TABLE IV

STRATIGRAPHY

		SOUTH AFRICA	ZAMBIA	EAST AFRICA
TRIASSIC	Upper	(Cave Sandstone (Red Beds		
	Middle	(Molteno	Red Marls	Manda Formation
	Lower	(Cynognathus zone (Lystrosaurus zone	N'tawere Formation ?Escarpment 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 x 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 and Plate I).

In the type species the snout breadth index (S:L) is 32. For Specimen A this value is 40, and 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 species, which may be due to their larger size compared with the type.

I have the opportunity of studying the almost complete skulls from the Ruhuhu Valley, now in the Cambridge Museum, and confirmed 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 new 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 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, (see figs. 16A and 16B). 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 venture to suggest that Specimen A, was older at death than the type specimen, causing ossification of the cartilage in this fossa.

The opening of the capitosaur jaw 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 (Watson, 1958) by the depressor mandibulae muscle, which inserted on the highest

point of the skull roof.

There are only two 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 occipito-vertebral muscles (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 attachment on the lower jaw being the slight medial inturning 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 capitosaurs were aquatic (the lateral line system and rete vasculosum found in capitosaurs 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 pl[illegible]s 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, the animal must have been totally bouyant. The modern animal with an analagous 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, then when it wants to snap 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 gap 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 capitosaurs preyed in a similar fashion to the crocodile, if there was a depressor mandibular muscle originating on the tabular horn flange and inserting on the roughened area of the retroarticular process, (Watson, 1958), this would mean 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 (see fig. 26). 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 bouyant.

Thus, to summerise, I have employed only one muscle system to open the mouth of capitosaurs, the depressor mandibular muscles, with the assumption that the capitosaurs fed in a similar fashion to the modern crocodile.

SUMMARY

1. I have described capitosaur material collected from the fossiliferous beds of the N'tawere Formation in the Upper Luangwa Valley, Zambia.

2. I have assigned the Capitosaur material to the genus and species Parotosaurus pronus on the basis of the vast 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).

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. Combining points 1, 2, and 3, I have corroborated 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. I have considered faunal units of the relevent horizons and on the assumption that the foregoing is correct, conclude 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 of the same age as the Cynognathus zone.

6. Assuming capitosaurs had a similar life-style to the modern crocodile, and the animals were neutrally bouyant, I have suggested that only the depressor mandibuae muscles were necessary to open the mouth, by lowering the lower jaw.

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LIST OF ABBREVIATIONS USED IN FIGURES

a - angular

aa - auxillary articulatory area

ac - anterior commissure

apv - anterior palatine vacuity

art - articular

bac - basioccipital chamber

bas - basal process

bcr - basioccipital crest

c - coronoid

ch - choana

cm - crista muscularis

con - condyle

cp - cultriform process

crb - conical recess for the basipterygoid process

d - dentary

dor - dorsal process

ec - ectopterygoid

eo - exoccipital

epi - epipterygoid

f - frontal

fad - adductor fossa

fcht - chorda tympani foramen

fm - foramen magnum

fma - anterior Meckelian foramen

fmp - posterior Meckelian foramen

fogl - glenoid fossa

fpsym - postsymphysial foramen

ic - intercoronoid

inl - infraorbital canal

ins - intercrestal sulcus

iv - interpterygoid vacuity

j - jugal

jf - jugalar foramen

jl - jugal canal

la - lacrimal

lam - lamellar process

mx - maxilla

n - nasal

nr - nare

obr - oblique ridge

p - parietal

paf - paraquadrate foramen

pafn - parietal foramen

pal - palatine

par - paroccipital process

parc - parapterygoid crest

pc - precoronoid

pca - internal opening of palatine branch of the

pca - continued internal carotid artery

pf - postfrontal

pmx - premaxilla

por - postorbital

pos - postsplenial

pp - postparietal

ppt - palatine ramus of pterygoid

pra - prearticular

pref - premaxillary foramen

prf - prefrontal

prh - hamate process of prearticular

prprc - precondylar process

prptc - postcondylar process

ps - parasphenoid

pt - pterygoid

ptf - post-temporal fossa

q - quadrate

qc - screw-shaped quadrate condyle

qj - quadratojugal

qpt - quadrate ramus of pterygoid

rae - roughened area for the attachment of the epipterygoid

rfo - ridge marking fenestra ovalis in the dorsal groove of the pterygoid

rp - retroarticular process

sa - surangular

sacc - sulcus accessorius

sf - subtemporal fenestra

smand - sulcus mandibularis

soral - sulcus oralis

sp - splenial

sq - squamosal

st - stapes

stp - supratemporal

sul - supraorbital canal

sym - symphysis

t - tabular

tl - temporal canal

tr - trough for depressor mandibular muscle

v - vomer

ven - ventral process

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 or foramen.
Light regular stipple	- Hollow or depression.
Parallel lines	- Worn broken surface.

