurus pronus* (Howie, 1969) is a roughened area of bone on the quadrate ramus of the pterygoid in an internal position adjacent to the quadrate. The feature is clearly seen in Specimen A (see Fig. 13). It appears, as Howie says, to be a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle.

The Braincase (Fig. 15)

Such elements of the braincase as remain have been to a greater or lesser degree distorted. In fact, the right exoccipital is so badly out of shape that pathological deformation seems to have occurred.

Anterior to the base of the paroccipital process there is an oblique ridge which is the median edge of the fenestra ovalis. Antero-lateral to the basioccipital chamber is a deep recess formed by the parasphenoid in front and the exoccipital behind, known as the intercrestal sulcus. Laterally, the intercrestal sulcus ends at the pterygoid beneath the longitudinal ridge marking the fenestra ovalis in the dorsal groove of the pterygoid. Anteriorly, the inter-

crestal sulcus is bounded by a ridge, the parapterygoid crest. This crest forms the posterior wall of the conical recess for the basipterygoid process of the basisphenoid. In front of the conical recess, the pterygoid and parasphenoid are roughened for the attachment to the epipterygoid. Medial to the conical recess is a posterolaterally directed recess in which lies a foramen for the internal opening of the palatine branch of the internal carotid artery.

A crushed and distorted bone, recognisable as the epipterygoid, shows the following features. Its base is attached to the pterygoid above the conical recess for the basipterygoid process of the basisphenoid. The ascending process of the epipterygoid is expanded to form a buttress which probably met the cartilaginous braincase just below the skull roof.

A small piece of stapes, 2,8 cm long and about 0,9 cm wide, was found sandwiched with matrix to the posterior surface of the epipterygoid.

Description of Lower Jaw of Specimen A (figs. 9, 10 and 11)

The left lower jaw measures 70 cm internally. There is a large hamate process of the prearticular as in *P. pronus*, which rises 3,5 cm from the dorsal surface of the adductor fossa. The jaw ramus is highest and broadest in its posterior half, measuring 13,5 cm at the hamate process and 4,0 cm at the symphyseal tusk.

The ramus is hollow in the middle, its cavity extending almost to the median symphysis. This cavity is very small anteriorly and was, in life, probably filled with Meckel's cartilage.

The prearticular fossa described by Howie (1969, p. 218, fig. 7 B) is not apparent in Specimen A.

Openings in the Lower Jaw

Anteriorly, a postsymphysial foramen is situated in a depression just behind the symphysis near the dentary-splenic suture. It is thought to be the exit of the n. lingualis (Nilsson, 1944).

The anterior Meckelian foramen is located in the anterior half of the lingual portion of the postsplenic, 19 cm from the postsymphysial foramen. It possibly served as the exit for the n. mylohyoideus anterior (Nilsson, 1944).

The posterior Meckelian foramen is bordered by the postsplenic antero-ventrally, the angular postero-ventrally and the prearticular dorsally. Only the ventral limit, smoothly rounded on the angular bone, remains to show the approximate size and position of this opening in this specimen. According to Nilsson (1944) the n. mylohyoideus posterior passes through it.

The adductor fossa is bounded lingually by the prearticular and laterally by the surangular. It is approximately 4 cm wide at its widest point, about half-way along its length, which is about 19 cm. The large adductor musculature of the jaw inserted here.

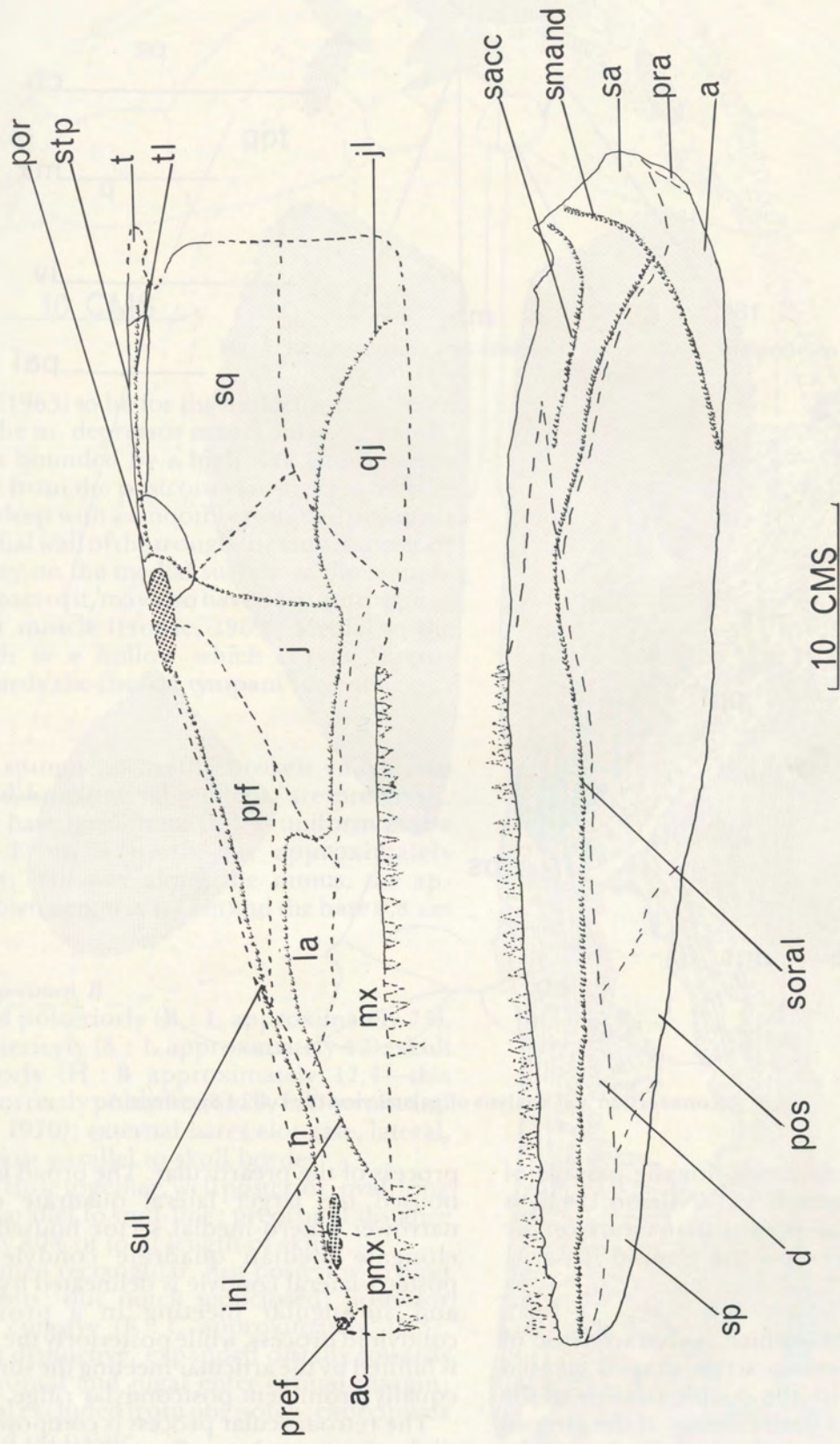


Fig. 3. Reconstruction of lateral view of Specimen A.

