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THREE CAPITOSAURS FROM THE TRIASSIC OF SOUTH AFRICA: *PAROTOSUCHUS AFRICANUS* (BROOM 1909); *KESTROSAURUS DREYERI* HAUGHTON 1925, AND *PAROTOSUCHUS DIRUS* SP. NOV.

by

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ABSTRACT

Two members of the family Capitosauridae are redescribed after further preparation, namely *Parotosuchus africanus* (Broom 1909) and *Kestrosaurus dreyeri* Haughton, 1925. New material consisting of a fragmentary lower jaw of a very large parotosaur from the *Cynognathus* zone of Aliwal North is described, upon which a new species, *Parotosuchus dirus*, is erected.

Parotosuchus africanus (Broom 1909) from the *Cynognathus* zone of Vaalbank, Albert, Cape Province, is redescribed and figured for the first time. It consists of most of the postorbital regions of the skull associated with part of the left lower jaw which are fairly well preserved and capable of being directly compared with the same parts of other taxa. Thus it is reconfirmed a valid member of the family Capitosauridae.

Kestrosaurus dreyeri is re-examined and found to consist of large areas of plaster of Paris in which the original bone has been embedded. The entire skull could be about 5 cm shorter than the original reconstruction. The position and shape of the orbits are not preserved and the reconstructed lateral position found in the specimen is arbitrary. The parietal foramen is also not preserved. The nature of the preserved palate and occipital area indicates that the material probably represents a primitive member of the family Capitosauridae, not only stratrigraphically (*Lystrosaurus* zone), but also morphologically. The taxonomic designation established by Welles and Cosgriff (1965) is retained. *Kestrosaurus* remains an enigma because it also displays certain trematosaurid characters.

A partial capitosaurid jaw from the *Cynognathus* zone of Aliwal North, Cape Province, is also described which when reconstructed represents one of the largest amphibians found in Southern Africa. Comparisons are made with *Parotosuchus pronus* (Howie 1970) and *Parotosuchus megarhinus* (Chernin and Cosgriff 1975), which share a few similar characteristics. It is suggested that the amphibian represented by this jaw may be ancestral to both *P. pronus* and *P. megarhinus*. Based on substantial morphological differences in the symphysial and articular regions between this jaw and those of the above-mentioned parotosaurs, it is hereby proposed to erect a new species, *Parotosuchus dirus* (dirus = Latin: fearful), for this material.

CONTENTS

INTRODUCTION

The capitosaurs were among the earliest fossil amphibians to be discovered. *Mastodonsaurus "giganteus"* (Jaeger, 1828) from the Lettenkohle of Gaildorf in Germany was the first labyrinthodont to be described. Since then, many new genera and species have been discovered and named. Watson (1962) discussed various evolutionary trends in the morphology of the group, e.g. progressive closure of the otic notch; progressive chondrification (especially noticeable in the neurocranium and limb bones); increase in dorso-ventral flattening of the skull; and an increase in size.

Welles and Cosgriff (1965) revised the group, relegating a large number of generic and specific names to the *nomen vanum* category and reducing the taxonomic content to 3 families, 6 genera and 18 species. The families retained by them within the superfamily Capitosauroidea are the Benthosuchidae, Mastodonsauridae and Capitosauridae. Within the Capitosauridae *Parotosuchus* Paton 1977, has 8 species: *P. nasutus* (Meyer 1858); *P. helgolandicus* (Schröder 1913); *P. haughtoni* (Broili and Schröder 1937); *P. semiclausus* (Swinton 1927); *P. angustifrons* (Riabinin 1930); *P. brookvalensis* (Watson 1958); *P. birdi* (Brown 1933) and *P. peabodyi* (Welles and Cosgriff, 1965). *Cyclotosaurus* has 4 species: *C. robustus* (Quenstedt 1850); *C. stantonensis* (Woodward 1904); *C. ebrachensis* (Kuhn 1932); and *C. hemprichi* (Kuhn, 1942). *Kestrosaurus* has 1 species, *K. dreyeri* (Haughton 1925), and *Paracyclotosaurus* has 1 species, *P. davidi* (Watson, 1958).

Since the revision by Welles and Cosgriff (1965) the context of the family has been enlarged and many changes in its structure have been proposed. Otchev (1966) was responsible for much of this, but his work is not generally available. These alterations and additions, although adding greatly to the knowledge of the morphology, diversity and geographic distribution of the group, have left capitosaurid taxonomy in a confused and unreconciled state. A complete new revision of the superfamily Capitosauroidea is therefore called for, but this is beyond the scope of the present paper, the aim here being the reconsideration of only three members of the Capitosauridae in the following order:

Parotosaurus africanus (Broom 1909) was considered *nomen vanum* by Welles and Cosgriff (1965) as they believed the holotype of this form was too incomplete for meaningful comparisons. The specimen, however, consists of most of the postorbital regions of the skull and part of the left lower jaw which are well prepared and capable of being directly compared with these parts in other taxa.

Kestrosaurus dreyeri Haughton, 1925, is tentatively retained in the Family Capitosauridae, as originally designated by Welles and Cosgriff (1965). It was the first capitosaur to be described from South Africa and has been retained in the Family Capitosauridae by Welles and Cosgriff (1965) notwithstanding the anomalous trematosaurid characteristics apparent in the animal. In addition, the specimen has been reconstructed in plaster of Paris resulting in the orbital position being artificial and the overall reconstructed length being too great by about 5 cm.

Parotosuchus dirus sp. nov. is based on a large capitosaur lower jaw from the *Cynognathus* zone of Aliwal North, Cape Province, R.S.A.

This fragmentary jaw shows a few affinities with the geologically later *Parotosuchus megarhinus* (Chernin and Cosgriff 1975) from Zambia and *Parotosuchus pronus* (Howie 1970) from Tanzania. The most obvious similarity which occurs in all three animals is the buccal projection of the prearticular to form a large hamate process.

Otchev (1966) contributed an extensive consideration and revision of capitosaurid systematics and phylogeny, summarised in Chernin and Cosgriff (1975). A discussion of his treatment of the Superfamily at species level is omitted here as none of it is relevant to a consideration of the Karoo amphibians discussed. The classification of the Capitosauroidea of Otchev (1966) down to generic level is as follows:

