CAPITOSAURID AMPHIBIANS

FROM

THE UPPER LUANGWA VALLEY
ZAMBIA

SHARON CHERNIN B.Sc. Hons.

I, the undersigned herewith declare that this thesis is entirely my own work and has not been presented for a degree at another University.

DATE: 14th Nov. 1972 ....

S. Chernin ....

CONTENTS

INTRODUCTION

Capitosaurs are extinct amphibians, which arose in the Lower Triassic and became extinct before the Jurassic. They were probably slow-moving animals, inhabiting the bottom of swamps or streams.

The type species is regarded as Capitosaurus nasutus Meyer, 1858, which exhibits a distinctive organization differing from other common Triassic forms, in that the preorbital region of the skull is greatly expanded; the external nares are small and anteriorly placed; the small, rather medially placed orbits are bounded partly by the frontals, separating the pre- and postfrontal elements; the postorbital tends to crowd the jugal out of its position along the rim of the orbit.

Fraas in 1889 (p. 121) proposed the term Cyclotosaurus for such animals of the Upper Triassic of Europe, in which the tabulars united with the squamosals to enclose the otic notch. For the less specialized forms from the Lower Trias, with an open otic notch and ancestral to the cyclotosaurs, the genus Capitosaurus was retained.

Romer (1947, p. 218) proposed the term Parotosaurus for the early Triassic "Capitosaurus" with an open otic notch and retained the term Cyclotosaurus for the closed-notched type of the European Upper Trias. He used as the type species Capitosaurus arenaceus, restricting the generic name Capitosaurus to this species.

Because the diagnostic otic notch of Capitosaurus arenaceus was not preserved, it was dropped as the type species, and Capitosaurus nasutus (Schroeder 1913, p. 263) took its place - a primitive form with an open otic notch, being called by the generic name Parotosaurus by Jaeckel in 1923.

Watson (1962, p.261) listed a number of evolutionary trends of the capitosaurs through the Triassic. Among those listed were the following: an increase in the size of the skull; a disproportionate increase in the length of the nasal region; and a tendency to close the otic notch - this latter character dividing the family into the Lower Triassic parotosaurs with open otic notches and the Upper Triassic cyclotosaurs with closed otic notches. The third genus of Capitosaurs, Paracyclotosaurus from the Upper Trias of New South Wales, was considered to have a closed otic notch and a deep skull line (Watson, 1958).

Welles and Cosgriff (1965) placed all members of the Family Capitosauridae in 3 genera: Parotosaurus, Paracyclotosaurus, and Cyclotosaurus, dropping the generic term Capitosaurus completely.

However, they maintained the term 'Capitosauridae' as the family name because of the long established usage of the name, and also because of the possibility that adequate material of Capitosaurus arenaceus may be found, upon which the Family was founded. If this species has an open otic notch Parotosaurus will then become synonymous with Capitosaurus; if it has a closed otic notch, Cyclotosaurus would then become synonymous with Capitosaurus. In either case, the term Capitosaurus will become more meaningful.

Welles and Cosgriff (1965), have also established newly observed trends in the evolution of capitosaurs. These are: the expansion of the skull table; the spreading apart of the orbits which also move forward; the increase in distance both from the orbits to the parietal foramen and from the parietal foramen to the otic notch; and the lengthening of the pterygoids. Chronologically, the genera are named as follows: Parotosaurus in the Bunter and early Muschelkalk; Cyclotosaurus in the Upper Muschelkalk and Lower Keuper; and Paracyclotosaurus in the Upper Keuper.

Howie (1969), distinguished Parotosaurus pronus from the other ten species described, 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 four of the eight species retained by Welles and Cosgriff, the tabulars have also grown laterally towards the squamosal. Of these P. semiclausus (Swinton, 1929) is quite different: the tabular is unexpanded distally and only just fails to meet the squamosal; the choanae, orbits and pineal foramen are rounder; and the jugal is excluded from the orbital margin. Howie (1969), points out that some of these characters could apply to a young individual of P. pronus, but in that case, the otic notch could be expected to be less closed, in the younger specimen, and not more closed as in P. semiclausus.