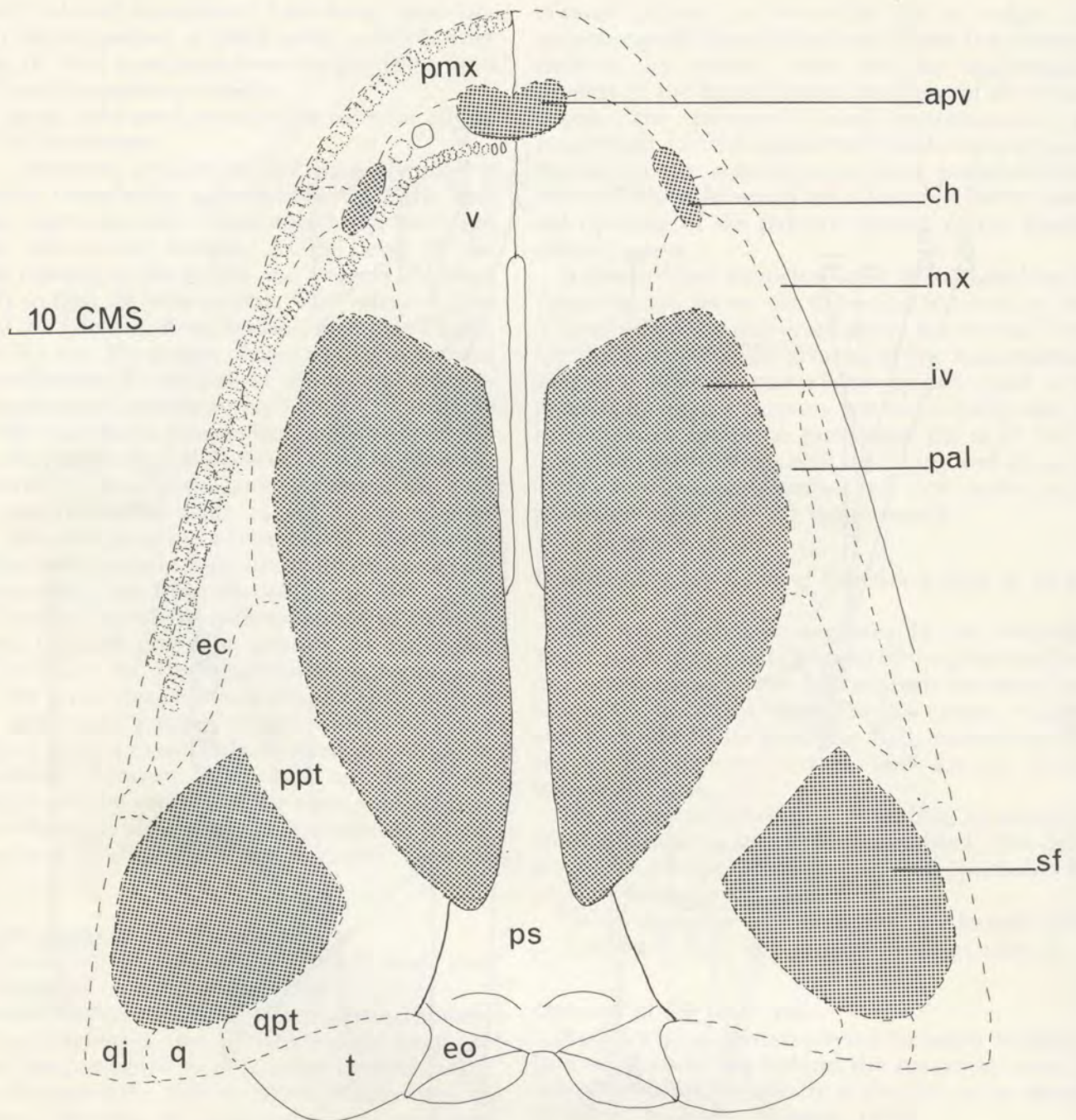


Fig. 4. Reconstruction and analysis of palatal view of skull of Specimen A.

The chorda tympani foramen, for the passage of the n. mandibularis internus VII (Nilsson, 1944), is situated in the surangular-prearticular suture on the medial surface, 1.5 cm below the glenoid fossa.

Bones of the Lower Jaw

The articular is pitted—which is characteristic of cartilage bone—and forms a screw-shaped glenoid fossa for articulation with the double condyle of the quadrate. There are two distinct areas of the glenoid fossa: a broad transverse groove entirely formed by articular and a narrower, more median groove at an angle to and in front of the former, composed of articular and prearticular. The median groove is contained by the roughened posterior face of the hamate

process of the prearticular. The broad lateral groove housed the larger lateral quadrate condyle; the narrower antero-medial sector housed the thinner elongate median quadrate condyle. The main postero-lateral condyle is delineated by the articular and surangular meeting in a prominent precondyloid process, while posteriorly the glenoid fossa is limited by the articular meeting the surangular at an equally prominent postcondylar ridge.

The retroarticular process is composed almost entirely of surangular; a flange of the angular extends along the ventral surface for about half of the length of the process to end in a sharp angle 1 cm anterior to the end of the jaw. The dorsal surface of the retroarticular process is occupied by a deep trough, said by Welles

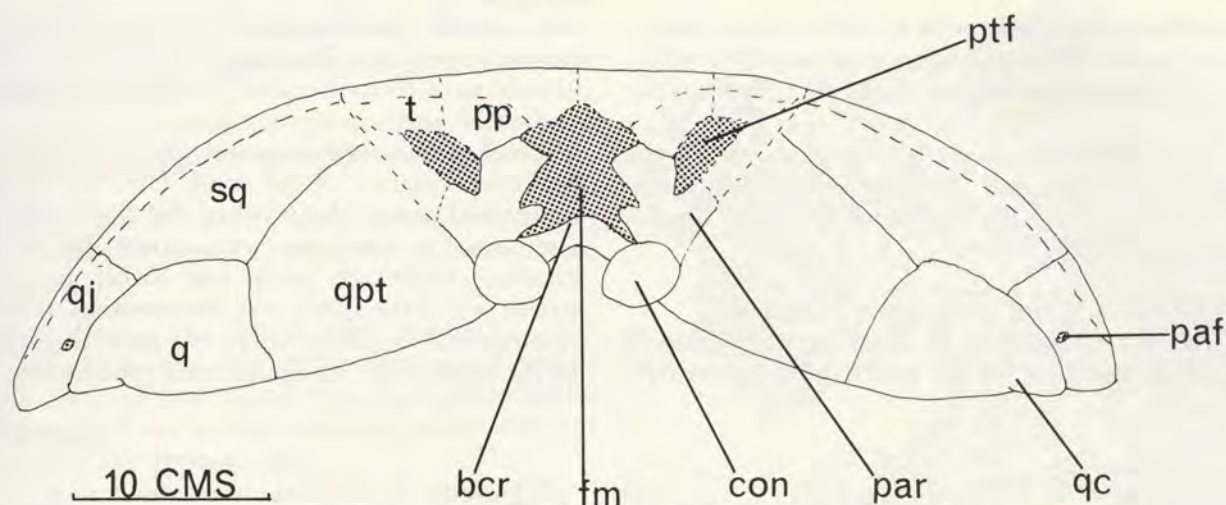


Fig. 5. Reconstruction and analysis of occipital view of Specimen A.

and Cosgriff (1965) to be for the adductor muscles of the jaw, viz. the *m. depressor mandibulae*. Laterally, this trough is bounded by a high wall which slopes down rapidly from the postcondylar process, so that the trough is deep with a smoothly rounded posterior wall. The medial wall of the trough rises to a sharp spur about half-way on the medial surface of the trough. This spur, or part of it, may also have been the origin of the depressor muscle (Howie, 1969). Medial to the dorsal trough is a hollow which curves antero-medially towards the chorda tympani foramen.

Teeth

Only the stumps of teeth, broken in various transverse and longitudinal sections, are preserved. They seem to have been more or less uniform in size and shape. From a tooth cut approximately longitudinally, half-way along the ramus, the approximate crown height is 1,7 cm and the base 0,8 cm wide.

Diagnosis of Specimen B

Skull broad posteriorly (B : L approximately 75), but tapers anteriorly (S : L approximately 42); skull deep posteriorly (H : B approximately 17,4—this figure was incorrectly published as 20, in Chernin and Cruickshank, 1970); external nares elongate, lateral, long axes almost parallel to skull border.

Orbits very close together, well posterior, oval, long axes almost parallel to mid-line; preorbital distance approximately 80% of total length of skull.

Pineal foramen rectangular, just posterior to hind border of orbits; otic notch semiclosed; posterior skull border concave (K : C approximately 19,3); tabular horns distinctive, expanded distally towards squamosal; frontal and jugal enter orbital margin; supratemporal excluded from otic notch; exoccipitals barely exposed on palate.

Description of skull roof of Specimen B (Figs. 6, 7 and 8)

The skull is greatly elongated in the preorbital region; the snout is rounded. As preserved, the shape



Fig. 6. Dorsal view of Specimen B.

of the skull is rectangular seen in dorsal view, due to the total absence of the quadrato-jugal and distortion whereby the jugal is pushed medially and overlaps the maxilla.

Only one half of the skull is preserved, with great gaps, bad distortion and virtually invisible sutures. The tip of the premaxilla is distorted so that the estimated length is 79,5 cm.

Openings in the skull roof of Specimen B

The external naris lies in the anterior one-eighth of the skull, surrounded by the premaxilla anteriorly,

the nasal posteromedially and the maxilla posterolaterally. The naris lies with its long axis almost parallel to the skull border. It is elongated and oval in shape.

Oval orbits are situated close together in the posterior quarter of the skull. The rims of the orbits are raised above the level of the skull table, so that the two orbits are separated by a shallow groove. Although only one orbit is completely preserved in the specimen, the position of the other is distinguishable. Anteriorly, the orbital rim is formed by the prefrontal; medially first by the frontal and then