Superfamily Capitosauroidea
- Family Rhinesuchidae Watson, 1919
  - *Rhinesuchus* Broom, 1908; *Rhinesuchoides* Broom and Olson, 1937; *? Jugosaurus* Riabinin, 1962.
- Family Uranocentrodontidae Romer, 1947
  - *Uranocentrodon* van Hoepen, 1917; *Laccocephalus* Watson, 1919; *? Muchocephalus* Watson, 1962; *? Gondwanosaurus* Lydekker, 1885; *? Pachygonia* Huxley, 1865.
- Family Rhinecepidae Otchev, 1965
  - *Rhineceps* Watson, 1963.
- Family Lydekkerinidae Watson, 1919
  - *Lydekkerina* Broom, 1915.
- Family Sclerothoracidae von Huene, 1931
  - *Sclerothorax* von Huene, 1931.
- Family Capitosauridae Watson, 1919
  - Subfamily Wetlugasaurinae Otchev, 1958
    - *Wetlugasaurus* Riabinin, 1930; *Sassenisaurus* Nilsson, 1942; *Parotosaurus* Jaekel, 1922; *Karoosuchus* Otchev, 1966; *Watsonisuchus* Otchev, 1966; *Stenotosaurus* Romer, 1947; *Eryosuchus* Otchev, 1966; *Mentosaurus* Roepke, 1930; *Capitosaurus* Münster, 1836.
  - Subfamily Cyclotosaurinae Otchev, 1966
    - *Procyclotosaurus* Watson, 1958; *Cyclotosaurus* Fraas, 1889.
  - Subfamily Paracyclotosaurinae Otchev, 1966
    - *Subcyclotosaurus* Watson, 1958; *Paracyclotosaurus* Watson, 1958; *Austropelor* Longman, 1941; *Stanocephalosaurus* Brown, 1933; *Moenkopisaurus* Shishkin, 1960; *Rhadalognathus* Welles, 1947.
- Family Mastodonsauridae Lydekker, 1885
  - *Heptasaurus* Säve-Söderbergh, 1935; *Mastodonsaurus* Jaeger, 1828; *Promastodonsaurus* Bonaparte, 1963.
- Family Bukobajidae Otchev, 1966
  - *Bukobaja* Otchev, 1966; *Kestrosaurus* Haughton, 1925; *Meyerosuchus* Otchev, 1966.

Family Benthosuchidae Efremov, 1931
Benthosuchus Efremov, 1929; *Yarengia* Shishkin, 1960

In comparing this classification with that of Welles and Cosgriff (1965) many differences will be noted. Among these are the much greater number of previously described genera recognised by Otchev, the addition of new genera and families, the inclusion of the families Rhinesuchidae, Uranocentrodontidae, Lydekkerinidae and Sclerothoracidae in the superfamily Capitosauroidea and the division of the Capitosauridae into subfamilies.

SYSTEMATIC PALAEONTOLOGY

Class Amphibia
Subclass Labyrinthodontia
Order Temnospondyli
Family Capitosauridae

Parotosuchus africanus (Broom 1909),
Synonym *Capitosaurus africanus* Broom 1909
(*Ann: S. Afr. Mus.*, 7, 270–273)

Type: Fragmentary skull and part of left lower jaw, S.A.M. Cat. No. 2360.

Locality: Vaalbank, Albert, C.P.

Horizon: Cynognathus zone.

Hypodigm: S.A.M. Cat. No. 3008 from Winnaarsbaken, Albert, C.P. (complete skull except for dorsal surface — this skull could not be traced in the Museum collection).

Diagnosis

A *Parotosuchus* with a skull of average breadth (B:L approximately ?70) and shallow posteriorly (H:B approximately 17); orbits close together (A:L approximately 16), separated by a shallow depression, well posterior, oval with long axes converging anteriorly; large circular pineal foramen, close to hind border of orbits (P:C = 14); otic notches semiclosed with tabular horns distinctive, expanded distally towards squamosal; supratemporal excluded from otic notch; postorbital not in contact with parietal; posterior skull border concave (K:C = 28); exoccipitals well exposed on palate; pterygoid bears fine sculpturing.

TABLE 1
Measurements of reconstructed skull of *Parotosuchus africanus*

Indices (from Welles and Cosgriff, 1965)		cm
Height of postparietals above parasphenoid	H	3,4
Breadth of skull across quadrates	B	20,0
Estimated length of skull	L	28,5*
Interorbital distance taken at midlength of orbit	A	4,6
Estimated distance from tip of snout to level of anterior edge of orbit	O	19,0*
Distance from level of posterior limit of orbit to level of centre limit of skull	D	6,5
Distance from posterolateral corner of eye to otic notch	N	5,7
Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn	K	2,8
Distance between otic notches	C	10,0
Distance from mid-length of orbit to lateral edge of same side	I	4,6
Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull	P	1,4
Mid-line distance from level of anterior limit of otic notch to parietal foramen	T	3,4

* From reconstruction.

Description of the material

Bones of the skull (figs. 1, 2 and 3). Unless otherwise stated, the left side of the skull is described because it is the better preserved.

Parietal. Anteriorly, the suture between the frontal and the parietal is almost straight transverse to the midline. Laterally, the suture with the postfrontal is first straight and parallel to the midline, so that the anterolateral corner of the parietal forms almost a right angle. Then, the anterolateral parietal-postfrontal suture slants towards the otic notch. The parietal meets the supratemporal posterolaterally in a sinuous suture concave to the midline. Posteriorly, the parietal abuts the postparietal in an almost straight suture transversely to the midline. A circular parietal foramen is situated on the midline almost in the centre of the two parietals.

Postparietal. The postparietal sutures anteriorly with the parietal as previously noted. Anterolaterally, the postparietal sutures with the supratemporal in a posterolaterally slanted suture, while posterolaterally the suture with the tabular slants oppositely in a posteromedial direction. The postparietal forms the centre limit of the skull. When viewed dorsally, this posterior border is curved. The postparietal also forms the upper median border of the occiput. The posterior edge of the skull roof is thickened. The ventral process which meets the postparietal process of the exoccipital is not preserved on the right side.

Postfrontal. The anterior limit of the postfrontal is missing. Anterolaterally, the postfrontal forms the posteromedial border of the orbit. Posterolaterally, the postfrontal sutures with the postorbital in a posteromedially slanted suture. Anteromedially, a small part of the postfrontal-frontal suture is preserved which is almost straight and parallel to the midline. Posteromedially, the suture with the parietal is first straight and parallel to the midline and then slants obliquely towards the otic notch. Posterolaterally, the postfrontal has a short suture with the supratemporal.

Supratemporal. The supratemporal has a roughly pentagonal shape. Anteriorly, it sutures with the postorbital and postfrontal in an irregular suture almost transverse to the midline. Laterally, the supratemporal meets the squamosal in a slightly posteromedially slanted suture. Anteromedially, the suture with the parietal is irregular and concave to the midline. Posteromedially, this suture is continued in a posterolateral direction. Posteriorly, the supratemporal joins with the tabular in an almost straight suture transverse to the midline. It is almost excluded from meeting the postfrontal by contact between postorbital and parietal, but just touches