The tabular horns of P. birdi (Brown, 1933) and P. peabodyi have also moved laterally, but still have no distal expansion. Also, P. peabodyi has a much shallower occiput. The occiput of P. birdi is much nearer to P. pronus, however, P. birdi has a greater exposure of exoccipital on the palate; the orbits are far apart and slope towards the otic notch; the cultriform process is sharply keeled; and the occipital area extends farther posteriorly, behind the level of the quadrates.

Parotosaurus brookvalensis is the only other parotosaur in which the tabular has expanded distally as it does in P. pronus, but this is a bulbous swelling of the tabular horn increasing its surface area, rather than causing the tabular to approach the squamosal.

Howie also raised the possibility that the unornamented closure of the otic notch of Paracyclotosaurus davidi may be a gap filled with matrix, and if the link between the tabular and squamosal is removed, Paracyclotosaurus davidi markedly resembles a parotosaur.

In Watson's reconstruction of Paracyclotosaurus davidi, he noted an absence of an anterior palatal vacuity, setting it apart from all other capitosaurs. However, Howie, on re-examination of the casts, proposed the likelihood of the presence of an anterior palatal vacuity. She has thus concluded that Parotosaurus pronus and Paracyclotosaurus davidi are remarkably similar and may be closely related.

In 1970, I described 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 another capitosaur found a few feet away from the one described in 1970. The new material although lacking the crucial tabular horns, displays proportions and other characters so similar to P. pronus (Howie, 1969) that I must assign it to that genus. I have also re-described the material discussed in 1970, which I still assign to P. promus, although I would have been more confident in this decision if more morphological details of the skull were available.

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 and 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 <u>Unio karooensis</u> (Drysdall and Kitching, 1963, p. 22). From the same Locality, two cynodonts were also collected; the smaller perhaps belonging to the genus <u>Trirachodon</u> and the larger is a <u>Scalenodon</u>-like form resembling material described by Crompton (1955), from the Manda Beds of Tanganyika.

The type material of <u>Parotosaurus pronus</u> 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 <u>Parotosaurus</u> 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 <u>Unio karooensis</u>, which was a shaky correlation, because <u>Unio karooensis</u> is not a true faunal indicator.

Crompton and Ellenberger (1957), described Scalenodontoides macrodontes 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 (in press) denies this; he believes that Scalenodontoides macrodontes comes from the Lower part of the Red Beds, in Lesotho, and not in 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 fauna are more advanced than those ~~in~~ of the Cynognathus zone, in keeping with the progressive nature of the cynodonts.

Therefore, although the Manda Formation in general is more advanced than those in 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 the foregoing, it would therefore 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.

To summarise, the Manda Formation has been thought of as occupying a position exactly in the middle of the time gap between the end of the Cynognathus zone times and the beginning of the Red Beds times, whereas on analysing the Manda Formation, it is obviously closer to the Cynognathus zone fauna than to the Red Beds fauna.

MATERIAL AND METHODS OF PREPARATION

The material studied was as follows:

FIELD NO.	MUSEUM NO.	IDENTITY	REMARKS	SPECIMEN
4221	B.P.I.* 424	*Parotosaurus pronus*, Howie	Broken skull & ~~right~~ left lower jaw	A
4223	B.P.I.* 414	*Parotosaurus pronus*, Howie	Broken skull	B

* Bernard Price Institute for Palaeontological Research

Both Specimen 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 is present. A fragmented braincase 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 + 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, ventral surface of the condyles and pterygoids. The ventral surface of the skull was not prepared, many specimens of a Unio karooensis 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. 19), 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 I, II and III, 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 figures 13 and 14 the illustrations of the lower jaw in Specimen A have been reversed left for right.

For key to abbreviations used in this thesis, see pages 63 and 64.

DESCRIPTION OF MATERIAL

DIAGNOSIS OF SPECIMEN A

Skull broad posteriorly (B:L approximately 81), 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 the skull roof of Specimen A (fig. 1 and 2)

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 elongate ridges. See fig. 1.

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.