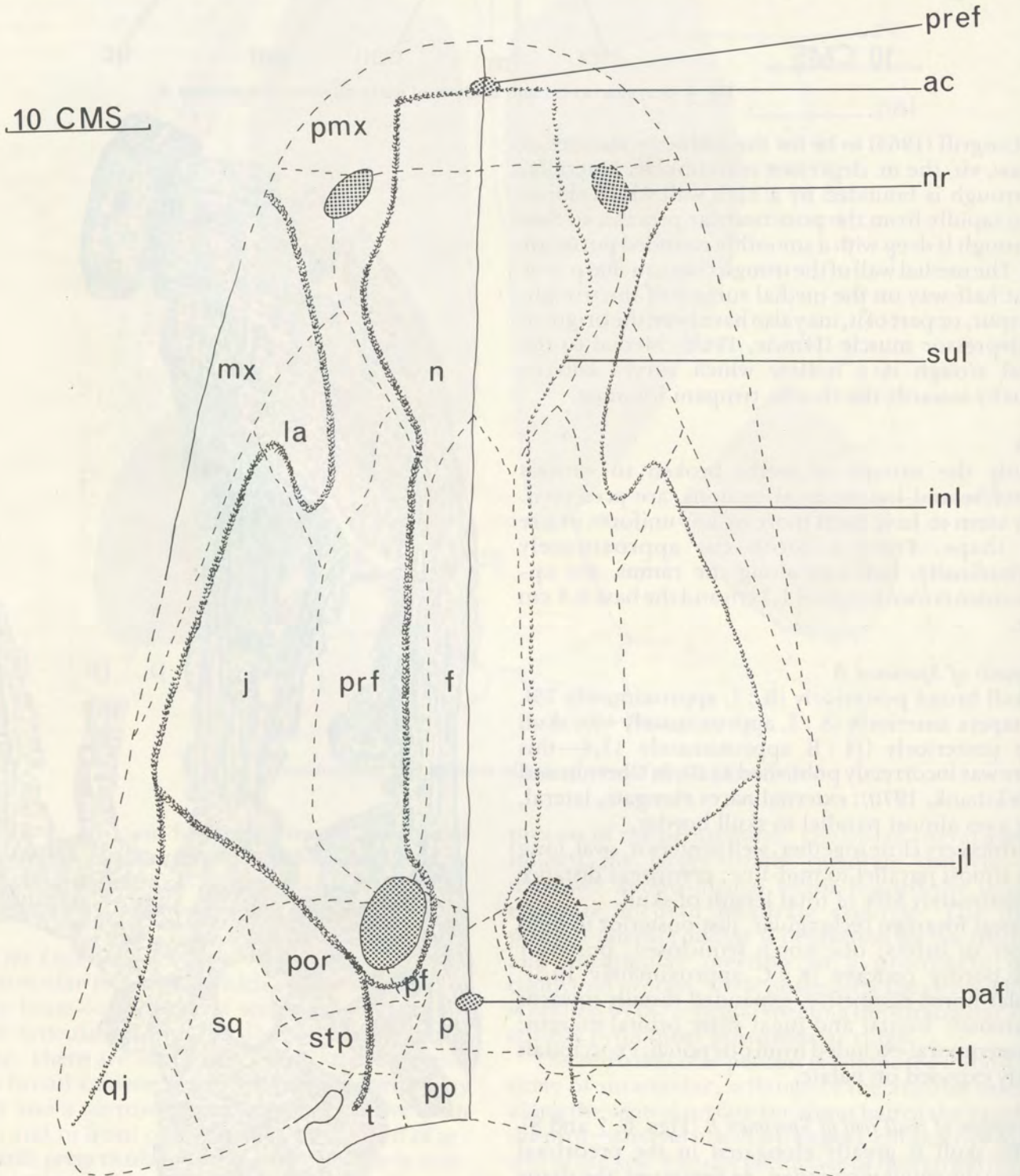


Fig. 7. Reconstruction and analysis of dorsal view of skull of Specimen B.

the postfrontal; anterolaterally first by the jugal and then, posterolaterally, the postorbital. The long axis of the orbit is slightly oblique, converging anteriorly towards the midline.

Close behind the orbits on the midline, in the centre of the parietals, lies the parietal foramen. It is rectangular.

The otic notch is oval in shape and the exterior meets via a narrow canal between the squamosal and tabular horn.

Lateral line system of Specimen B (Figs. 6 and 7)

As described by Moodie (1908) there are 4 sets of canals on the skull roof: jugal, temporal, infraorbital and supraorbital, the last three joining at the centre of ossification of the postorbital.

The course of the canals is distinctly marked by a series of enlarged pits and grooves.

Occiput of Specimen B (see Fig. 16)

Anterior to the dorsal and paroccipital process of the exoccipital only the more prominent structural features are visible. The left half of the dorsal occipital region and the right half of the ventral occipital region are preserved; thus the description is based on a combination of the two elements which not only are on opposite sides of the midline, but also lack visible sutures. This leads to a lack of continuation from the dorsal to the ventral elements.

Ventral surface of the occipital region

Only the basal plate of the parasphenoid is preserved together with crescent-shaped bars of the pterygoids.

The basal plate of the parasphenoid is bounded by oblique sutures to the pterygoid and, posteriorly, the parasphenoid has a slanted suture with the exoccipital. The parasphenoid has a small free margin in the posterior midline between the exoccipital condyles. Ventrally, the parasphenoid plate is concave.

The crista muscularis crosses the posterior portion of the basal plate of the parasphenoid transversely, just anterior to the exoccipital-parasphenoid suture. The crista muscularis consists of two anteriorly convex ridges which join medially to form a peaked posterior projection in the midline. Between each half of the crista muscularis and the condyle of the same side there is a shallow fossa, which is the pocket for the insertion of the rectus capitis muscle (Watson, 1962; Welles and Cosgriff, 1965).

The body of the pterygoid joins the parasphenoid in an oblique suture which issues from the centre of the posterior border of the interpterygoid vacuity and runs to the posterior margin of the skull just lateral to the exoccipital-parasphenoid suture. Anterolaterally, the palatine ramus of the pterygoid extends from the body of the pterygoid. The medial edge of this palatine process is the lateral border of the interpterygoid vacuity. The quadrate ramus of the pterygoid extends posterolaterally. The lateral edge of the palatine and quadrate processes of the pterygoid form the median rim of the subtemporal fenestra.



5 CMS

Fig. 8.

Dorsal view of otic notch of Specimen B, showing superficial sculpture.

Posterior view of the occiput

The paired exoccipital condyles face slightly inwards and downwards. The foramen magnum between the exoccipitals is the centre of the occiput proper. The tabulars form the dorsolateral corners of the occiput and the quadrate rami of the pterygoids dominate the lateral regions of the back of the skull.

Each exoccipital consists of a central condyle above which is a dorsal process and, lateral to the dorsal process, a paroccipital process. Each condyle is almost round and is surrounded by a raised ridge which is believed to have supported a cartilaginous cap.

Medially, the dorsal process forms the sloping dorsolateral limit of the foramen magnum. A lateral ridge of the dorsal process of the exoccipital forms the median border of the post-temporal fossa. The paroccipital process of the exoccipital rises beneath the post-temporal fossa to meet the tabular. The post-temporal fossa is bounded ventrally and laterally by the paroccipital process. The jugular foramen which transmits nerves IX and X opens externally in a foramen postero-latero-ventral to the paroccipital process. The external opening for the hypoglossal nerve XII is near the anterolateral edge of the condylar rim (neither foramen is seen in the illustrations.).

Between and below the exoccipitals is the parasphenoid. Posteriorly, the free margin of the parasphenoid is raised in the midline to form the basioccipital crest and in this region forms the floor of the chamber in which the cartilaginous basioccipital is believed to have been situated.

The tabular forms the dorsolateral corner of the occiput. The dorsal part of the tabular is the tabular horn. A thick arm of the tabular runs ventromedially to meet the exoccipital and sutures with the paroccipital process. A rugose area is present immediately below the distal end of the tabular horn. A prominent

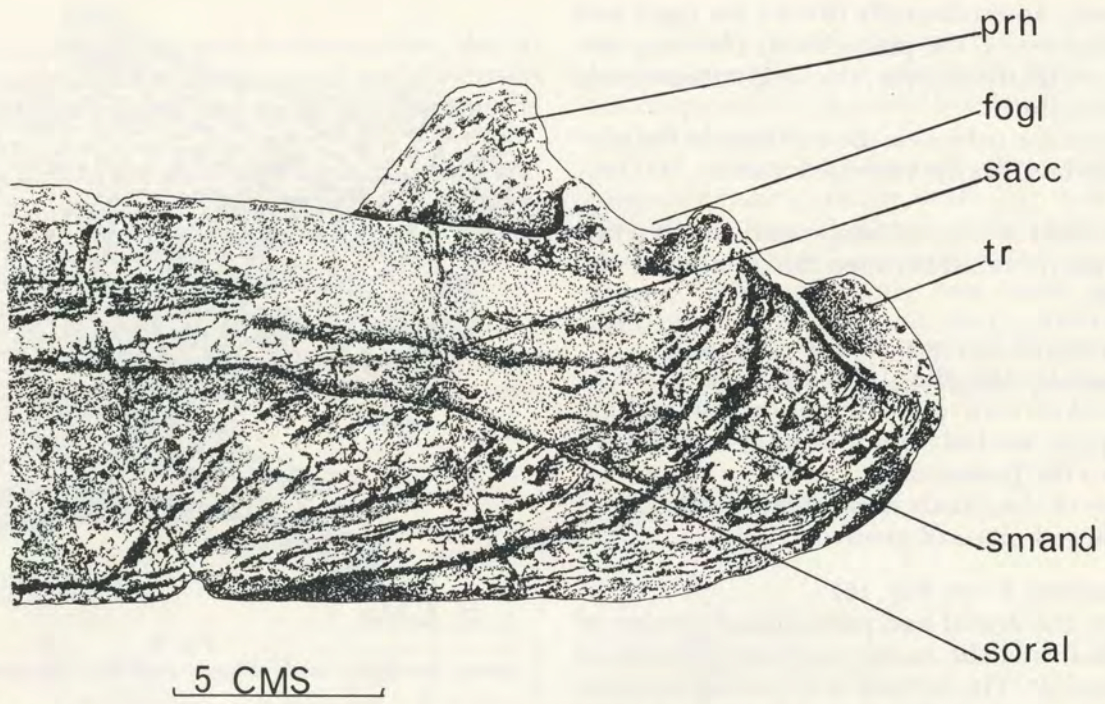
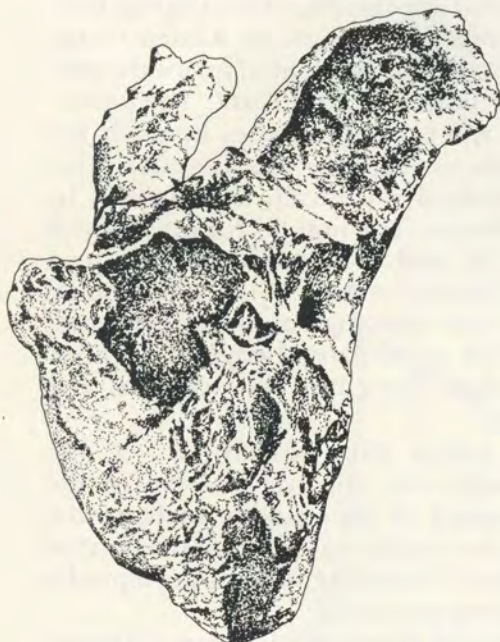


Fig. 9. Lateral view of posterior end of left lower ramus of Specimen A, showing lateral line complex.