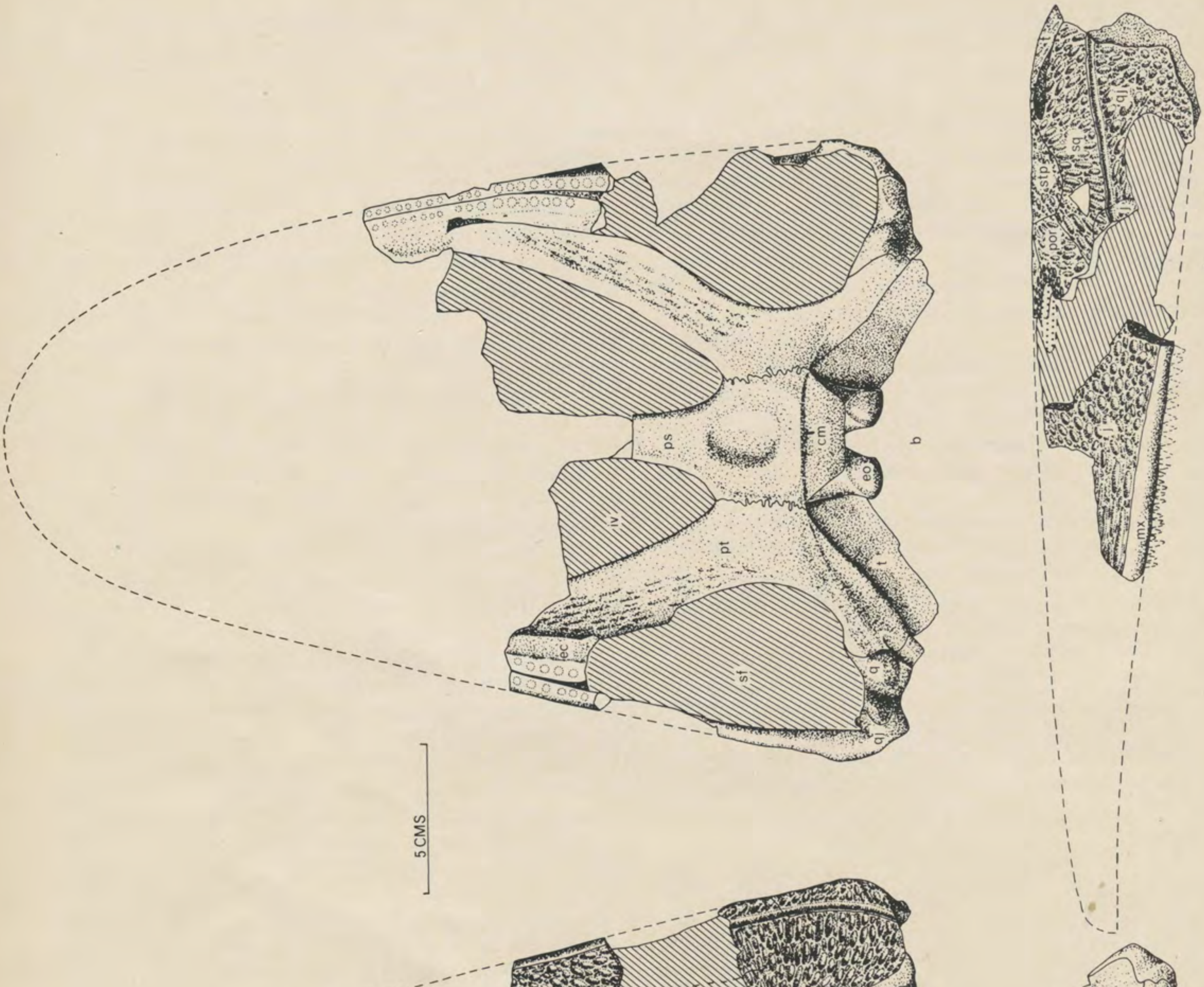

Figure 1. (A) Dorsal view of *Parotosuchus africanus;*
(B) Palatal view of *Parotosuchus africanus;*
(C) Posterior view of *Parotosuchus africanus;*
(D) Lateral view of *Parotosuchus africanus.*

the postfrontal anterolaterally, thus preventing the meeting of the parietal and postorbital.

Tabular. Anteriorly, the tabular meets a small part of the squamosal laterally and then continues medially with the supratemporal in a more or less straight suture transverse to the midline. Medially, the tabular meets the postparietal in a posteromedially slanted suture. The tabular forms a rounded posterolateral projection which is the tabular horn. This forms the posteromedial border of the otic notch. The distal portion of the tabular horn is slightly expanded anteriorly and laterally, thus constricting the posterior opening of the otic notch, behind the tympanic area. The tabular also forms the upper border of the occiput lateral to the postparietal.

It forms a process ventromedially which probably met the exoccipital but which is disarticulated in the specimen. This region of the skull is slightly distorted due to dorso-ventral flattening.

Postorbital. Anteriorly, the postorbital forms the posterior border of the orbit. The anterolateral limit of the postorbital is not preserved. Posterolaterally, the postorbital meets the squamosal in a sinuous posteromedially slanted suture. It meets the supratemporal posteriorly in an irregular suture almost transverse to the midline.

Squamosal. The anterior limits of the squamosal are not preserved. Anteromedially, the squamosal meets the postorbital in a sinuous posteromedially directed suture, then continues to suture with the supratemporal in an almost straight slightly posteromedially slanted suture. The posteromedial corner of the squamosal has a short straight suture with the tabular. Posterolaterally the squamosal meets the quadratojugal in a straight suture almost parallel to the midline which lies in the depression of the jugal lateral-line canal. Laterally, a small curved section of the suture with the jugal is preserved. Posteriorly, the squamosal forms the anterolateral border of the otic notch. In occipital view, the squamosal has a descending flange which forms the dorsal portion of the anterior wall of the stapedial groove. This flange meets the ascending ramus of the pterygoid. Laterally to this flange, the squamosal forms the entire occipital wall above the quadrate and medial to the quadratojugal.

Quadratojugal. The quadratojugal forms the posterolateral limit of the skull table. Medially, it sutures with the squamosal in a straight suture parallel to the midline. This suture lies in the depression of a lateral-line canal. Anteriorly, the quadratojugal meets the jugal in an almost straight suture transverse to the midline. The quadratojugal forms the posterolateral corner of the palatal surface and in occipital view it forms the extreme lateral part of the posterior wall of the skull. It is perforated by the paraquadrate foramen. In occipital view the quadratojugal sutures medially with the quadrate and is dorsally overlapped by the squamosal.

Jugal and Maxilla. Small fragments of the jugals and the maxillae are preserved.

Sculpture

The sculpture is of the type found throughout the Capitosauroidea. In the centre of each bone are small irregular pits from which, in the larger bones, ridges and grooves radiate outwards.

Lateral Line System

The supraorbital canal is partially preserved, following the curve along the posteromedial border of the orbit, as a series of enlarged pits surrounded by broader than average ridges.

The jugal canal is partially preserved as a deep groove running along the quadratojugal-squamosal suture.

The temporal canal is not evident, probably due to the large number of cracks in the supratemporal region.

Orbits

Only the posteromedial borders of the orbits are preserved, but the impression of both orbits is quite clear on the matrix. They are oval with their long axes oblique to the midline, converging anteriorly. The orbits measure approximately 3 cm by 2 cm.

