TABLE III

COMPARISON OF INDICES OF THREE PAROTOSAURS

Indices (Welles and Cosgriff 1965)	Range of Parotosaurs from Table X Welles and Cosgriff, 1965	P. pronus Howie, 1970	P. africanus (Broom) 1909	P. megarhinus Chernin and Cosgriff, 1975
Breadth of skull index B:L	59.3-91	75	?70	73
Interorbital breadth index A:L	11-17	13	?16	11
Interotic breadth index C:L	21.5-42	30	?30	24
Interorbital length to interotic length index A:C	36-56.5	45	46	45
Orbit to otic notch index N:C	42-68.5	43	57	45
Distance behind orbits of parietal foramen index P:C	0-27	8	14	9
Distance of parietal foramen in front of otic notch index T:C	25-50	28	34	28
Concavity index K:C	0-38	30	28	24

2.2 *Kestrosaurus dreyeri* Haughton, 1925

Ann. S. Afr. Mus., 22, 227-261

Type: Incomplete skull and small piece of the right articular region of the lower jaw. S.A.M. Cat. No. 3452.

Locality: Harmonia, Senekal, O.F.S.

Horizon: From a sandstone horizon in the upper part of the Middle Beaufort or *Lystrosaurus* zone.

2.2.1 Diagnosis

A primitive member of the Capitosauridae with a triangular skull (B : L approximately 66); snout narrow (S : L an estimated 32); narrow interotic breadth (C : L approximately 23); posterior skull border straight (K : C = 0); interfrontal present; narrow frontals; broad otic notch; tabular horn projects at right angles to midline; supratemporal has short suture with tabular; paired anterior palatine vacuities; extremely long vomerine plate; palatal rami of pterygoid rugose; short parasphenoid-pterygoid suture; basioccipital present; single vertical exoccipital process; epipterygoid present on occiput; sculpture consists of oblong pits arranged in radiating rows; lower jaw relatively shallow; short retroarticular process.

2.2.2 Description of the material

The Dorsal Skull Roof: (figs. 5 & 6)

The nares: The posterior borders of the nares are curved, thus it is possible to conclude that the nostrils were small, rounded and wholly on top of the snout.

The nasals: The nasals, although incompletely preserved, are large. Anterolaterally, the nasal forms the curved posteromedial border of the nares. Laterally, the suture with the maxilla is almost straight and parallel to the midline. Where the nasal meets the lachrymal, the suture slants slightly medially. Posterolaterally, the nasal meets the prefrontal in a highly sinuous suture which is posteromedially directed. The nasals are separated by the interfrontal which seems to extend further forward than the limit described in Haughton, 1925 p.243. Also in the latter description, the nasal/frontal suture is slanted posterolaterally, but is actually seen to be a highly interdigitated suture transverse to the midline.

The maxilla: The limits of the maxilla are not visible. Anteromedially, it sutures with the nasal in an almost straight suture parallel to the midline. Posteromedially, a small part of the maxilla-lachrymal suture is visible. This suture is very sinuous and posterolaterally directed.

The interfrontal: The interfrontal lies medially between the frontals posteriorly and the nasals anteriorly. The anterior limit is missing.

The lachrymal: The lachrymal lies between the nasal and maxilla anteriorly and the prefrontal and jugal posteriorly. The posteromedial suture with the prefrontal is sinuous and is angled halfway along its length.

The prefrontal: Anteriorly the prefrontal forms a blunt spear-head between the nasal medially and the lachrymal laterally. Both anterior sutures are sinuous. Posteriorly, the prefrontal meets the frontal medially and the jugal laterally in almost straight sutures, running parallel to the midline. The posterior limits of the prefrontal are not preserved.

The frontal: The frontal is much narrower than the prefrontal and anteriorly it sutures with the nasal in a highly sinuous suture transverse to the midline. Anteromedially the frontals are separated by the interfrontal for 5,2cm. Posterior to this position, the frontals meet in the midline, the posterior limits of which are not preserved.

The jugal: The anteromedial suture of the jugal with the lachrymal is preserved. This suture is posteromedially slanted. Medially, the jugal meets the prefrontal in an almost straight suture parallel to the midline. The posterior limits of the former are not preserved.

The tabular: The right tabular horn is almost completely preserved. The posterior skull border is straight (K : C = 0) and the tabular horn projects almost at right angles to the midline and not 45 degrees posterolaterally, as noted in Welles and Cosgriff 1965, p.60. Although the posterolateral border of the tabular is not preserved, it undoubtedly tapers to a blunt point and does not expand to any degree. Anteriorly, the tabular meets the squamosal in a posterolaterally slanted suture. The tabular meets the supratemporal anteromedially and the postparietal posteriorly in posteromedially directed sutures so that the tabular has a similar pattern of sutures in this area as in other parotosaurs, except that the supratemporal-tabular suture is extremely short.

The tabular extends on to the occiput as a thick ventromedially directed process which meets the lateral process of the exoccipital. The suture with the exoccipital is not discernible. The tabular forms the anterolateral border of the triangular posttemporal foramen. The lateral suture with the postparietal is not visible in occipital view.

The otic notch: The otic notch is broad and its anterior and lateral limits are not preserved on either side of the skull but there is indication of a slight constriction at the opening.

The Lateral Line System

Small sections of three lateral-line canals can be seen:

The supraorbital canal: This canal is discernible posteromedial to the right naris where it follows the curvature of the latter and crosses the maxilla-premaxilla suture.