FIG. 10 A.



10 B.

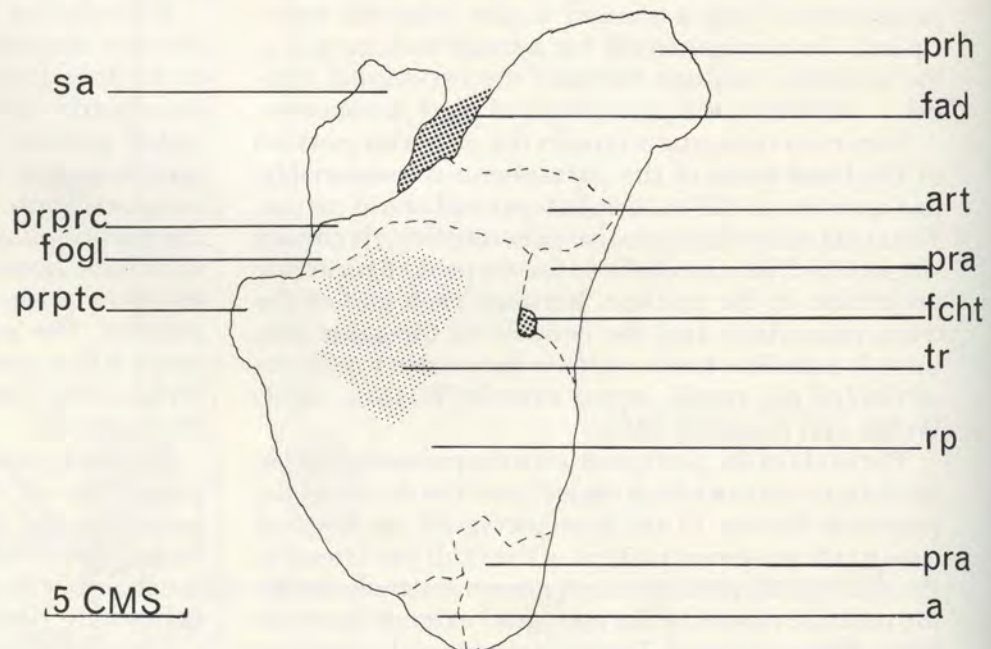


Fig. 10A. Posterior view of left lower jaw of Specimen A.

Fig. 10B. Analysis of posterior view of left lower jaw.

muscle ridge on the tabular runs posterolaterally along the paroccipital process. Just lateral to the exoccipital-pterygoid suture, the pterygoid curves anteriorly to form a cup-shaped region beneath the otic notch, the subtympanic cavity.

Teeth

No teeth have been preserved, but a few uniform tooth sockets are visible on the premaxilla and maxilla.

Table 1

Measurements of reconstructed skull

(N.B. The reconstructed skull is used to obtain measurements due to the large degree of distortion in the material.)

Specimen	A	B
	cm	cm
1. Height of postparietals above the parasphenoid (H)—	9,6	10,4
2. Breadth of skull across quadrates (B) —	55,8	59,5
3. Length of skull (L) —	64,4	79,5
4. Interorbital distance taken at mid-length of orbit (A) —	10,4	7,0
5. Distance from tip of snout to level of anterior edge of orbit (O) —	45,4	60,5
6. Distance from level of posterior limit of orbit to level of centre limit of skull (D) —	12,5	11,5
7. Distance from postero-lateral corner of eye to otic notch (N) —	10,4	9,5
8. Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn (K) —	5,6	3,0
9. Distance between otic notches (C) —	17,5	15,5
10. Distance from mid-length of orbit to lateral edge of same side (I)	14,1	19,0
11. Distance from posterior mid-point of nare to anterior mid-point of orbit (F) —	34,1	48,5
12. Distance between nares at mid-length of same (J) —	14,1	17,0
13. Distance from level of anterior limit of nares to edge of snout (M) —	4,1	9,0
14. Breadth of snout 1/5th of skull length from tip (S) —	25,8	38,5
15. Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull (P) —	2,9	1,5
16. Midline distance from level of anterior limit of otic notch to parietal foramen (T) —	5,8	6,0

Table 2

Habitus Characteristics of Capitosaur. (Chosen from Welles and Cosgriff, 1965)

Specimen	A	B
	Approx.	Approx.
1. Breadth of skull index: $B : L \times 100$ —	81	75
2. Breadth of snout index: $S : L \times 100$ As juveniles tend to have a relatively broader snout (Bystrow and Efremov, 1940), breadth is only significant when comparing skulls of a similar degree of maturity —	40	42
3. Height of skull index: $H : L \times 100$ A division could be made at about 16 and above (deep skulls), and below 16 as shallow skulls	17,2	17,4
4. Interorbital breadth index: $A : L \times 100$ The difference between the two indices is due to the excessive length of Specimen B—it must be remembered that severe distortion of this specimen in the snout area may have produced this difference —	16,1	8,8
5. Interotic breadth index: $C : L \times 100$ —	27,1	19,5
6. Index of interorbital breadth relative to interotic breadth: $A : C \times 100$	59,4	45,1
7. Orbit to otic notch: Interotic breadth index: $N : C \times 100$	59,4	61,2
8. Midline distance behind orbits of parietal foramen: Interotic breadth index: $P : C \times 100$ —	16,5	9,6
9. Midline distance in front of otic notches of parietal foramen: Interotic breadth index: $T : C \times 100$ —	33,1	38,7
10. Posterior skull border concavity index: $K : C \times 100$ —	19,3	32,0

Table 3

**Comparison of Specimen A and B to type specimens
of *Parotosaurus pronus* (Howie, 1969)**

<i>Characters</i>	<i>Type Specimens</i>	<i>Specimen A</i>	<i>Specimen B</i>
Otic Notch	Semiclosed	Not known	Semiclosed
Tabular Horns	Expanded distally towards squamosal	Not known	Expanded distally towards squamosal
H : B x 100	23	17,2	17,4 (this figure was incorrectly printed as 20 in Chernin and Cruickshank, 1970)
Nares	Elongate, lateral, long axes parallel to skull border	Elongate, lateral, long axes parallel to skull border	Elongate, lateral, long axes almost parallel to skull border
Orbits	Close together well posterior oval, long axes parallel to midline	Close together well posterior, oval, long axes parallel to midline	Very close together posterior, oval, long axes almost parallel to midline
Pineal Foramen	Rectangular, just posterior to hind border of orbits	Shape unknown, just posterior to hind border of orbits	Rectangular, just posterior to hind border of orbits
Skull breadth B : L index	Skull broad posteriorly 75	Skull broad posteriorly 81	Skull broad posteriorly 75
Frontal and jugal enter orbital margin	Yes	Yes	Not known
Supratemporal excluded from otic notch	Yes	Yes	Not known
Snout breadth S : L index	Skull tapers anteriorly 32	Skull tapers anteriorly 40	Skull tapers anteriorly 42
Exoccipital barely exposed on palate	Yes	Yes	Yes
Pterygoid with facet for jaw articulation	Yes	Yes	Not known
Processus lamellosus of exoccipital present	Yes	Yes	Not known

Table 4
Stratigraphy

		<i>South Africa</i>	<i>Zambia</i>	<i>East Africa</i>
T R I A S S I C	Upper	{ <i>Cave Sandstone</i> <i>Red Beds</i>		
	Middle	<i>Molteno</i>	Red Marls	Manda Formation
	Lower	{ <i>Cynognathus zone</i> <i>Lystrosaurus zone</i>	N'tawere Formation ?Escarment Grits	?Kingori Sandstone

DISCUSSION

Briefly reviewing the four other species of *Parotosaurus* in which the tabular has grown laterally towards the squamosal, it is found that in *P. semiclausus* (Swinton, 1927) the tabular is unexpanded distally and only just fails to meet the squamosal. The orbits are more rounded and the jugal is excluded from the orbital margin. Although the tabular horn of *P. birdi* (Brown, 1933) and *P. peabodyi* (Welles and Cosgriff, 1965) have moved laterally, they still do not expand distally. Also *P. peabodyi* has a much shallower occiput and Howie (1969) has pointed out that the vertebrae of *P. peabodyi* differ from those of *P. pronus*. *P. birdi* has a greater exposure of exoccipital on the palate than *P. pronus* and the orbits are further apart in *P. birdi*.