Palate

Parasphenoid. The parasphenoid consists of a posterior basal plate which has been severely distorted and a small posterior portion of the narrow cultriform process. The ventral surface of the cultriform process is badly cracked. The basal plate of the parasphenoid is concave in cross-section. It meets the pterygoids laterally in interdigitated oblique sutures. The basal plate has a short free edge between the exoccipital condyles. The *crista muscularis* is preserved as a ridge of bone. Posterior to this ridge, the medial part of the parasphenoid is deflected towards the skull roof. This distortion is probably due to post-mortem damage.

Pterygoid. The pterygoid consists of a body with a palatine ramus and a quadrate ramus. The body meets the basal plate of the parasphenoid in an interdigitated oblique suture which runs posterolaterally from the centre of the posterior border of the interpterygoid vacuity to the posterior edge of the palate. This region, as noted previously, has been distorted but, as it is preserved, the pterygoid does not seem to meet the exoccipital in palatal view. Fine sculpturing is present on the lateral surface of the body where it borders the subtemporal fossa, and on the lateral part of the palatine ramus. The medial side of the palatine ramus is curved and is not sculptured. Anteriorly the limits of the palatine ramus are missing. The quadrate ramus bears no sculpturing. It ends on the left side of the skull in a sinuous suture with the quadrate. In occipital view the dorsal surface of the quadrate ramus is extended into an ascending ramus which meets the descending flange of the squamosal. The pterygoids, seen posteriorly,

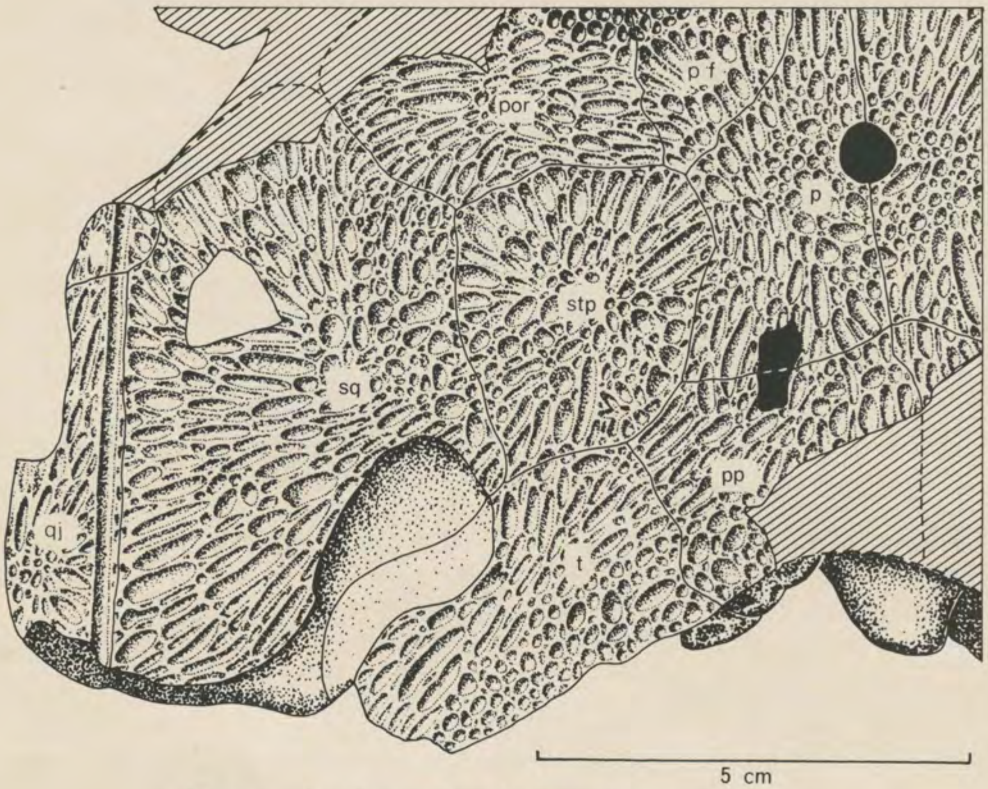

Figure 2. Dorsal view of tabular horn of *Parotosuchus africanus*.

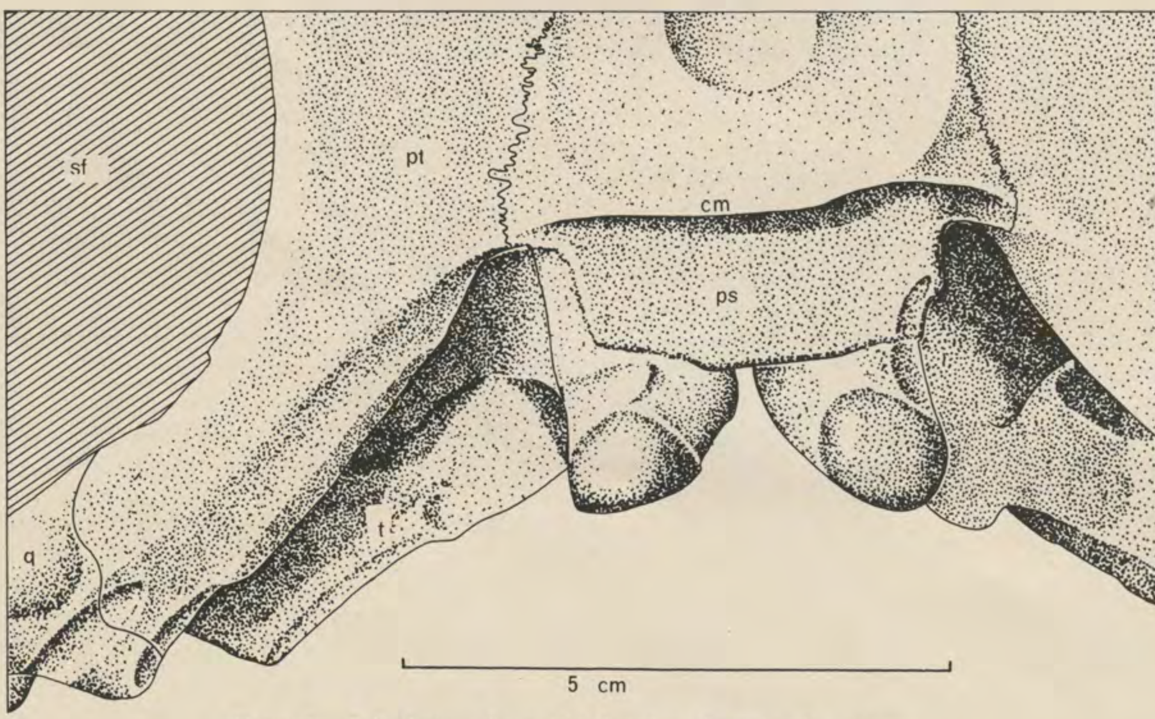

Figure 3. Palatal view of exoccipital region of *Parotosuchus africanus*.

cover different areas on the left and right of the skull, probably due to distortion.

Interpterygoid vacuities. These converge posteriorly to a broad point. The anterior borders are missing.