From front to back, the paired elements bordering the mid-line, are the premaxillae (not preserved), the nasals, frontals, parietals and postparietals.

Posteriorly, the nasal wedges between the frontal medially and the prefrontal laterally. It forms a part of the posterior border of the naris and then runs in a straight-line posteriorly, suturing first with the maxilla and then with the lacrimal, before meeting the prefrontal.

The two frontals form a spear-head between the nasals and cover the central area to midway between the orbits. Anteriorly, the frontal meets the nasal in a gently curved suture, while further back it forms a straight-line suture with the prefrontal. The frontal also forms part of the medial border of the orbit. Posteriorly, the frontal sutures first with the postfrontal and then with the parietal.

The parietals enclose a presumably rectangular parietal foramen, which is situated about 3.1 cm behind the level of the back of the orbits. The anterior suture with the frontals is angled on the left and more transverse on the right hand side of the skull. Antero-laterally, the parietal meets the postfrontal in a curved suture, which is directed towards the otic notch. Postero-laterally, the parietal forms a straight-line suture with the supratemporal. The posterior border of the parietal is a transverse suture with the postparietal.

The pentagonal postparietals form the posterior limits of the central skull area. The anterior suture is a transverse one with the parietal, while the posterior edge is curved, making the central border concave. The postparietal has a slanted contact with the supratemporal, which points towards the otic notch, while postero-laterally, the postparietal suture reverses direction to form a suture with the tabular, obtuse to the former suture, forming thus the pentagonal shape of the postparietal.

The maxilla forms part of the posterior border of the naris, and extends backwards to an oblique suture with the jugal. It forms part of the lateral border of the skull roof, the edge curving gently antero-medially. Behind the naris, the maxilla medially forms a straight-line suture with the nasal and then turns abruptly in a laterally slanted suture first with the lacrimal and then with the jugal.

Between the maxilla and the nasal is a sharp wedge of bone which is the anterior limit of the lacrimal. It is a diamond-shaped bone, the posterior wedge of which lies between the prefrontal medially and the jugal laterally, and does not enter the orbit.

The prefrontal begins anteriorly as a sharp point between the lacrimal and nasal and then forms a straight-line suture medially with the frontal, a slightly outward-bulging suture with the jugal and posteriorly it forms the anterior border of the orbit.

Forming the postero-medial border of the orbit is the postfrontal. Anteriorly, this bone has a sloping suture with the frontal and medially, an outwardly curving suture with the parietal. Postero-laterally, it has a straight-line suture, first with the postorbital and then with the supratemporal.

The postorbital forms the postero-lateral border of the orbit from the anterior transverse suture with the jugal around to the straight-line suture with the postfrontal. Posteriorly, the postorbital forms a wedge between the squamosal laterally and the supratemporal medially. The antero-lateral corner of the postorbital lies within the jugal, so that the jugal forms a small part of the lateral border of the orbit.

Between the postorbital and postfrontal lies the sharp point of the supratemporal. Medially, the supratemporal sutures anteriorly with the postfrontal, then the parietal and this suture turns sharply towards the otic notch, when it meets the postparietal. Postero-laterally, the supratemporal meets the squamosal in a suture at right angles to the postorbital-supratemporal suture. On the right side of the skull, the supratemporal does not seem to extend anteriorly to a sharp point, but to have a rather more wavy anterior margin, but here the sutures are very vaguely seen.

Lateral to the postparietal, forming the postero-medial border of the otic notch lies the tabular. The diagnostic tabular horn is missing. Anteriorly, the tabular forms a transverse suture with the supratemporal. It has a short suture with the squamosal, which points to the centre of the otic notch.

The jugal is a large bone forming part of the lateral margin of the skull, and a small part of the lateral margin of the orbit. Anteriorly, it forms a sharp wedge between the maxilla and the lachrimal. Medially, it forms a slightly concave suture with the prefrontal and then dips into the orbit. Posteriorly, it forms a sharp point between the quadratojugal and the squamosal.

Forming a part of the posterior border of the skull, lateral to the tabular is the squamosal. It tapers anteriorly between the jugal laterally and the supratemporal and postorbital medially. The medial suture of the squamosal slants to meet the antero-lateral corner of the tabular.