P. brookvalensis (Watson, 1958) has a distal expansion of the tabular, but this is a bulbous swelling, which increases the surface area rather than causing it to approach the squamosal. Howie (1969) has discounted the proposal that *P. brookvalensis* is a juvenile of *P. pronus*, because of the character of its ornament and the length of the snout, which are both adult in proportion.

In the type specimen of *Parotosaurus pronus* (Howie, 1969), the tabular is expanded laterally towards the squamosal. Although this expansion is greater in the type specimen of *P. pronus* than in Specimen B, the significance lies not in the absolute size (Welles and Cosgriff, 1965), but in the distinct shape of the tabular horn, which in Specimen B is just about the only region not distorted or damaged, and corresponds to that region in the type species. The difference in the size of the distal expansion of the tabular and the whole skull could be due to genetic variability in populations.

The height to breadth ratio ($H : B \times 100$) is 23 in the type specimen and 17.2 and 17.4 in Specimen A and B respectively. This difference is largely due to post-mortem deformation which also included dorso-ventral flattening, which is discussed more fully below.

The fact that in Specimen B the nares and orbits are not quite parallel to the skull border as they are in Specimen A and the type specimen is almost certainly due to post-mortem lateral compression.

Specimen B corresponds exactly to the type species with regard to the skull breadth index ($B : L$ is 75). However, Specimen A has a greater skull breadth index (81). This is due, mostly, to the great difficulty in joining the small fragments in that area; small gaps remain between abutting fragments which, added together, caused this difference (see Fig. 1).

In the type species the snout breadth index ($S : L$) is 32. For Specimen A this value is 40, and for Specimen B 42. There seems no doubt that even taking into consideration the lack of the snout in Specimen A and the distortion of that area in Specimen B, the Luangwa Valley animals have

broader snouts than the type specimen, which may be due to their larger size compared with the type.

I have had the opportunity of studying the almost complete skulls from the Ruhuhu Valley, now in the Cambridge Museum, and can confirm the triangular nature of their shape. With regard to Specimen B, the great expansion of the preorbital region makes the shape of the skull almost oval (without, of course, considering the quadrate region). This could mean that, with better material, new facts may emerge to cast doubt on the taxonomy and Specimen B could be a different species. With the available material this latter conclusion would presume too much.

With regard to Specimen A, however, the total lack of the snout and the difficulty involved in fitting the fragments together explain the difference in the snout index. As the indices were obtained from direct measurement, not taking into account the many small gaps, the morphological details (of the braincase (for example) convince me that Specimen A is most likely to be *Parotosaurus pronus*.

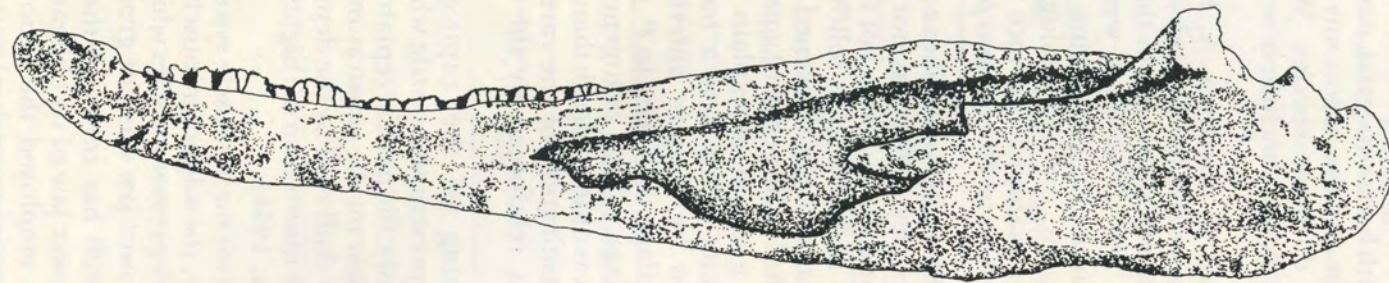
Howie (1969, p. 215) describes a pre-articular fossa in the type species, which has not been described in other labyrinthodonts and is not found in Specimen A. This fossa is described as follows: "The (hamate) process is transversely thickened and is excavated medially by the leading edge of a pre-articular fossa". Howie then goes on to explain that in the other labyrinthodonts which have a hamate process this fossa is filled by a more anterior ossification of Meckel's cartilage than seen in *P. pronus*. As ossification of cartilage is also ontogenetic, I suggest that Specimen A was older at death than the type specimen, and hence ossification of the cartilage filled in this fossa. This is reinforced by the larger size of the specimen.

The opening of the capitosaur mouth has traditionally presented a puzzle which former writers solved variously, the most acceptable being the resting of the lower jaw on the substratum together with the raising of the skull roof by the depressor mandibulae muscle, which inserted on the highest point of the skull roof (Watson, 1958).

There are two main muscle systems which support the lower jaw, the adductor muscles (which close the jaw) and the depressor muscles which would open the jaw—if the lower jaw was not grounded.

Howie (1969) has reviewed the problem and, in freeing the lower jaw of its obligation to hit the substratum, has employed the action of three muscle systems; the occipitovertebral muscle (which insert on the more or less vertical occiput and run to the cervical vertebrae); the cleidomastoideus muscle (which originates on the dorsal process of the clavicle and inserts on a projecting flange of the tabular) and the depressor muscle, which inserted along the cheek region of the occiput on the squamosal and quadratojugal—so that origin and insertion of the muscle are in the same vertical plane—the point of at-

FIG. 11 A.



11 B.

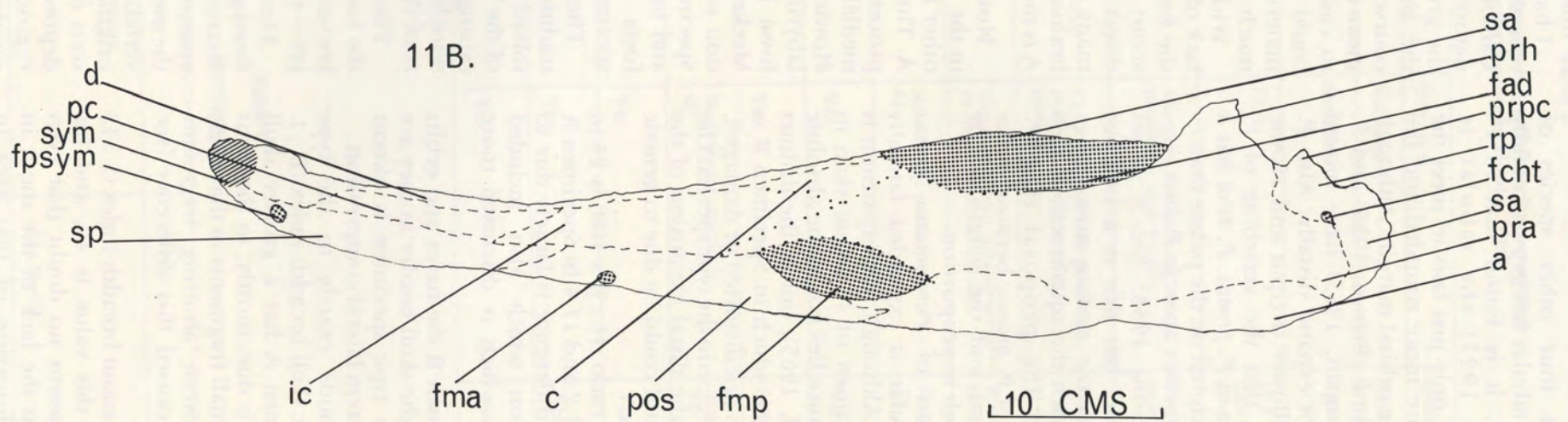


Fig. 11A. Lower jaw of Specimen A, seen lingually. (Reversed from left side)
 Fig. 11B. Reconstruction and analysis of lower jaw of Specimen A, seen lingually.