The infraorbital canal: This canal follows the medial suture of the lachrymal before forming the sigmoid loop of the lachrymal flexure. It continues forward to cross from the prefrontal into the nasal where it fades.

The jugal canal: Only a small section is seen on the right side of the skull on a small piece of bone embedded in plaster.

The Palate

The premaxillae: The posterior limits of the premaxillae are not preserved. Two circular anterior palatal vacuities are almost completely preserved.

The vomer: Anteriorly, the suture between the vomer and the premaxiliae is not preserved. However, a small piece of vomer carrying 4 tooth-bases is preserved lying posterior to the anterior palatine vacuities. A very sinuous midline suture bisects this bone. Anterior to the choana, a large tusk is preserved. Posterolaterally to this tusk 3 small tooth-bases lie in a row which is directed in the same plane. Posterior to the tusk lies the large oval choana. The palatine probably sutures with the vomer halfway along its lateral border but this suture is not discernible. The vomer meets the palatine posteromedial to the choana in a suture which starts at the anterior limit of the interpterygoid vacuity and is straight and parallel to the midline anterior to this point; then turns anterolaterally to enter the choanal rim approximately two-thirds down its length. Posteromedial to the choana is part of a row of small tooth-bases which follow the curvature of the choana and continues posteriorly onto the palatine to end at a position just behind the posterior limit of the choana.

Posteriorly the vomer forms the anteromedial border of the interpterygoid vacuity; the suture with the cultriform process of the parasphenoid is not preserved.

The palatine: The anteromedial suture with the vomer slants at the anterior limit of the interpterygoid vacuity and slants anterolaterally to pass through a row of small tooth-bases and enters the choanal rim. Posterolateral to the choana is a large tusk together with a tusk pit. Behind this tusk a row of small tooth-bases passes backwards parallel to the external row of teeth. The posterior suture with the ectopterygoid is not visible.

The pterygoid: Medially the pterygoid meets the parasphenoid in a short, interdigitated and slanted suture. The palatal rami of the pterygoid are narrow compared with the parotosaurs, and lightly sculptured. The anterior sutures with the ectopterygoids are not discernible. The quadrate ramus of the pterygoid is visible in occipital view, and sutures laterally with the quadrate in a curved suture. Dorsolaterally the pterygoid has a short suture with the squamosal and dorsomedially the former sutures with the epipterygoid; dorsomedially, the pterygoid has another suture with the squamosal. The entire dorsal suture is almost straight and transverse to the midline.

The parasphenoid: The cultriform process of the parasphenoid is not well-preserved, but has been reconstructed as being long and narrow.

The parasphenoid plate meets the pterygoids laterally in very interdigitated slanted sutures. The parasphenoid plate is widest posteriorly. The crista muscularis extends across the plate between the ends of the pterygoidal sutures. Posteriorly the parasphenoid forms a free edge between the exoccipital condyles. In occipital view this free edge supports a circular basioccipital bone.

The quadrates: Both quadrate condyles are exposed in palatal view. Each side has two gently rounded projections with a fairly wide groove between them. In occipital view, the quadrate forms the ventrolateral corner of the occiput. Just dorsal to the quadrate condyle is a groove in which lies the paraquadrate foramen. This foramen is on the quadrate-quadratojugal suture. Dorsal and medial to the foramen the quadrate-quadratojugal suture slants dorsomedially. The quadrate then meets the squamosal in a ventromedially slanted suture. Medially, the quadrate sutures with the pterygoid in a curved suture convex to the midline.

The Occiput

The basioccipital: This is a small, almost circular bone lying on the hollowed dorsal surface of the parasphenoid. It lies between the parasphenoid and a bridge of bone joining the exoccipitals which forms the floor of the foramen magnum.

The exoccipital: The exoccipital condyles are convex, with lateral and ventral ridged edges. Laterally, the exoccipital meets the pterygoid in a straight suture parallel to the midline, while the exoccipital meets its neighbour by means of a bridge of bone which lies above the basioccipital and forms the floor of the foramen magnum. The exoccipital has two dorsal processes. The medial process is not expanded as in the parotosaurs and meets the ventral process of the postparietal. The suture between the postparietal and exoccipital is not discernible. The lateral dorsal process of the exoccipital meets the ventral process of the tabular. This suture is also not visible. The two dorsal processes form the postero-ventral border of the posttemporal fenestra. On the lateral margin of the exoccipital just dorsal to the condyle lie two foramina, the larger for the opening of the Xth nerve and the smaller for the hypoglossal nerve.

The epipterygoid: The epipterygoid lies between the squamosal and the pterygoid as a long, low ridge of bone being thin laterally and thickening medially.

The squamosal: The squamosal forms most of the dorso-lateral part of the occiput. It has a short suture with the pterygoid ventrolaterally and then meets the epipterygoid in an almost straight suture, transverse to the midline. The squamosal sutures medially and ventrally with the pterygoid in a straight suture transverse to the midline.

The quadratojugal: The quadratojugal forms the dorsolateral corner of the occiput. It has a wavy suture with the quadrate ventrally which passes through the paraquadrate foramen and then slants dorsomedially. The quadratojugal meets the squamosal in a ventromedially directed suture.