Ectopterygoid. Lateral and anterior to the palatine rami of the pterygoids displaced ectopterygoids carrying tooth bases are present.

Quadrate. The quadrate forms the articular surface for the lower jaw. Anteriorly, in palatal view, it forms the posterior border of the subtemporal vacuity. Its medial suture with the quadrate ramus of the pterygoid is sinuous and posteromedially slanted. Laterally, the quadratojugal clasps the quadrate with anterior and posterior flanges which surround the lateral extremity of the bone. This lateral part of the quadrate is a rounded condyle. Anteromedially, a larger condyle is present with a groove just posterior to it. Behind this groove the posteromedial corner of the quadrate forms a distinct angle of smooth-surfaced bone which perhaps assisted as an auxiliary articulatory area. Between the lateral and anteromedial condyles is the trochlear which lies parallel to the medial condyle.

In occipital view, the quadrate forms about a quarter of the wall of the back of the skull. Dorsally, it meets the squamosal in a wavy, ventrolaterally directed suture. Medially, it meets the quadrate ramus of the pterygoid in an irregular suture almost perpendicular to the skull. Laterally, the quadratojugal meets the quadrate with a dorsal and ventral flange which surrounds the lateral margin of that bone.

Occiput

Exoccipital. The left exoccipital, which is better preserved, is subcircular. It faces inward and downward and has a roughened surface that evidently bore a cap of cartilage. In palatal view the exoccipital extends forwards to meet the parasphenoid and not the pterygoid. However, this area is distorted. In occipital view, the exoccipital sends up a stout process that bifurcates to form the vertical postparietal process and the dorsolateral tabular process. The left exoccipital is different from the right and seems less distorted. The vertical postparietal process has two medial extensions. The upper one, the *processus lamellosus,* evidently underlay a cartilaginous supraoccipital. It resembles a vertebral prezygapophysis. It is noted here that the left exoccipital seems to have two vertical dorsal postparietal processes with a distinct groove between them. This may be due to distortion, but the two pillars are smooth and intact. The lower medial process of the postparietal process, the *processus basalis,* approaches the midline and overlies the space presumably occupied by the cartilaginous basioccipital. On the lateral wall of the exoccipital, just above the condyle, lies the posterior opening for the XIIth nerve. Its internal opening is on the anteromedial face of the dorsal process just above the *processus basalis.* Laterally and ventral to the posterior opening for the XIIth nerve lies the smaller foramen, presumably for the Xth nerve, which is not seen in the illustrations. The tabular process of the exoccipital projects dorsolaterally and somewhat posteriorly to meet the tabular. This area on both sides of the skull is badly distorted. Between the postparietal and tabular processes of the exoccipital lies the triangular posttemporal fenestra.

Lower Jaw

About 22 cm of the left lower jaw is preserved. The piece tapers from 5 cm posteriorly to 1,5 cm anteriorly. Lingually, an anterior Meckelian foramen is present on what is presumably the postsplenial. Although the two bones are disarticulated, it is clear that lingually the postsplenial met the splenial in an almost straight ventromedially slanted suture. Above the postsplenial lies the intercoronoid. Its sutures with the postsplenial ventrally and the dentary dorsally are not discernible. Between the splenial dorsally and the dentary ventrally lies the precoronoid which forms a thin ribbon of bone. Its posterior suture with the intercoronoid is not discernible, and anteriorly its limits are not preserved.

Labially, the dentary, which dorsally bears a single row of uniform tooth-bases, forms most of the jaw fragment. Posteroventrally lies the anterior part of the angular which is sculptured. The angular meets the unsculptured dentary dorsally in an irregular anteroventrally directed suture. The posterior limits of the angular are not preserved. Anteriorly, the angular meets the postsplenial in an irregular posteroventrally oblique suture. The postsplenial meets the dentary dorsally in an almost straight suture parallel with the ventral surface of the jaw fragment. Anteriorly, the postsplenial meets the splenial in an irregular suture which dorsally slants posteroventrally, but ventrally is not discernible. Dorsally, the splenial meets the dentary in an almost straight suture parallel to the ventral edge of the jaw fragment. The labial side of the splenial and postsplenial is sculptured in radial high and sharp ridges and broad, flat grooves.

Discussion

Welles and Cosgriff (1965) stated that "*Capitosaurus africanus*" was never figured and the description was not adequate for generic or specific determination. The species was therefore designated *nomen vanum.* As shown, however, the specimen consists of most of the postorbital parts of the skull which are fairly well preserved and may be directly compared with the same parts on other taxa.

Howie (1970) states that four species of parotosaurs have a tabular horn which has grown laterally towards the squamosal. These are *P. semiclausus* (Swinton 1927), *P. birdi* (Brown 1933), *P. peabodyi* (Welles and Cosgriff 1965), and *P. brookvalensis* (Watson 1958). In *P. pronus* (Howie 1970), the tabular horn is expanded anteriorly and laterally towards the squamosal so that the otic notch is semiclosed. This distal expansion of the tabular horn occurs also in *P. rajareddyi* (Chowdhury 1970), *P. megarhinus* (Chernin and Cosgriff 1975), and *P. africanus* (Broom 1909) (Figs. 1a, 3).

In Table 2 a comparison is made between *P. pronus, P. africanus* and *P. megarhinus.* The measurements for *P. africanus* are derived from the reconstruction to overcome the limitations of distortion during fossilization. From the range of indices shown in this Table, it is probable that these three parotosaurs are closely related. *P. africanus* probably had a narrower skull than the other two forms. (It is noted here that the skull length is only an estimated figure.) The interorbital breadth is probably greater than that of both the other forms. The interotic breadth is

TABLE 2
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

greater than *P. megarhinus* but the same as that of *P. pronus*. The interorbital length to interotic length index is slightly greater than for both *P. pronus* and *P. megarhinus* which have the same index value. The distance between the orbit and the otic notch is greater than that of the other two forms in which this value is approximately the same. The distance behind the orbits of the parietal foramen is also greater than that of the other two forms for which this value is also more or less the same. The distance between the parietal foramen and the front of the otic notch is greater than that of the other two forms. The concavity of the posterior border of the skull is less than in *P. pronus*, but greater than that of *P. megarhinus*.

Thus in three out of eight indices, *P. africanus* is closer to *P. pronus* (i.e. A:L, C:L and K:C); in two indices *P. africanus* is closer to *P. megarhinus* (i.e. B:L and N:C). In two indices it is equally apart from both (T:C and P:C) and finally in one index it has approximately the same value (A:C).

Thus it would seem that these three parotosaurs are on very much the same evolutionary level. *P. pronus* is thought to be Mid-Triassic, *P. megarhinus* to be on the border of the Lower-Middle Triassic, and *P. africanus* is from the *Cynognathus* zone. Thus, on the basis of the comparative morphology of these three species, the *Cynognathus* zone would seem to be close to the Lower-Middle Triassic boundary.

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.

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.