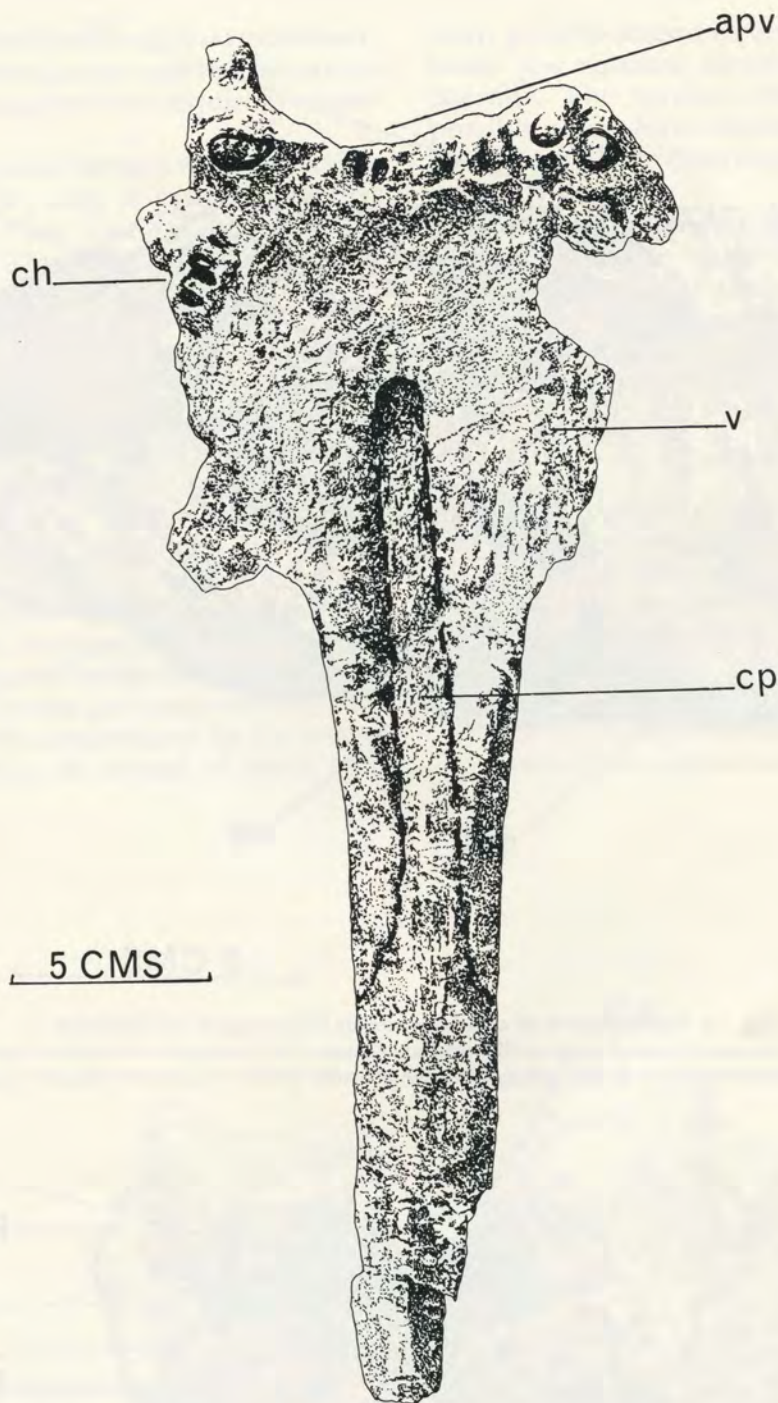


Fig. 12. Palatal view of vomer and clutiform process of Specimen A, as preserved.

tachment on the lower jaw being the slight medial in-turning of the retroarticular process.

Howie's solution has two phases; firstly the skull is raised using the occipito-vertebral muscles and then the cleidomastoideus muscles, and secondly the jaw is lowered by the action of the depressor muscles.

I suggest another simpler mechanism. There is no doubt the capitosaur were aquatic (the lateral line system and rete vasculosum found in capitosaur are habitus characters of aquatic animals). If they did venture on land their progress would have been ponderously slow, leaving little doubt that they had little need to open their mouths on land with a view to

catching prey. The position of their eyes (on the top of their heads and also centrally placed) makes it difficult to believe they could see, stalk, lie in wait and therefore catch a meal on land.

So, assuming the animals fed in water, on fish, which they could see, they must have been totally buoyant. The modern animal with an analogous way of life is the crocodile. On observation of these animals in glass tanks, it is clear that at no time is the jaw firmly closed. Whether resting, swimming or just walking on the bottom, there is a small gap between the jaws. This allows water to be continuously in the mouth, thus equalizing the pressures inside and outside the mouth;

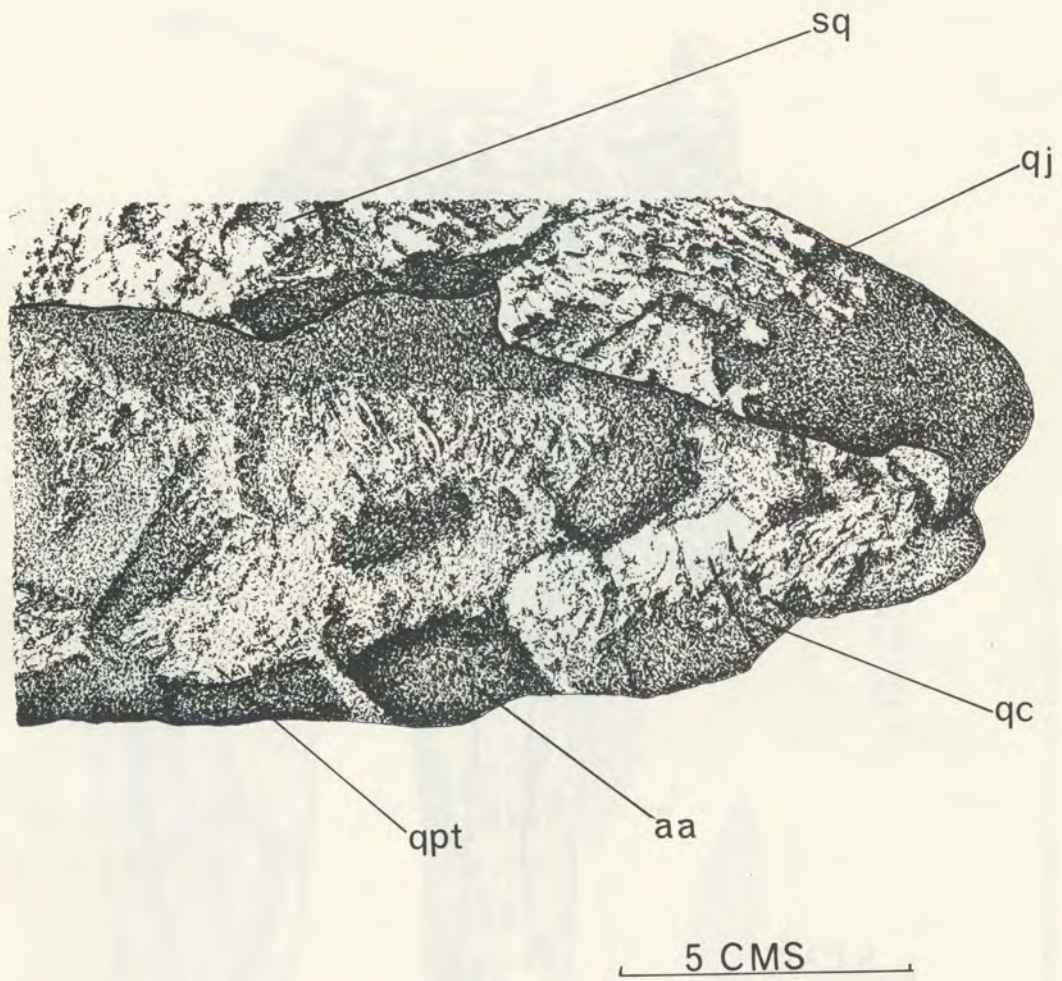


Fig. 13. Internal view of quadrate ramus of pterygoid of Specimen A.

N.B. A distinction of *P. pronus* is a roughened area of bone on the quadrate ramus of the pterygoid in an internal position adjacent to the quadrate. This appears to have been a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle. (Howie, 1969)

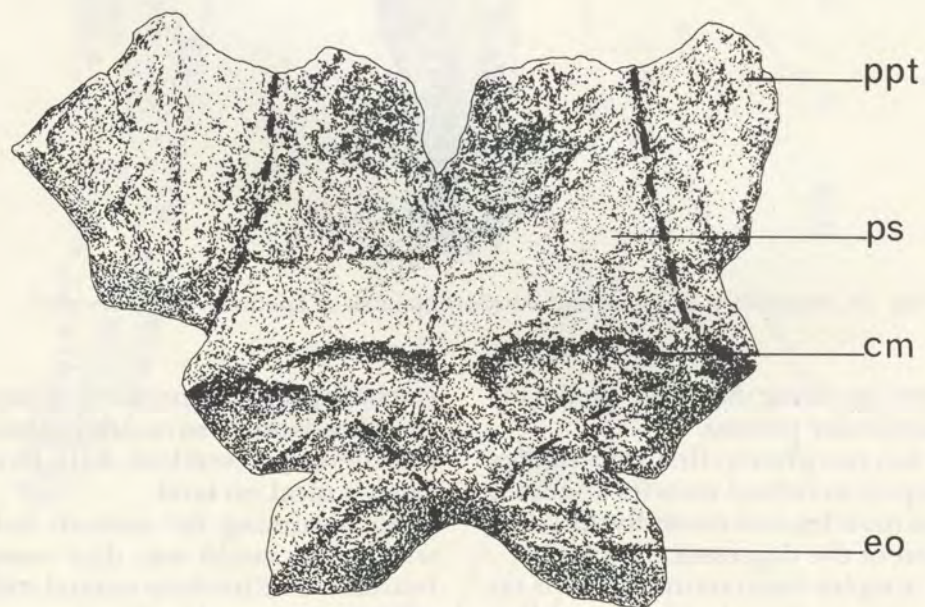


Fig. 14. Ventral view of occipital region of Specimen A.

then when it wants to open the mouth less resistance is applied by the water acting against a partial vacuum in the mouth, thus decreasing the force required to open the mouth.