LIST OF ILLUSTRATIONS

15. A) Posterior view of left lower jaw of Specimen A.
B) Analysis of posterior view of left lower jaw of Specimen A.

16. A) Postero-dorsal view of left lower ramus of Specimen A.
B) Analysis of postero-dorsal view of left lower ramus of Specimen A.

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

18. Lingual view of posterior end of left lower ramus of Specimen A to show hamate process.

19. Dorsal view of Specimen B.

20. Reconstruction and analysis of dorsal view of skull of Specimen B.

21. Reconstruction and analysis of lateral view of skull of Specimen B.

22. Reconstruction and analysis of posterior view of skull of Specimen B.

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

24. Ventral view of occipital region of Specimen B.

25. Posterior view of occipital view of Specimen B.

26. Semi-diagramatic representation of a suggested mechanism for opening the mouth in Capitosaurs, if the animals are neutrally bouyant.

PLATE I Dorsal view of skull roof of Specimen A.

PLATE II Dorsal view of skull roof of Specimen B.

FIG. 1.

Dorsal view of Specimen A, showing superficial sculpture.

FIG. 1.

FIG. 2.

Reconstruction and analysis of the dorsal view of Specimen A.

FIG. 2.

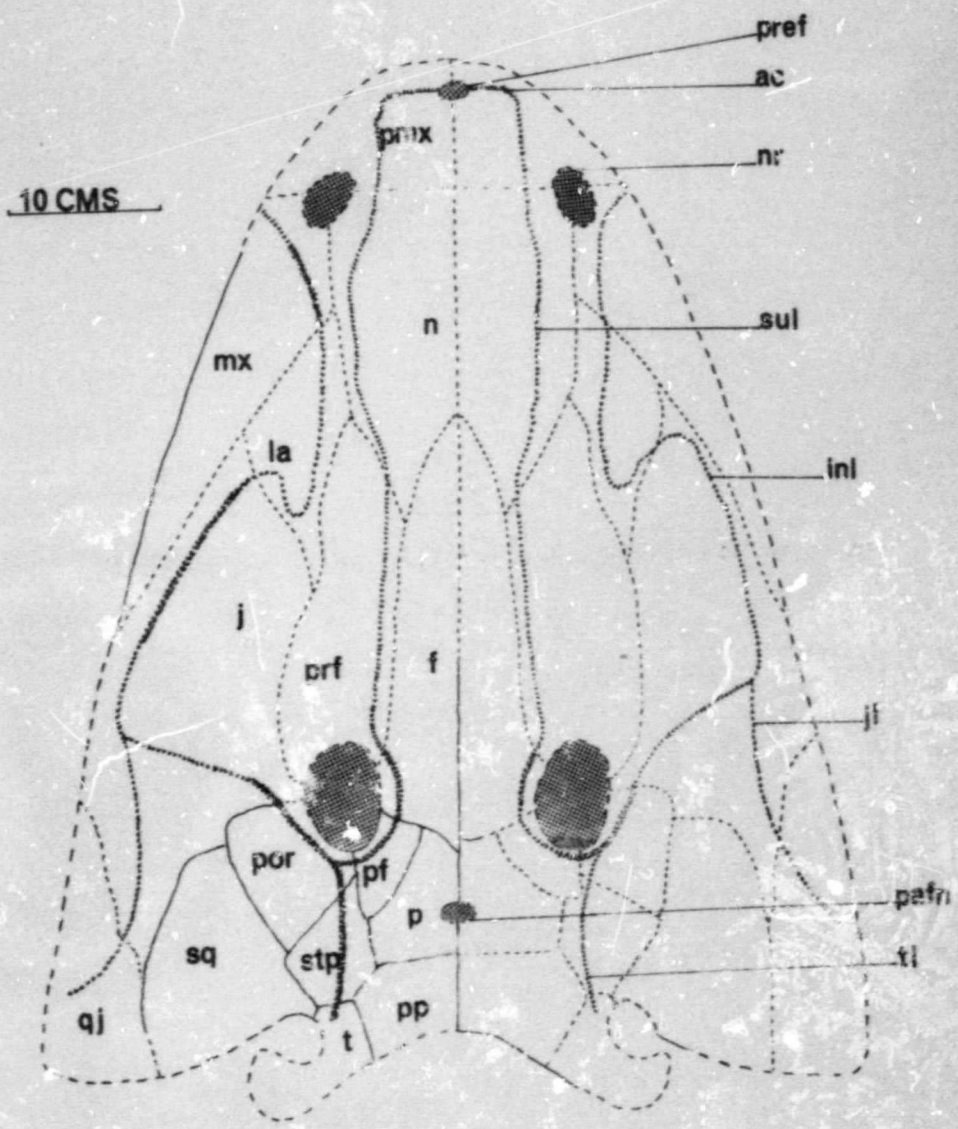
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FIG. 3.

Reconstruction of lateral view of Specimen A.

FIG.3.

FIG. 3.

ction of lateral view of Specimen A.