The Lower Jaw

Only the posterior part of the right lower jaw is preserved. The dimensions of this region are far less robust than would normally be expected for a skull of this size and length. In Table X comparisons are made with two parotosaurs with similar skull lengths. The jaw of Kestrosaurus is almost 50% smaller than those of the parotosaurs.

The glenoid fossa: The glenoid fossa is a smooth, transverse rectangular groove 3,2cm wide which slants slightly downward on the labial side. This fossa was presumably formed by the articular whose exact limits are not preserved.

The adductor fossa: This is very narrow and thins to a sharp corner posteriorly. This shape could be due in part to distortion.

The prearticular: From the anterodorsal border of the chorda tympani foramen a suture runs anteriorly. This is the prearticular-articular suture, the articular presumably forming the groove and median part of the missing hamate process and the prearticular forming a flange both lingually and medially of this process. The prearticular probably occupied all of the median edge of the adductor fossa.

From the posteroventral rim of the chorda tympani foramen, the prearticular meets the surangular in a suture which is sharply angled. The prearticular also meets the angular in an almost straight suture parallel to the main axis of the jaw.

The surangular: The surangular forms the dorsoposterior and lingual surface of the retroarticular process. In lateral view the surangular-angular suture is visible in part as it runs along the groove of the sulcus mandibularis. Two small foramina probably for blood vessels lie in a smooth groove which is slanted laterally to the main axis of the jaw. This groove is also found to a lesser extent in P. dirus in the same relative position. Two foramina are found on the anterodorsal surface of the trough of the retroarticular process in P. dirus. The surangular probably formed the entire wall of the adductor fossa. Anterolateral to the precondyloid process is a rectangular foramen which slants anterodorsally; this is continuous with another foramen seen on the medial surface of the labial wall of the adductor fossa. This latter foramen of which only the circular ventral rim is preserved, lies on the opposite side of the jaw to the prearticular fossa (Howie 1970, fig.7). The surangular forms the postcondylar process which forms the posterior limit of the glenoid fossa and is on a lower level than the precondyloid process. This latter process is a low ridge which forms the posterior limit of the adductor fossa. From the postcondylar process, the dorsal border of the jaw slopes sharply downward so that the retroarticular process is very short. The trough for the adductor mandibular muscles lies on the lingual side of the retroarticular process.

The angular: The angular forms the posteroventral surface of the jaw both labially and lingually. The ventral surface of the angular curves gently upward at its posterior limit so that the shape of the retroarticular process seen labially is that of a blunt arrowhead. The angular-surangular suture is seen in part sloping posterodorsally as it follows the groove of the sulcus mandibularis. It is lost posterior to the position of the postcondyloid process. It is unlikely, however, that the angular plays any part in the construction of the trough.

The lateral line canals: Three sets of canals are preserved on the labial surface of the surangular. These are the sulcus accessorius, the sulcus mandibularis which curves upwards to end in a position just lateral to the postcondylar process , and from a point ventral to the midlength of the glenoid fossa, the sulcus oralis which branches out anteriorly from the sulcus mandibularis parallel to the more dorsal sulcus accessorius.

2.2.3 Discussion

This was the first capitosaur described from South Africa (Haughton 1925). The skull was found in a weathered condition, palate upwards in a sandstone band or horizon at a slightly higher elevation than the one at Senekal which yielded Uranocentrodon senekalensis (Van Hoepen, 1917). The sculpture of K. dreyeri is interesting in that it seems to represent an intermediary stage between U. senekalensis and the more advanced parotosaurs such as Parotosaurus haughtoni (Broili and Schroeder, 1937). In the more advanced parotosaurs, the sculpture consists of rounded ridges and broad grooves which radiate out from the centres of ossification of individual bones. Cross bars are found in older individuals between the ridges, forming oblong depressions surrounded by high walls. Where growth is slow (or in older individuals) the development of the cross-bars seem to be able to keep pace with the growth of the various skull bones and the sculpture consists mainly of pits. Thus the central area of each bone carries a sculpture of small irregular pits and on the larger bones of medium and large-sized skulls, this central region is surrounded by radiating ridges and grooves. In the Rhinesuchidae and in the Uranocentrodontidae, the sculpture consists entirely of pits surrounded by walls with rounded crests. This sculpture occurs without variation on all bones in skulls of varying size (and age). In *Kestrosaurus dreyeri*, the sculpture on the anterior roof of the skull consists of radiating grooves with many cross-bars giving the bone a pitted appearance as in the family Rhinesuchidae, but in the latter family, the pits are not organized in rows as in *K. dreyeri*.

Kestrosaurus has an elongated vomerine plate which is characteristic of the Trematosauridae. However, *Parotosaurus haughtoni* (Broili and Schroeder, 1937) from the *Cynognathus* zone also has a long vomerine plate. Both genera have extremely narrow skulls when compared with most other parotosaurs.

The presence of an interfrontal in *Kestrosaurus*, a trematosaur character, is unique among the parotosaurs. One is present for example in *Trematosuchus sobeyi* (Haughton, 1915) from the *Cynognathus* zone.

Kestrosaurus has paired anterior palatal vacuities unlike *Parotosaurus* but similar to *Trematosuchus sobeyi*.

Kestrosaurus displays four characteristics which are primitive but can be found in several species of *Parotosaurus*. These are (1) the short pterygoid-parasphenoid suture (trematosaurs display an exceedingly long parasphenoid-pterygoid contact which is not found in the capitosaurs until the later Triassic); (2) the sculptured palatine ramus of the pterygoid; (3) the open otic notch; (4) the posterior position of the quadrate (all trematosaurs have the quadrates posterior to the exoccipitals).