Description of the material (figs. 4 and 5)

Dorsal Skull Roof (fig. 4)

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

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

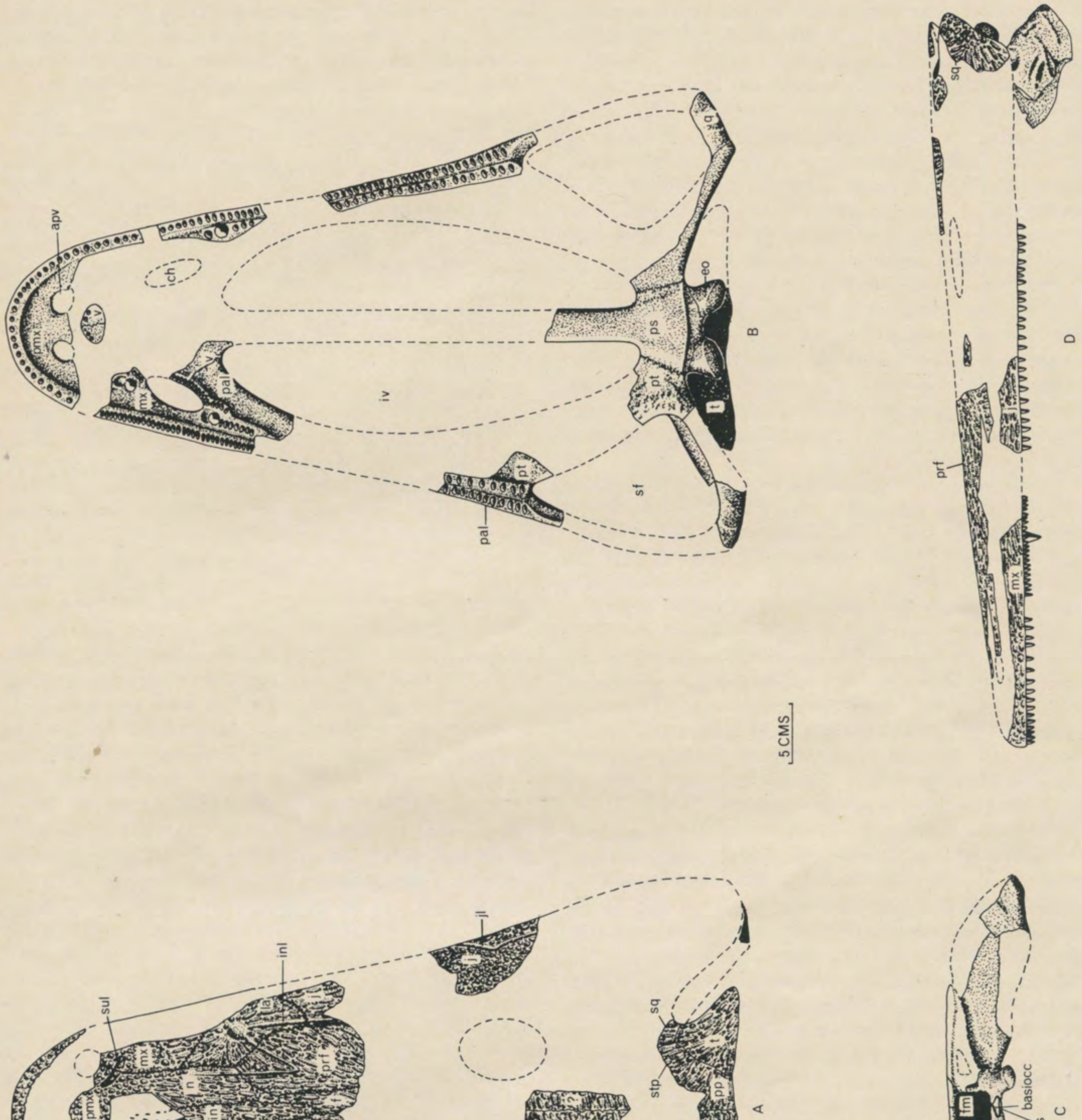

Figure 4. (A) Dorsal view of *Kestrosaurus dreyeri;*
(B) Palatal view of *Kestrosaurus dreyeri;*
(C) Occipital view of *Kestrosaurus dreyeri;*
(D) Lateral view of *Kestrosaurus dreyeri.*

which seems to extend farther 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.

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.

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

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.

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.

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 5,2 cm. Posterior to this position, the frontals meet in the midline, the posterior limits of which are not preserved.

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.

Tabular. The right tabular horn is almost completely preserved. The posterior skull border is straight (K:C = O) 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.

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.

Lateral Line System

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

The supraorbital canal. This 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 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.

Palate (Fig. 4b)

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

Vomer. Anteriorly, the suture between the vomer and the premaxillae is not preserved. However, a small piece of vomer carrying four 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 three 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 half-way 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; it 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 follows the curvature of the choana and continues posteriorly on to 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.

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 to enter 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.

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.

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.

Quadrate. 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.

Occiput (fig. 4c)

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.

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 posteroventral 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.

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

Squamosal. The squamosal forms most of the dorsolateral 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.

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.

Lower Jaw (fig. 5)

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. The jaw of *Kestrosaurus* is almost 50 per cent smaller than those of the parotosaurs.

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

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

Prearticular. From the anterodorsal border of the *chorda tympani* fossa 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.

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 fossa which slants anterodorsally; this is

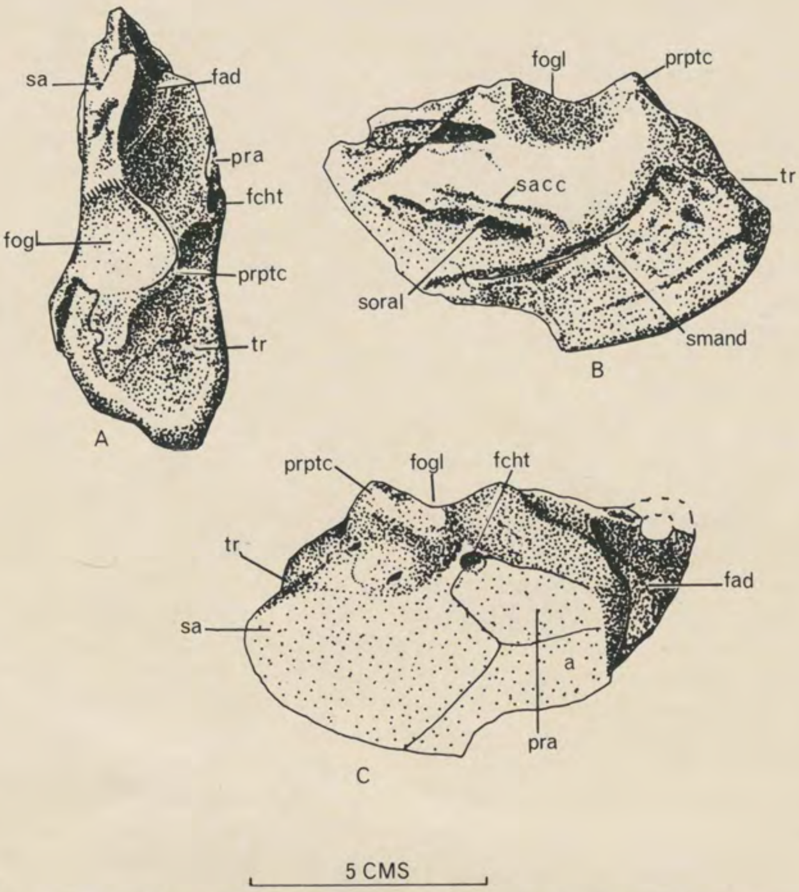

Figure 5. (A) Dorso-posterior view of posterior portion of lower jaw of *Kestrosaurus dreyeri;*
(B) Lateral view of posterior portion of lower jaw of *Kestrosaurus dreyeri;*
(C) Lingual view of posterior portion of lower jaw of *Kestrosaurus dreyeri.*

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.