The quadratojugal forms the postero-lateral margin of the skull. Medially, it forms a slanted suture first with the jugal and more posteriorly with the squamosal.

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 about 10 cm apart in the posterior one-third of the skull. The long axes are probably parallel. The 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 horn is missing. The skull is badly distorted in this area.

Lateral Line System

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

From the centre of ossification of the postorbital, three sets of canals emerge. They are marked by a clearly distinguishable set of rounded pits, which resemble a chain. The supraorbital canal arises from the postorbital, circles the orbit, crosses the postfrontal and frontal, enters the prefrontal and follows its medial border. It is then lost as damage to the bones is severe.

The infraorbital canal issues from the postorbital anterolaterally, crosses the jugal till it almost reaches the lateral limit of the skull, turns forward and follows the antero-lateral suture of the jugal, enters the lacrimal and then its course is lost.

The temporal canal emerges posteriorly from the postorbital, leads straight across the supratemporal and terminates after entering the tabular.

The jugal canal leads off posteriorly from the infraorbital canal as the latter changes direction anteriorly. It is barely discernable in the remnants of bone present in the area.

<u>The Palate</u> (figs. 4, 6, 8, and 9)

The premaxillae are not preserved.

The vomers join to form a flat plate across the palate, see fig. 6. The vomer flanks the cultriform process of the parasphenoid anteriorly, and widens out more, anteriorly, to form a square flat platform, the vomerine plate, 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 antero-lateral corner of the vomer. The vomers are divided posteriorly by the anterior projection of the cultriform process. This separation extends to about half the length of the plate. The vomers then extend posteriorly on either side of the cultriform process about one-third of the length of the interpterygoid vacuity.

The parasphenoid (figs. 4 and 6) consists of a posterior basal plate and a narrow cultriform process, which divides the interpterygoid vacuities.

The cultriform process of the parasphenoid is quite wide posteriorly, approximately 5.2 cm and the edges curve dorsally. More anteriorly, the edges become developed 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 the medial edge of the interpterygoid vacuity is about 34 cm. The anterior end of the cultriform process lies in the body of the vomer as a finger-shaped depression. As it moves 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 becomes the outwardly directed keel approximately 7 cm from its deepest point (see figs. 4 and 6).

The basal plate of the parasphenoid is bounded laterally by the slanted sutures with the pterygoids (see fig. 9). Posteriorly, the parasphenoid has a short free margin between the exoccipital condyles and then curved sutures with the exoccipitals. The basal plate 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 maxilla on the left side is partially preserved, although severely distorted on the ventral surface. A row of teeth of more or less the same size are present along the outer margin. The maxilla forms part of the lateral limit of the palate. No sutures with the palatine, ectopterygoid and premaxilla have been preserved.

No palatine or ectopterygoid has been preserved, so Howie, 1969, has been followed in the reconstruction. Thus the palatine meets the ectopterygoid (see fig. 4). A second row of teeth parallel to the maxillary teeth occur vertically on the distorted maxilla; these are probably the ectopterygoid and palatine teeth.

Only a very small piece of bone suturing with the parasphenoid remains to represent the body of the pterygoid. No palatal ramus is preserved. The quadrate ramus of the pterygoid is discussed later. The conical recess for the cartilaginous basipteryoid process of the basisphenoid is formed by the medial side of the body of the pterygoid and the antero-lateral part of the body of the parasphenoid. A roughened area on the dorsal surface alongside the parasphenoid suture extending from just anterior to the conical recess to the level of the posterior border of the interpterygoid vacuity is the articular surface for the epipterygoid.

No limits of the subtemporal vacuity have been preserved.

The quadrate extends between the pterygoid and the quadratojugal. This is the articular surface for the lower jaw and consists of a screw-shaped condyle (see fig. 8).

The quadratojugal forms the postero-lateral corner of the palatal surface.