A second interesting point emerged while observing crocodiles; whenever they snap at prey the jaw first opens a distance away from the prey and then the animal lurches forward. This means that the inrush of water completes the widening of the gape without great muscular exertion.

The opening of the capitosaur jaw by lowering of the jaw instead of raising the skull roof would also enable the animal to keep sight of its prey.

Assuming that capitosaur preyed in a similar fashion to the crocodile, if there was a depressor mandibularis muscle originating on the tabular horn flange and inserting on the roughened area of the retroarticular process, (Watson, 1958), this would mean that, when the muscle was contracted, a force would be exerted which, resolved into vectors, would have a vertical and horizontal component, the latter of which would tend to move the jaw rami medially. This latter force is adequately counteracted by the screw-shaped quadrate condyle, the thread of which runs

from postero-lateral to antero-medial directions. A lower jaw rotating about this condyle must move laterally. The vertical component of the force is possibly all the force necessary to open the jaw in the conditions I have described, with the animal floating neutrally buoyant.

Thus, to summarize, it is necessary to employ only one muscle system to open the mouth of capitosaur, the depressor mandibularis muscles, with the assumption that the capitosaur fed in a similar fashion to the modern crocodile.

SUMMARY

1. Capitosaur material collected from the fossiliferous beds of the N'tawere Formation in the Upper Luangwa Valley, Zambia is described.
2. These are tentatively assigned to the genus and species *Parotosaurus pronus* Howie, on the basis of the similarity in proportions as well as other details (Specimen A), and the diagnostic otic notch, in which the tabular has expanded laterally towards the squamosal (Specimen B).

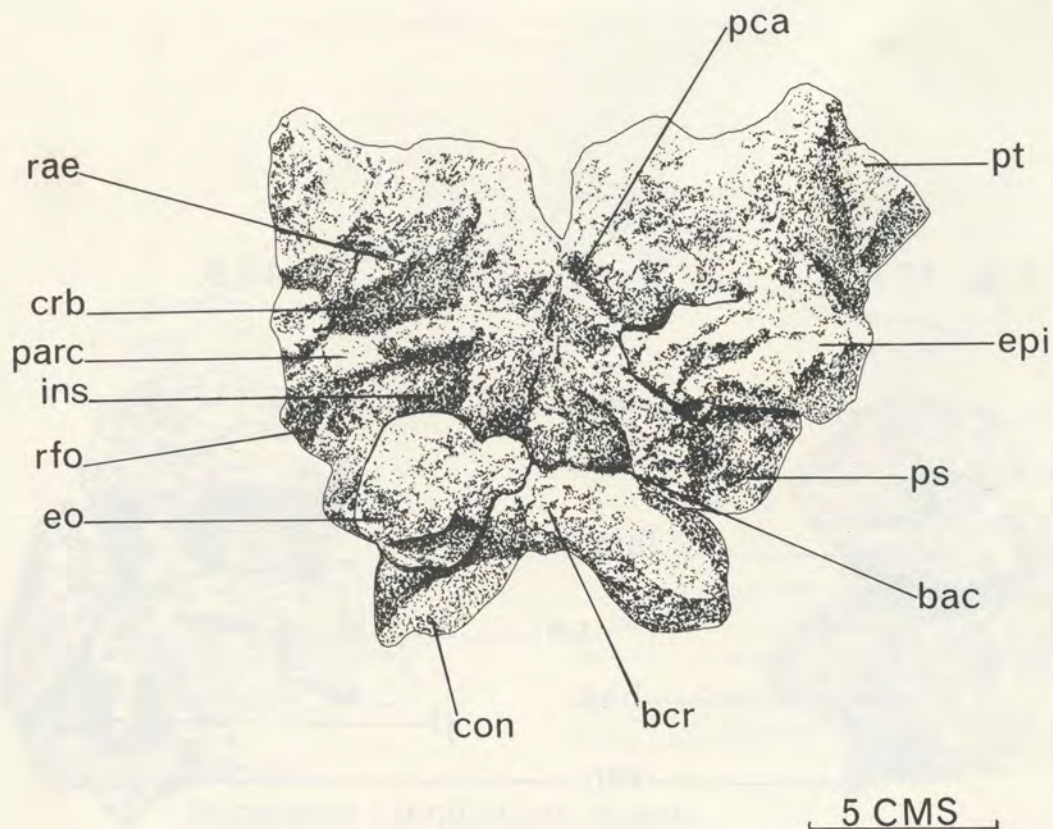


Fig. 15. Dorsal view of Braincase of Specimen A.
N.B. The right exoccipital is missing.

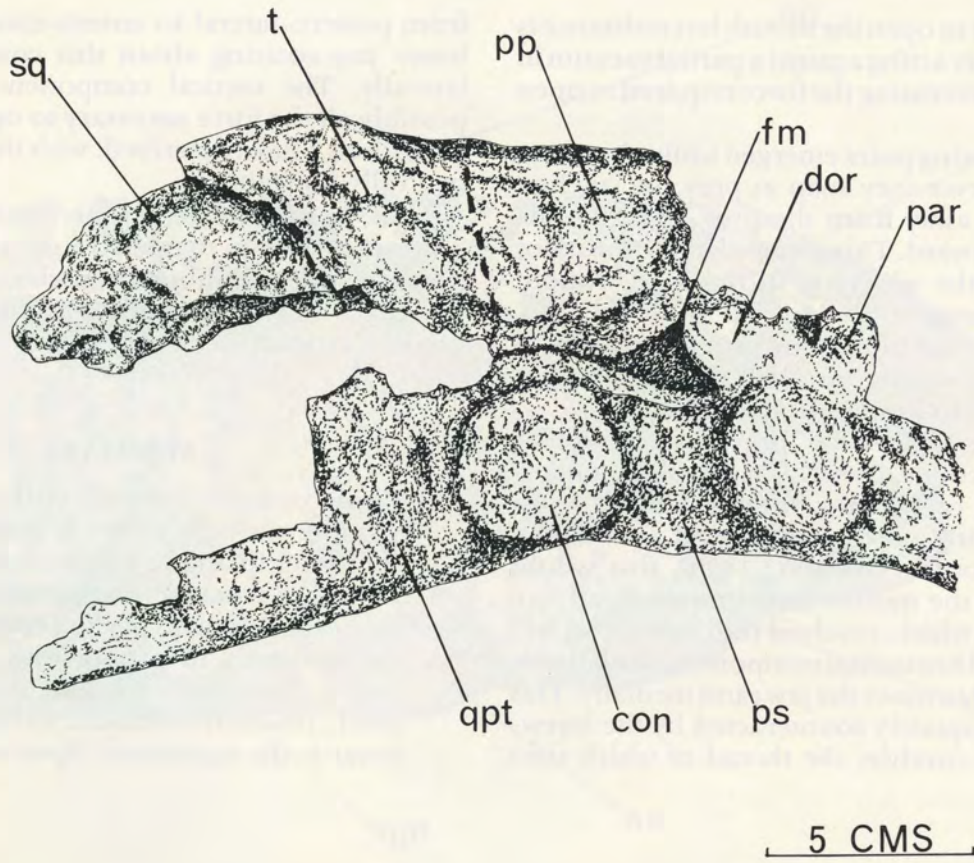


Fig. 16. Posterior view of occipital view of Specimen B.

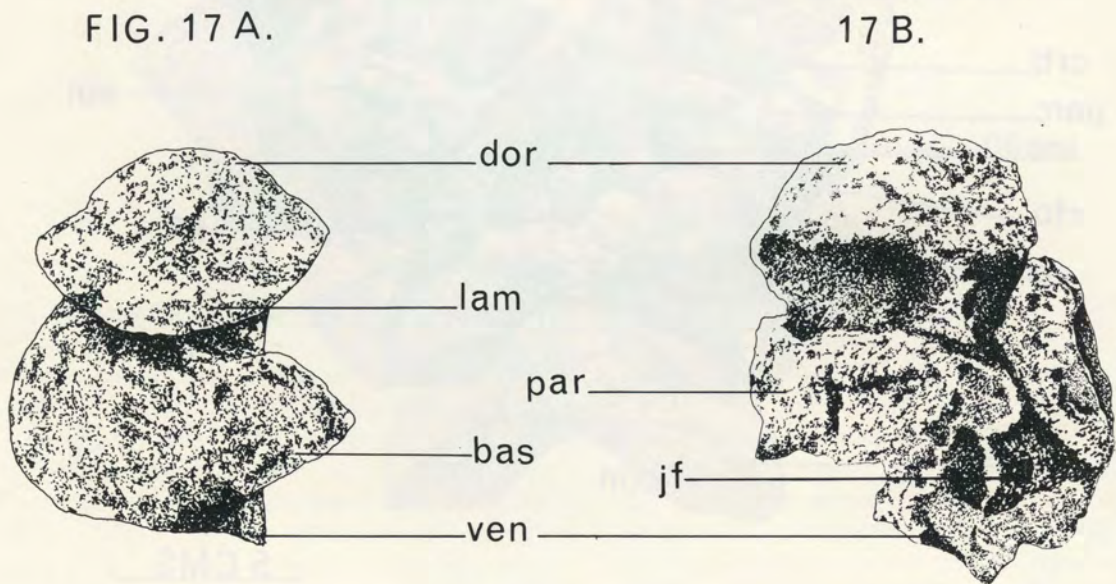


Fig. 17A. Median view of left exoccipital of Specimen A.