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.

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.*

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 intermediate stage between *U. senekalensis* and the more advanced parotosaurs such as *Parotosuchus 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 seems 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, *Parotosuchus 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 *Parotosuchus* 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 4,8 cm and the length from the posterior limit of the glenoid fossa to the end of the retroarticular process is only 4,4 cm; the greatest width of the retroarticular process is 3,2 cm. This is highly unusual for a specimen whose skull length is estimated at approximately 60 cm. 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.

TABLE 3

Table of comparison of measurements of the lower jaws of *Parotosuchus megarhinus*, Chernin and Cosgriff 1975; *Kestrosaurus dreyeri*, Haughton 1925 and *Parotosuchus dirus* sp. nov.

	P. megarhinus cm	*K. dreyeri* cm	*P. dirus* cm
(1) Width of retroarticular process posterior to post-condylar 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

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*, which have similar skull lengths, the jaw proportions of *Kestrosaurus* are 50 per cent smaller. (See table 3).

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).

Parotosuchus dirus sp. nov.

Type: S.A.M. Cat. No. K434
Locality: Aliwal North, N.E. Cape Province, South Africa
Material: Fragments of a lower jaw
Collected by: South African Museum Expedition

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 degrees 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 line canals converge to depression in sculpture.

Description of the material (figs. 6–8)

The fragments were prepared by means of a vibrotool. From the texture of the bone, it is evident

Figure 6. (A) Dorsal view of symphysial region of *Parotosuchus dirus;*
(B) Dorsal view of symphysial region of *Parotosuchus megarhinus.*

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.

Symphysial region (fig. 6)

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 26 cm and the left 17 cm. The breadth across the two fragments at the position of the posterior edge of the symphysial region when joined measures 20,5 cm.

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 5,3 cm across and approximately 2,8 cm anteroposteriorly. The whole of the lingual tooth row consists of six tooth-bases and six replacement pits. The lingual row of teeth measures approximately 9 cm as compared with the measurement of 11 cm 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 8 cm. 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*.

The mid-line length of the symphysis of *P. megarhinus* is 3,5 cm and the entire configuration of this area is completely different. In *P. megarhinus* the breadth of the ramus remains constant from a position 10 cm posterior to the anterior edge of the jaw to the symphysis, whereas in *P. dirus* it expands from 4,9 cm to 9 cm 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 cm at the base compared to 1,6 cm 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 7 cm, as compared with 11 cm 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 posterolateral 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.

Precoronoid

On the left side the precoronoid forms a conspicuous ridge of bone 6 cm long on the lingual side of the jaw approximately 5 cm posterior to the lingual row of symphysial teeth. This ridge expands to a thickness of 1,8 cm and four 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 three 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 3 cm posterior to its anterior limit the bone thickens to form the above-mentioned tooth-bearing ridge. This ridge is thickest approximately 7 cm posterior to its anterior limit. Posterior to this thickened area, the bone flattens approximately 10 cm 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.

Articular region (figs. 7 and 8)

The posterior part of the right ramus measures 20 cm 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.

Viewed 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 5,2 cm 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 1,2 cm by 0,6 cm with its long axis facing anterodorsally, and is the internal opening of the *nervus chorda tympani*. The chorda tympani foramen lies in a depression 4 cm long by 3 cm wide, the mid-length of which is immediately lateral to the precondyloid process, with the foramen lying anterior to this position.

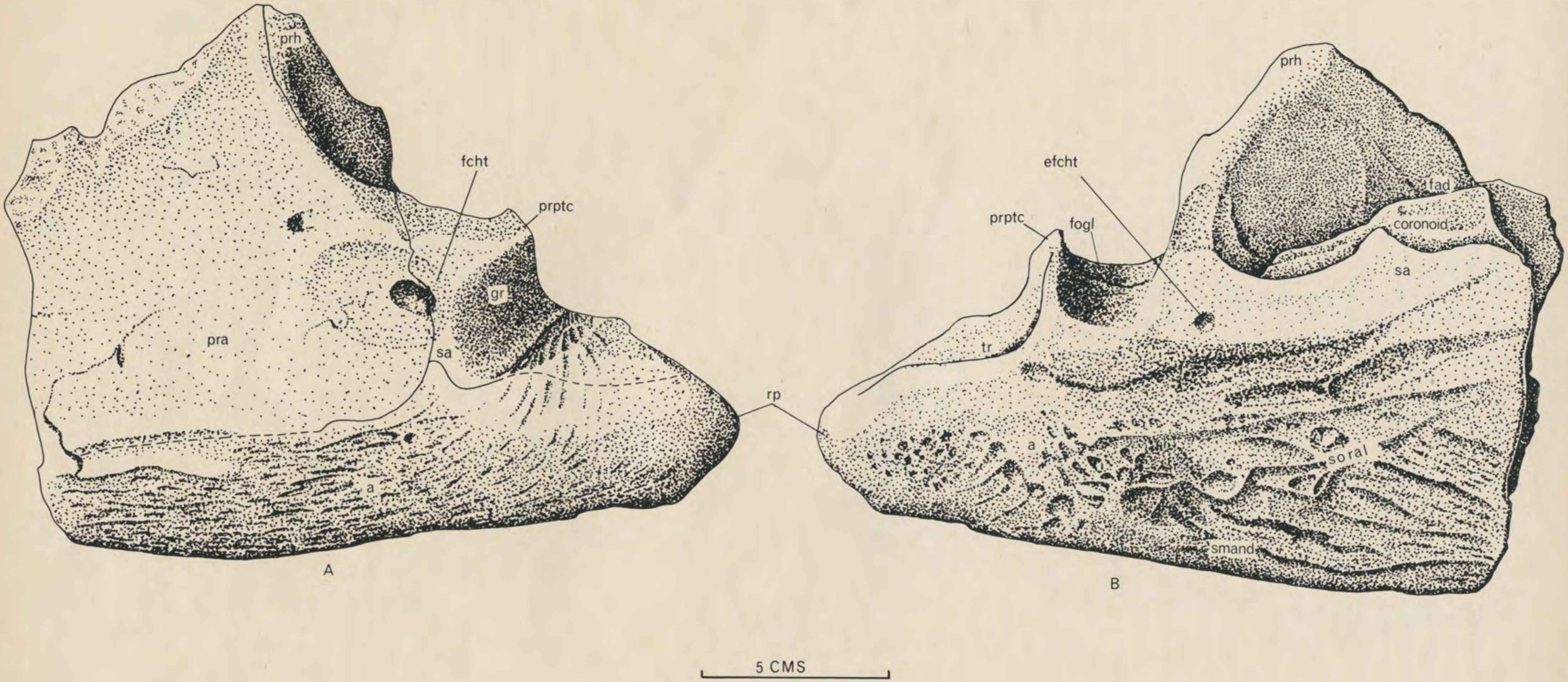

Figure 7. (A) Lingual view of posterior portion of jaw ramus of *Parotosuchus dirus;*
(B) Lateral view of posterior portion of jaw ramus of *Parotosuchus dirus.*