The other two characters in *Kestrosaurus* which are primitive in comparison to all temnospondyls are an ossified basioccipital and the presence of the epipterygoid on the occiput.

A small part of the posterior end of the right jaw ramus is preserved which seems to be exceptionally small. The height from the ventral surface of the jaw to the floor of the glenoid fossa is 4,8cm and the length from the posterior limit of the glenoid fossa to the end of the retroarticular process is only 4,4cm; the greatest width of the retroarticular process is 3,2cm. This is highly unusual for a specimen whose skull length is estimated at approximately 60cm. In fact, the skull as a whole is distinctly less robust than that of the known parotosaurs.

Primitive characters, not seen in either of the more advanced parotosaurs or the trematosaurs, are displayed in what is preserved of the ramus. In Trematosaurus kannemeyeri Broom, 1909 the posterior part of the jaw is deep and there is a very highly developed retroarticular process. Watson (1962) noted the trend towards increased size and complexity of the retroarticular process in the capitosaurid lineage, while Nilsson (1944) mentions that this trend is shared in parallel degrees by various lineages of the temnospondyls. Watson (1962) relates the increased length and massiveness of the retroarticular process with the progressive flattening of the skull as a whole - which is contrary to the evidence in Kestrosaurus. Watson believes that the retroarticular process was important because it gave attachment to muscles whose contraction raises the upper jaw, whilst the lower rested on the ground.

Thus, not only the small size, but the lack of complexity of this portion attests to its primitive nature.

Kestrosaurus remains an enigma. Welles and Cosgriff (1965, Table 3 p.132) retain this genus in the family Capitosauridae with the comment that it is aberrant and has so few characters relating it to other members of the family that it probably belongs in another family.

In the foregoing description, some new morphological characters are described, none of which, however, clarify the state of confusion with regard to the taxonomy, thus Kestrosaurus is tentatively left in the family Capitosauridae.

Kestrosaurus may belong in an evolutionary series as follows:

Rhinesuchidae
Uranocentrodontidae
Kestrosaurus dreyeri
Parotosaurus haughtoni

The last species resembles Kestrosaurus superficially, but is more advanced and is a 'true' parotosaur. The sculpture and other characteristics seem to agree with this hypothesis.

Kestrosaurus also shares some characters diagnostic of trematosaurs, i.e. the long vomerine plate and the presence of the interfrontal.

There are indications of a very delicate and frail lower jaw relative to the size of the skull. Compared with P. megarhinus and P.dirus who have similar skull lengths, the jaw proportions of Kestrosaurus are 50% smaller. See Table III.

Because the taxonomy of the capitosaurs is in a confused and unreconciled state, the enigmatic Kestrosaurus is retained in the Family Capitosauridae as was originally suggested by Welles and Cosgriff, (1965).

2.3 Parotosaurus dirus sp. nov.

Type: S.A.M. Cat. No. K434

Locality: Aliwal North, North-eastern Cape Province, South Africa

Material: Fragments of a lower jaw

Collected by: South African Museum Expedition

2.3.1 Diagnosis

A large parotosaur with three rows of symphysial teeth; medial symphysial tooth row bears two large tusks and two large hemispherical replacement pits; teeth posterior to symphysis medium-sized, orientated both dorsally and lingually with medium-sized replacement pits; not regular and widely spaced: precoronoid forms a thickened ridge bearing teeth; hamate process has no lingual projection dorsally; ventral limit of retroarticular process straight; long retroarticular process which slopes posteroventrally at 45° angle; transverse articular area present, lying lingual to main trough of retroarticular process just posterior to postcondylar process; coronoid extends to posterolateral region of adductor fossa; dorsolingual border of adductor fossa anterior to hamate process drawn out to form ridge; glenoid fossa forms two articular facets separated by a low ridge; the lingual half of the postcondyloid process expanded to form large hump; sculpture represented by thin high ridges separated by deep broad grooves; lateral to retroarticular region sculpture consists of very deep pits; lateral line canals converge to depression in sculpture.

2.3.2 Description of material (figs. 7-9)

The fragments were prepared by means of a vibrotool. From the texture of the bone, it is evident that at some stage acid had been employed in an attempt to prepare the material. Of the number of pieces collected, only three are of morphological interest: the left and the right anterior symphysial regions which join medially and the posterior portion of the right ramus, the left ramus having lost most of the hamate and articular processes.

The Symphysial region: (fig. 7a)

At the symphysis three rows of teeth are borne by the dentary. The suture between the dorsal dentary and the ventral splenial is not clear. The length of the right anterior portion of the jaw measures 26cm. and the left 17cm. The breadth across the two fragments at the position of the posterior edge of the symphysial region when joined measures 20,5cm.

The labial row of teeth at the symphysis has tooth-bases that seem to be of the same size as the rest of the outer tooth row; the middle row consists of two large tusk-bases and two pits, each tusk-base and pit measuring 5,3cm across and approximately 2,8cm antero-posteriorly. The whole of the lingual tooth row consists of 6 tooth-bases and 6 replacement pits. The lingual row of teeth measures approximately 9cm. as compared with the measurement of 11cm. for both the medial tusks and pits. Two levels of teeth are present in the lingual row, a dorsal series with the teeth facing inwards or lingually and a ventral series where the two outer teeth face lingually and the two medial teeth dorsally.