<u>The Occiput</u> (figs 5, 7 and 10)

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

Seen in posterior view, each exoccipital consists of a large round condyle, above which a stout pillar rises to make contact with a ventral extension of the postparietal. The condyle is hemispherical, the diameter of the sphere being about 3.8 cm. Each condyle is surrounded by a raised ridge, probably for the support of a cartilaginous cap. The condyles face inwards and downwards. The pillar of exoccipital bone seen posteriorly, consists of a dorsal process which forms a suture laterally with a descending process of the postparietal; a ventral process which sutures with the parasphenoid postero-ventrally and the pterygoid antero-laterally; a basal process extending medially, which probably covered the cartilaginous basioccipital, and a paroccipital process which extends out laterally and probably dorsally to meet a ventro-medial process of the tabular beneath a post-temporal fossa. (This latter area is not preserved.)

Medially, the dorsal process forms a prominent lamellar process, which probably served to support the cartilaginous supraoccipital. The dorsal process is a pyramidal shape seen clearly in fig. 7, with an anterior triangular face, a postero-lateral, diamond-shaped face and the rhomboidal dorso-medial face (this latter face being the lamellar process). The lateral face of the dorsal process forms the medial border of the post-temporal fossa. There is a channel between the dorsal and basal processes which probably bordered the posterior medulla oblongata region of the brain (Howie, 1969).

The parasphenoid lies below and between the exoccipitals. It forms the floor of the braincase in this area. Posteriorly, the free margin is raised in the midline as the basioccipital crest and forms the ventral surface of the chamber, probably housing the cartilaginous basioccipital.

The postparietal forms the dorsal median border of the occiput. It roofs a space which was probably occupied by the cartilaginous supraoccipital. Lateral to this, the post-parietal sends down a short cylindrical process to meet the exoccipital. The lateral suture with the tabular lies above the post-temporal fossa.

The tabular forms the dorso-lateral corner of the occiput proper, and also the post-temporal fossa. The dorsal part of the bone forms the tabular horn and a thick ventral process of the tabular probably runs ventro-medially to suture with the paroccipital process of the exoccipital and thus form the lateral limit of the post-temporal fossa. (This latter area is not preserved.) Only one ridge of the tabular is preserved.

It protrudes ventrally along the posterior surface of the tabular, forming a suture with the lateral part of the dorsal process of the exoccipital. This ridge probably served for the cleidomastoideus muscle (Howie, 1969).

The squamosal forms the dorsal limit of the skull between the tabular and quadratojugal. The suture between the squamosal and tabular is directed towards the centre of the otic notch. The squamosal sends down a descending flange which forms the dorsal portion of the anterior wall of the stapedial groove. The descending flange of the squamosal is approximately perpendicular to the ventral surface of the dorsal plate of the squamosal. The squamosal has a ventro-laterally directed suture with the supratemporal just anterior to the otic notch, and from this point, the descending flange of the squamosal sutures with the quadrate ramus of the pterygoid to the quadrate. The descending flange of the squamosal becomes larger laterally and forms the entire occipital wall above the quadrate, medial to the quadratojugal.

The quadrate ramus of the pterygoid forms most of the lateral area of the back of the skull, extending from a median suture with the exoccipital to a lateral suture with the quadrate, and from the rounded postero-ventral border of the skull, up to a dorsal suture with the squamosal. The combined pterygoid and squamosal form a wall anterior to the otic notch. The pterygoid in this area develops a strong projecting shelf, the oblique ridge, which forms a trough for the stapes. Its function was probably to protect the stapes from pressure by the m. depressor mandibularis, (Welles and Cosgriff, 1965). There is distortion in this area, see fig. 8.

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. This feature is clearly seen in Specimen A (see fig. 11). It appears, as Howie says, to be a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle.

The quadrate forms part of the dorso-lateral limit of the skull between the pterygoid medially and the quadratojugal laterally. It is overlain dorsally by the squamosal. The screw-shaped quadrate condyle occupies the ventro-lateral corner of the quadrate.

The quadratojugal forms the extreme lateral part of the posterior wall of the skull. It is perforated by the paraquadrate foramen. It is limited by the squamosal dorsally and the quadrate medially and ventrally.

The Braincase (fig. 12)

Such elements of the braincase which 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 intercrestal sulcus is bounded by a ridge,