Fig. 17B. Lateral view of left exoccipital of Specimen A.

17C.

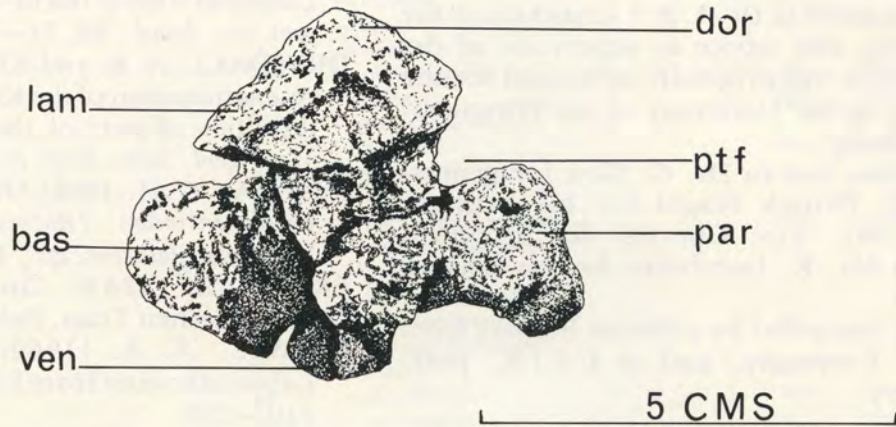


Fig. 17C. Anterior view of left exoccipital of Specimen A.

3. The only other *Parotosaurus pronus* from another locality, described to date, is that described by Howie (1969), which was collected from Mkongoleko, Ruhuhu Valley, Tanzania, in the Manda Formation.
4. Points 1, 2 and 3 corroborate evidence put forward by Dixey (1937), Crompton (1955), Crompton and Ellenberger (1957) and Drysdall and Kitching (1969) that the N'tawere Formation in the Upper Luangwa Valley and the Manda Beds represent the same horizon.
5. A consideration of faunal units of the relevant

horizons and on the assumption that the foregoing is correct leads to the conclusion that the "Red Marl" horizon of N'tawere is largely equivalent to that of the Mkongoleko area of the Manda Formation and that both of these post-date the *Cynognathus* zone only slightly. The lower of the two N'tawere horizons may, in fact, be of the same age as the *Cynognathus* zone.

6. Assuming capitosaur had a similar life-style to the modern crocodile, and the animals were neutrally buoyant, it is suggested that only the depressor mandibulae muscles were necessary to open the mouth, by lowering the lower jaw.

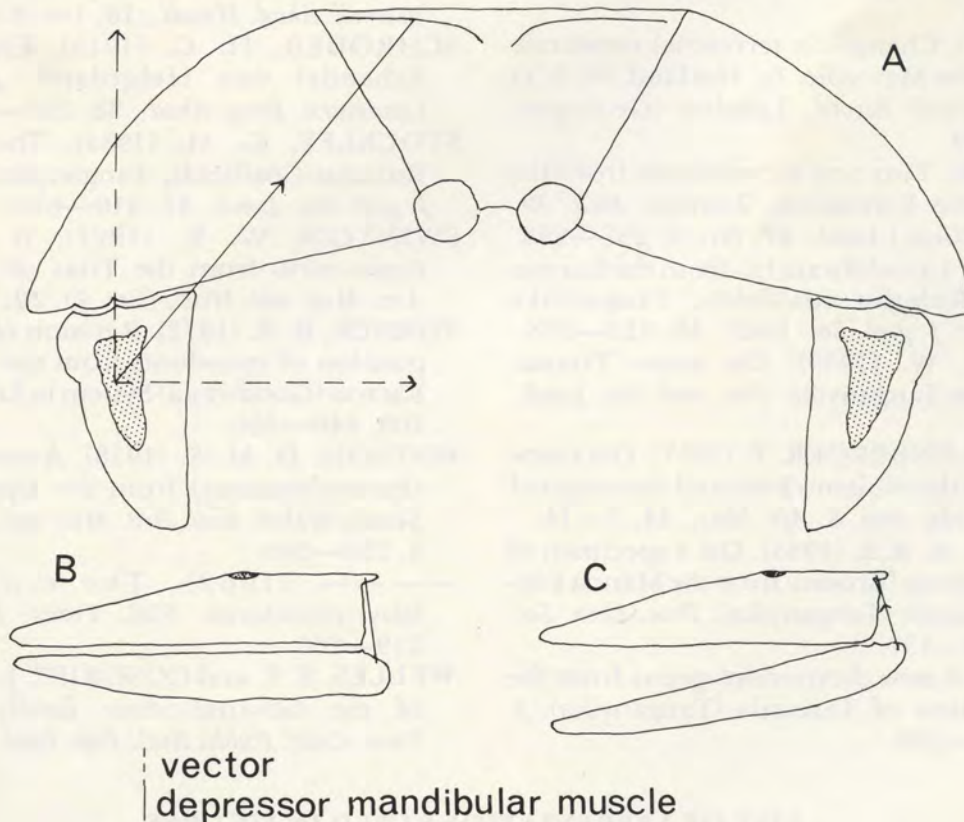


Fig. 18. Semi-diagrammatic representation of a suggested mechanism for opening the mouth in capitosaur, if the animals are neutrally buoyant.

- A. Posterior view of skull and jaw, showing line of action of force exerted by the depressor mandibular muscle. This force is also shown resolved into its vertical and horizontal vectors.
- B. Lateral view of relaxed skull and jaw, showing position of depressor mandibular muscle.
- C. Lateral view of skull with jaw lowered, showing line of action of depressor mandibular muscle when contracted.

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LIST OF ABBREVIATIONS USED IN FIGURES

a	— angular	apv	— anterior palatine vacuity	bas	— basal process
aa	— auxiliary articular area	art	— articular	bcr	— basioccipital crest
ac	— anterior commissure	bac	— basioccipital chamber	c	— coronoid

ch	— choana	lam	— lamellar process	ptf	— post-temporal fossa
cm	— crista muscularis	mx	— maxilla	q	— quadrate
con	— condyle	n	— nasal	qc	— screw-shaped quadrate
cp	— cultriform process	nr	— nare	qj	— quadratojugal
crb	— conical recess for the basipterygoid process	obr	— oblique ridge	qpt	— quadrate ramus of pterygoid
d	— dentary	p	— parietal	rae	— roughened area for the attachment of the epipterygoid
dor	— dorsal process	paf	— paraquadrate foramen	rfo	— ridge marking fenestra ovalis in the dorsal groove of the pterygoid
ec	— ectopterygoid	pafn	— parietal foramen	rp	— retroarticular process
eo	— exoccipital	pal	— palatine	sa	— surangular
epi	— epipterygoid	par	— paroccipital process	sacc	— sulcus accessorius
f	— frontal	parc	— parapterygoid crest	sf	— subtemporal fenestra
fad	— adductor fossa	pc	— precoronoid	smand	— sulcus mandibularis
fcht	— chorda tympani foramen	pca	— internal opening of palatine branch of the internal carotid artery	soral	— sulcus oralis
fm	— foramen magnum	pf	— postfrontal	sp	— splenial
fma	— anterior Meckelian foramen	pmx	— premaxilla	sq	— squamosal
fmp	— posterior Meckelian foramen	por	— postorbital	st	— stapes
fogl	— glenoid fossa	pos	— postsplenial	stp	— supratemporal
fpsym	— postsymphysial foramen	pp	— postparietal	sul	— supraorbital canal
ic	— intercoronoid	ppt	— palatine ramus of pterygoid	sym	— symphysis
inl	— infraorbital canal	pra	— prearticular	t	— tabular
ins	— intercrestal sulcus	prf	— premaxillary foramen	tl	— temporal canal
iv	— interpterygoid vacuity	prh	— hamate process of prearticular	tr	— trough for depressor mandibular muscle
j	— jugal	prprc	— precondylar process	v	— vomer
jf	— jugular foramen	prptc	— postcondylar process	ven	— ventral process
jl	— jugal canal	ps	— parasphenoid		
la	— lacrimal	pt	— pterygoid		

INTRODUCTION

The Anomodontia were the numerically dominant terrestrial herbivores during the Permian between Palaeomex and Mesomex stages, but almost their greatest diversity during the Upper Permian as it drew from the abundance of large articular surfaces in the Lower stages of the Permian faunas of the Karoo system of South Africa (see Diller, 1967). Permian faunas in Africa including the Mazonian, Mazonian of Zambia and those in the Karoo area of Tanzania.

Most of the Permian species of Dicynodontia were relatively small, but giant forms developed in the Upper Permian. Permian repletan faunas are well known on both sides of the continents and are only known from the Permian of Africa, India, U.S.S.R., Scotland and possibly China. As far as is known most of the Permian species are relatively small (Kerry, 1952).

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