The mid-line length of the symphysial region is approximately 8cm. Posterior to the symphysis on both portions, the labial tooth row becomes an irregular series of large tooth-bases and replacement pits. This arrangement contrasts with the regular row found in *P. megarhinus* and *P. pronus*. This is probably due to an adaptation to the size and nature of the prey of *P. dirus*.

TABLE IV

Table of Comparison of Measurements of the lower jaws of Parotosaurus megarhinus, Chernin and Cosgriff 1975; Kestrosaurus dreyeri, Haughton 1925 and Parotosaurus dirus sp. nov.

	P. megarhinus cms.	K. dreyeri cms.	P. dirus cms.
(1) Width of retroarticular process posterior to postcondylar process	5	3.1	5.5
(2) Total breadth of glenoid fossa	5.3	3.2	6.5
(3) Distance from ventral surface to floor of glenoid fossa	9.6	4.8	8
(4) Distance from posterior limit of glenoid fossa to end of retroarticular process	6.8	4.4	9.6
(5) Greatest width of retroarticular process	5.5	3.2	5.6

The mid-line length of the symphysis of P. megarhinus is 3,5cm. and the entire configuration of this area is completely different. In P. megarhinus the breadth of the ramus remains constant from a position 10cm. posterior to the anterior edge of the jaw to the symphysis, whereas in P. dirus it expands from 4,9cm. to 9cm. in the same relative positions.

The labial row of teeth at the symphysis is similar in both animals. The teeth are set at right angles to the curve of the ramus, but the teeth of P. dirus are larger, measuring 2,0cm. at the base compared to 1,6cm. in P. megarhinus.

With regard to the medial row of teeth in P. megarhinus, there are no replacement pits of the hemispherical nature like those in P. dirus. The maximum breadth across the tusks of P. megarhinus is approximately 7cm., as compared with 11cm. in P. dirus. The lingual row of teeth in P. megarhinus is not as conspicuous as that of P. dirus. On either side only two small tooth-bases are visible, facing lingually, just postero-lateral to the medial tusks.

Posterior to the symphysis, the teeth of P. megarhinus are similar to those on the labial symphysial region, lying transverse to the curvature of the ramus, facing dorsally with small replacement pits set at irregular intervals.

The precoronoid:

On the left side the precoronoid forms a conspicuous ridge of bone 6cm. long on the lingual side of the jaw approximately 5cm. posterior to the lingual row of symphysial teeth. This ridge expands to a thickness of 1,8cm. and 4 tooth-bases are confined to the thickened area. These teeth face dorsally. On the right side of the ramus, the ridge is visible but badly damaged and only 3 tooth-bases are barely visible. The sutures on the left ramus are clear. Anteriorly, and immediately posteroventrally to the lingual row of symphysial teeth, the precoronoid is an almost triangular wedge of bone. The dorsal suture slants upwards and approximately 3cm. posterior to its anterior limit, the bone thickens to form the above mentioned tooth-bearing ridge. This ridge is thickest approximately 7cm. posterior to its anterior limit. Posterior to this thickened area, the bone flattens approximately 10cm. from its anterior limit and the dorsal suture of the precoronoid slants gradually in a posteroventral direction until it reaches the edge of the broken-off portion.

The precoronoid ridge is absent in P. megarhinus and the precoronoid is completely fused with the dentary. It reaches almost to the dorsal surface of the jaw from where it slants gently anteriorly, while in P. dirus it slants almost abruptly downwards in the same region.

The articular region: (figs. 8a, 9b, 9d)

The posterior part of the right ramus measures 20cm. in length. Few sutures can be traced in the fragment due to the fusion of the bones which could probably be attributed to the advanced age of the animal at death.

Seen dorsally, part of the coronoid bone is seen on the inner surface of the lateroposterior part of the adductor fossa. The suture with the outer surangular is clear as the two bones are slightly separated by matrix filling the intervening space.

In the adductor fossa of P. megarhinus, the posterior limit of the coronoid lies 5,2cm. anterior to the posterior border of the fossa.

When the posterior ramus region of P. dirus is viewed lingually, the suture between the prearticular and the surangular can be traced from the base of the hamate process ventrally through the chorda tympani foramen. The latter is oval, measuring 1,2cm. by 0,6cm. with its long axis facing anterodorsally, and is the internal opening of the nervus chorda tympani. The chorda tympani foramen lies in a depression 4cm. long by 3cm. wide, the mid-length of which is immediately lateral to the precondyloid process, with the foramen lying anterior to this position.

Beneath the above-mentioned foramen, the prearticular surangular suture continues vertically until it meets the angular. The latter sutures with the prearticular in a curved horizontal suture where visible. The angular-surangular suture runs posteriorly in a sinuous horizontal line which cannot be traced to the end of the retroarticular process.

From the dorsal limit of the prearticular-surangular suture, as seen lingually, a suture runs upwards along the dorsolingual border of the hamate process. The groove of the prearticular is thus composed of an extension of the articular with the prearticular forming a flange on either side of it. The medial wall of the adductor fossa is thus formed by part of the prearticular.

In describing the fragment from back to front: the length of the retroarticular process measured from the anterior edge of the postcondyloid process measures 9,3cm. The width of the retroarticular process measured immediately posterior to the postcondyloid process is 5,5cm. The trough for the abductor muscles is visible lying within the retroarticular process which has a downward slope of approximately 45°. This trough lies on the labial half of the retroarticular process when seen dorsally. Lingually there is a smooth-edged groove with a labial-lingual axis. This smooth-edged area lies posterior to the large lingual hump of the postcondyloid process. The posterior limit of the retroarticular process is bluntly rounded and its ventral limit almost straight, curving upward only at the very end. The ventral and dorsal aspects combine in an almost complete triangle.

This type of retroarticular process is best exemplified by Cyclotosaurus robustus Quenstedt 1850, in which the process is low relative to the long axis, with the lower border being straight. Contrasted to this type of process, is that exemplified by Parotosaurus peabodyi Welles and Cosgriff, 1965; Parotosaurus pronus Howie, 1970; Parotosaurus megarhinus Chernin and Cosgriff 1975, and Paracyclotosaurus davidi Watson, 1958 in which the retroarticular process is set high relative to the long axis of the lower jaw and has a rounded lower border. In front of the trough the postcondylar process rises,seen dorsally; this process is not straight but is concave anteriorly on either side and convex anteriorly in the centre. The whole upper limit is smoothly rounded. Lingually, the process is enlarged anteroposteriorly to form the lingual hump mentioned above.

Anterior to the postcondylar process lies the glenoid fossa whose lingual to labial limits extend 6,3cm. The greatest anteroposterior width of the glenoid fossa measures 2,3cm. The articular forms the glenoid fossa which is pitted and characteristic of a cartilaginous bony structure. The fossa is rectangular and articulates with the quadrate condyle. The articular was probably bound laterally, anteriorly and posteriorly by the surangular and medially by the prearticular. The glenoid fossa is a broad groove, transverse to the long axis of the jaw, which is continued lingually by the roughened posterior face of the hamate process of the prearticular. The inner half of the glenoid fossa is more elongate than the outer half, being a capitosaurid character mentioned by Watson (1962). Between the inner and outer halves of the glenoid fossa is a well defined low and narrow ridge.

In front of the glenoid fossa, the precondyloid process rises upwards to form the posterior limit of the adductor fossa. The prearticular probably occupied most of the median edge of the adductor fossa. Posteromedially to the adductor fossa, the prearticular rises to form the large hamate process which reaches a height of 9cm. measured from the 'floor' of the glenoid fossa. The total depth from the top of the hamate process to the ventral surface of the jaw measures approximately 16cm. Along the lingual and dorsal border of the adductor fossa and from the hamate process anteriorly a distinct ridge is present. In P. megarhinus this border is smoothly rounded.

The hamate process of P. dirus is transversely thickened and forms a trough posteriorly surrounded by smooth walls dorsally, laterally and medially. The entire hamate process resembles the shape of a right hand thumb seen from above and the texture of the bone of the trough suggests an extensive cartilaginous cover in life. This surface presumably represents an accessory articular surface which lies immediately anterior to the inner part of the glenoid articulation. Howie (1970) suggests that the hamate articulatory area met a roughened region on the pterygoid, thus elongating the latter area between the lower jaw and the skull. The hamate process seems to be characteristic of the Capitosauridae although developed to an extreme in P. dirus, P. pronus and P. megarhinus.

In P. peabodyi Welles and Cosgriff, 1965 the upper border of the prearticular produces a high sharp process, in contrast to the rounded limits of P. pronus, P. megarhinus and P. dirus.

In P. megarhinus, the upper part of the hamate process turns lingually almost 90 degrees from the vertical.

The surangular in P. dirus probably formed most of the dorsoposterior labial surface and retroarticular process. It may also have formed the labial wall of the adductor fossa. The external foramen for the nervus chorda tympani is present on the labial surface just lateral to the precondyloid process.

Sculpture and Lateral line system

Seen labially, the sculpture pattern and lateral line system is as follows: The sulcus mandibularis slants from a ventral position 18cm. in front of the posterior edge of the jaw to a dorsal position 7,5cm. below the precondyloid process. Above the latter canal, a continuous groove is visible which may be a second canal. This canal parallels the ventral canal and lies just dorsal to a very high ridge marking the dorsal border of the ventral canal. The two canals converge to a large oval depression in the sculpture, which lies transverse to the long axis of the jaw measuring 2cm. by 2,5cm. This depression lies well below the precondyloid process. From this depression another canal, the sulcus oralis, emerges and slants anterodorsally. With regard to the remainder of the sculpture pattern in the posterior portion of the jaw, the ridges are thin and high with deep, broad grooves between them. There are deep pits in the posterior region dorsal to an unsculptured area; in P. megarhinus the area is only lightly sculptured. The ventral and posterior part of the angular of P. dirus is not sculptured, nor is the dorsal surface anterior to the postcondyloid process.

In P. megarhinus, the ventral and single sulcus mandibularis curves from a ventral position 17cm. anterior to the posterior edge of the jaw to a dorsal position 1,2cm. posterior to the postcondylar process. The curvature of the canal runs parallel to the posterior curve of the retroarticular process. The sulcus oralis meets the sulcus mandibularis 5cm below the mid-length of the glenoid fossa and no depression is visible at this junction.

The general sculpture pattern is similar in P. dirus and P. megarhinus, in that neither the ventral posterior part of the angular is sculptured, nor is the dorsal area anterior to the postcondyloid process.

Seen labially, the sculpture at the anterior end of both jaw rami is similar in that the dentary is quite smooth while the splenials are sculptured with ridges and grooves. However, in P. megarhinus, the ridges are wide and rounded and the grooves are slender, deep indentations, whereas in P. dirus the ridges are thin, high and the grooves are broad and deep. In both animals the sulcus mandibularis runs along the length of the ramus between the sculptured ventral region and the smooth dorsal region.

2.3.3 Discussion

The robust size and peculiar hamate process of P. dirus make a comparison with P. megarhinus inevitable. The two jaws seem to be superficially alike but there are substantial morphological differences as pointed out above. In size, P. dirus is also approximately 10% larger than P. megarhinus. This approximation is taken from the following measurements:

	P. megarhinus cm.	P. dirus cm.
1. Width of retroarticular process posterior to postcondylar process	5	5,5
2. Total breadth of glenoid fossa	5,3	6,5
3. Height of hamate process from base of glenoid fossa	8,3	9
4. Total height of hamate process from ventral jaw surface	13,5	16

Thus it seems evident that although the jaw of K434 is undoubtedly capitosaurid, it shows characters which indicate differences at least at specific level.

In Southern Africa, three capitosaur jaws show the large finger-shaped hamate process: *P. pronus* Howie, 1970, p.219; *P. megarhinus* op. cit. and *P. dirus*.

P. pronus seems to be closely related to P. megarhinus by displaying the following similarities in the lower jaw morphology:

1. In *P. pronus* the hamate process turns lingually in the same manner as in *P. megarhinus*, while in *P. dirus* it faces dorsally.
2. The ventral limit of the retroarticular process curves upwards, as in *P. megarhinus*; in *P. dirus* it is almost straight.
3. When viewed lingually, the retroarticular process of *P. pronus* follows a smooth curve as in *P. megarhinus*, unlike that of *P. dirus* where it forms a triangle.

In one detail *P. pronus* differs from both *P. dirus* and *P. megarhinus*, namely in possessing a prearticular fossa which is listed as one of its diagnostic features. This fossa which has not yet been described in other parotosaurs, is found on the medial surface of the hamate process. In *P. dirus*, a small prearticular foramen is found on the lingual surface approximately 3,5cm. anterodorsal to the chorda tympanic foramen. This is not comparable with the fossa in *P. pronus*, which is situated on the opposite side of the hamate process.

P. dirus is less advanced than both *P. pronus* and *P. megarhinus*. Not only is the retroarticular process of *P. dirus* less complicated, but the configuration of the symphysial region bears superficial resemblance to the palatal and lower jaw regions of the Rhinesuchidae, where the 3 rows of teeth are mirrored in '*Muchocephalus muchos*' Watson, 1962 and B.P.I. No. 771, an unidentified - but undoubted - member of the Permian Rhinesuchidae.

In *P. dirus* this thus indicates a closer relationship with the Rhinesuchidae than either *P. megarhinus* or *P. pronus*, which stratigraphically correlates with the position suggested by Chernin and Cosgriff, 1975.

P. megarhinus from Locality 15, N'tawere Formation, Upper Luangwa Valley, Zambia is believed to be Middle Triassic while the *Cynognathus* zone is considered to be Early-Middle Triassic.

Kitching,(May 1963) and Drysdall and Kitching,(November 1963) state that the N'tawere Formation is later than the *Cynognathus* zone and correlates with the Manda Beds. P. pronus from the latter beds of the Ruhuhu Valley, Tanzania, is thus more or less of the same geological age as the N'tawere Formation.

P. megarhinus thus seems to be more advanced than P. dirus and is probably adapted to smaller and less aggressive prey than was P. dirus.

2.4 Summary and Conclusions

1. Three specimens of the family Capitosauridae have been described, one for the first time.
2. Parotosaurus africanus Broom is a valid taxon comprising most of the posterior part of a well-preserved skull and a fragment of lower jaw.
3. Kestrosaurus dreyeri Haughton, is an unusual and primitive member of the family Capitosauridae with some trematosaurid characters which may be an adaptation to a fast-swimming, fish-eating habitat.
4. A very large fragmentary Capitosaurid jaw from Aliwal North in the Cape Province is ascribed to Parotosaurus dirus sp. nov. This is believed to be closely related to Parotosaurus pronus Howie, and Parotosaurus megarhinus Chernin and Cosgriff, and probably ancestral to both.

3. THE FAMILY BRACHYOPIDAE

In the following paragraphs *Batrachosuchus concordi* sp. nov. from the Upper Luangwa Valley, Zambia is described. Also, *Batrachosuchus browni* Haughton is redescribed as the type specimen has been further prepared revealing more detail and some new characters.

3.1 *Batrachosuchus concordi* sp. nov.

Holotype: BPI Cat. No. F3728. Imperfect skull, lower jaws and some postcranial material

Locality: The N'tawere Formation, Upper Luangwa Valley, Zambia. Locality 15 (Drysdall and Kitching, 1961)

Horizon: ? Lower Middle Triassic

3.1.1 Diagnosis

Small *Batrachosuchus* with skull narrower than *B. browni* and much narrower than *B. watsoni*; interorbital breadth very much narrower than both *B. browni* and *B. watsoni*; shorter preorbital length than both *B. browni* and *B. watsoni*; orbit slightly smaller than *B. browni*; postorbital length greater than *B. browni*, but shorter than *B. watsoni*; interpterygoid vacuity shorter than *B. browni* and much shorter than *B. watsoni*; interpterygoid vacuity narrower than both *B. watsoni* and *B. browni*; distance of parietal foramen in front of end of skull table greater than *B. browni* (T : L = 23) and *B. watsoni* (T : L = 23), (*B. concordi* T : L = 37); lateral line canals weakly defined; parasphenoid extends to basal limit of skull; exoccipital does not reach as far posteriorly as in either *B. watsoni* or *B. browni*; a lingual process of the angular is present.

3.1.2 Stratigraphy (see Table VI)

This specimen was collected from the Upper Horizon of the N'tawere Formation by Drysdall and Kitching in 1961. The fossiliferous beds of their Locality 15 consist of dark red, soft mudstones with characteristic feldspathic grit bands, containing angular vein-quartz fragments. The N'tawere Formation contains two fossiliferous zones, the lower with *Diademodon*, and an Upper (Red Marl) horizon which includes Locality 15. Towards the base of the beds, amphibians and molluscs are present. The molluscs have been identified as *Unio karrooensis* by 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 is a Scalenodon-like form resembling material described by Crompton (1955) from the Manda Beds of Tanganyika.

The author has previously described two large capitosaurs from Locality 15 (Chernin and Cruickshank 1970; Chernin 1974; Chernin and Cosgriff, 1975) which were assigned to the species Parotosaurus megarhinus. This species is very similar to P. pronus (Howie, 1970) but distinct from it and perhaps somewhat stratigraphically older. P. pronus was collected from Mkongoleko, Ruhuhu Valley, Tanzania in the Manda Formation of East Africa (Middle Triassic) by Parrington, 1933.

Welles and Estes (1969) state that comparison of certain indices obtained by measuring the brachyopids, show trends which are probably indicative of the relative evolutionary level of the various genera. Of the 10 values obtained for the indices of B. concordi , one is more advanced than that of the Cynognathus zone batrachosuchians as given by Welles and Estes (the author has included her own values obtained by measurement of B. browni; Welles and Estes 1969 indices appear in parenthesis) :

U : L =	23	-	B. watsoni
	23	-	B. browni (24)
	25	-	B. concordi

Two values lie between the other species:

Q : R =	31	-	B. watsoni
	27	-	B. browni (26)
	30	-	B. concordi
D : L =	58	-	B. watsoni
	50	-	B. browni (55)
	57	-	B. concordi

Five values are more primitive than the other two species:

B : L =	149	-	B. watsoni
	120	-	B. browni (133)
	118	-	B. concordi
A : L =	46	-	B. watsoni
	45	-	B. browni (43)
	28	-	B. concordi

O : L =	25	-	<u>B. watsoni</u>
	24	-	<u>B. browni</u> (21)
	17	-	<u>B. concordi</u>
Y : L =	53	-	<u>B. watsoni</u>
	50	-	<u>B. browni</u> (49)
	46	-	<u>B. concordi</u>
Z : Y =	56	-	<u>B. watsoni</u>
	66	-	<u>B. browni</u> (55)
	52	-	<u>B. concordi</u>

Finally two values are so much more advanced as to be out of the range of the Brachyopidae as considered by Welles and Estes:

P : A =	69	-	<u>B. watsoni</u>
	55	-	<u>B. browni</u> (55)
	80	-	<u>B. concordi</u>
T : A =	49	-	<u>B. watsoni</u>
	55	-	<u>B. browni</u> (53)
	107	-	<u>B. concordi</u>

The latter two values are the result of the interorbital breadth being so small in <u>B. concordi</u> . This could be a juvenile feature (no growth series of the brachyopidae is available for study). However, taking the other indices as evolutionary guides, it seems that <u>B. concordi</u> is more or less on the same level as the <u>Cynognathus</u> zone forms. Welles and Estes (1969) place the batrachosuchians between Early and Middle Triassic. This confirms the report that the N'tawere Formation is probably Early Middle Triassic age as stated by Chernin and Cosgriff, 1975. (see Table VI).

3.1.3 <u>Material and Method of Preparation</u>

The material consists of a weathered and badly shattered skull, slightly dorsoventrally compressed with the anterolateral borders missing. Both lower jaw rami are present, the left one being firmly attached to the skull; the right one has been freed. The anterior parts of these are missing. A little of the postcranial skeleton is preserved, including parts of the pectoral girdle and forelimbs.

The skull is badly cracked, making the sutures difficult to discern. The material was prepared by Dr. C. Gow who used a weak acid solution.

TABLE V

COMPARISON OF THE INDICES OF THE GENUS BATRACHOSUCHUS

* Indices	B. watsoni*	B. browni*	B. browni***	B. concordi	From direct skull measurements of B. concordi
B : L	149	133	120	118	107
A : L	41.6	43	45	28	33
O : L	25	21	24	17	9
U : L	23	24	43	25	-
D : L	58	55	50	57	64
P : A	69	55	55	75	80**
T : A	49	53	50	107**	100**
Q : R	31	26	27	30	29
Y : L	53	49	50	46	52
Z : Y	56	55	66	52	50

* From Welles and Estes (1969)

** Out of range of Brachyopsidae as stated by Welles and Estes (1969)

*** As measured in the new reconstruction of B. browni