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 9,3 cm. The width of the retroarticular process measured immediately posterior to the postcondyloid process is 5,5 cm. The trough for the abductor muscles is visible lying within the retroarticular process which has a downward slope of approximately 45 degrees. 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 *Parotosuchus peabodyi* (Welles and Cosgriff 1965); *Parotosuchus pronus* (Howie 1970); *Parotosuchus 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 6,3 cm. The greatest anteroposterior width of the glenoid fossa measures 2,3 cm. 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 9 cm 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 16 cm. 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 18 cm in front of the posterior edge of the jaw to a dorsal position 7,5 cm 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

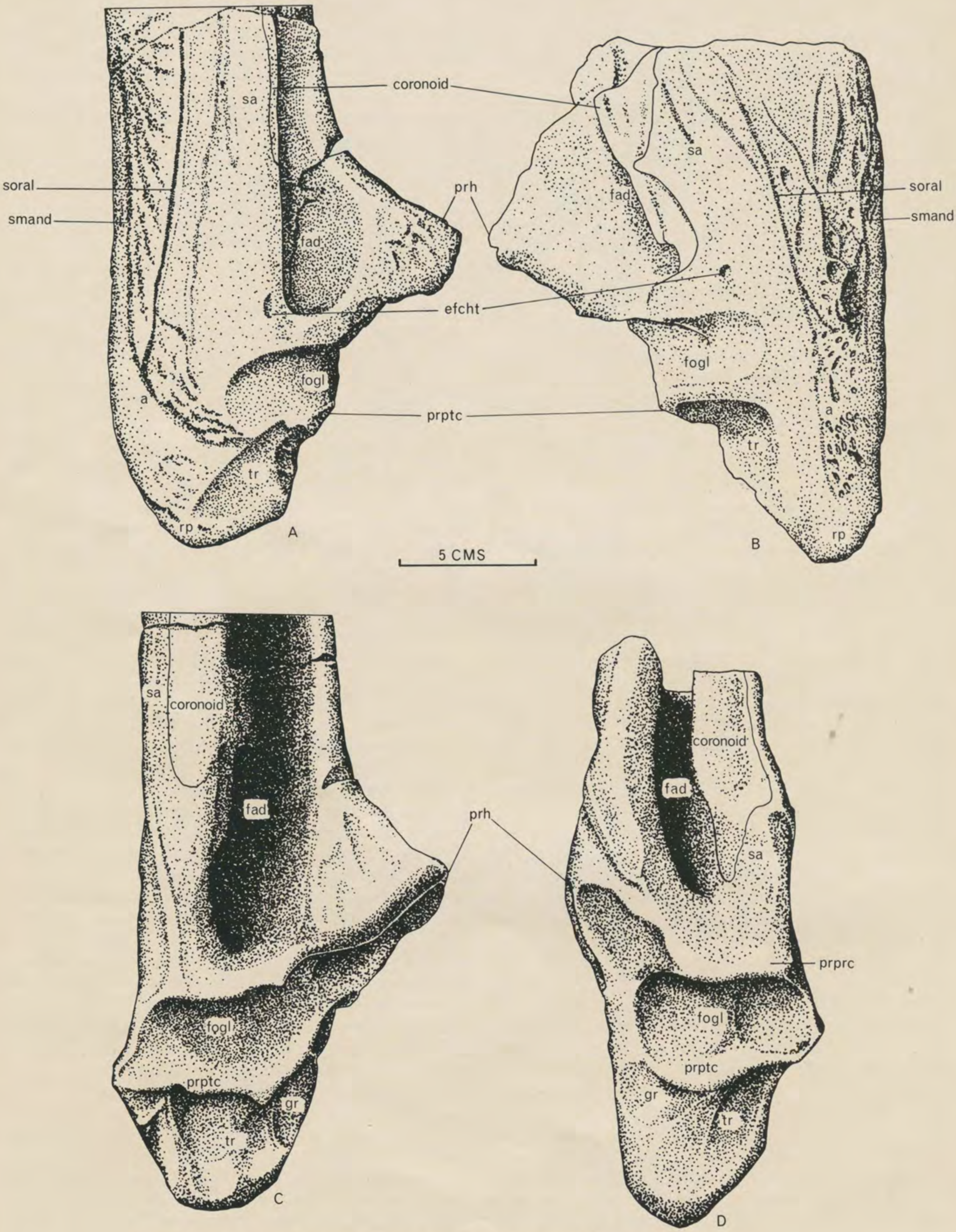

Figure 8. (A) External view of posterior portion of lower jaw of *Parotosuchus megarhinus;*
(B) External view of posterior portion of lower jaw of *Parotosuchus dirus;*
(C) Dorso-posterior view of posterior portion of lower jaw of *Parotosuchus megarhinus;*
(D) Dorso-posterior view of posterior portion of lower jaw of *Parotosuchus dirus.*

converge to a large oval depression in the sculpture, which lies transverse to the long axis of the jaw measuring 2 cm by 2,5 cm. 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 17 cm anterior to the posterior edge of the jaw to a dorsal position 1,2 cm 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* 5 cm 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.

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 per cent 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 3,5 cm 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 three 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 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*.

SUMMARY AND CONCLUSIONS

1. Three specimens of the family Capitosauridae have been described, one for the first time.

2. *Parotosuchus 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 *Parotosuchus dirus* sp. nov. This is believed to be closely related to *Parotosuchus pronus* (Howie) and *Parotosuchus megarhinus* (Chernin and Cosgriff), and probably ancestral to both.

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LIST OF ABBREVIATIONS

a	— angular	ec	— ectopterygoid	fogl	— glenoid fossa
apv	— anterior palatal vacuity	efcht	— external opening for the nervus chorda tympani	if	— interfrontal
art	— articular	eo	— exoccipital	inl	— infraorbital canal
basiocc	— basioccipital	epi	— epipterygoid	iv	— interpterygoid vacuity
c	— coronoid	f	— frontal	j	— jugal
ch	— choana	fad	— adductor fossa	jl	— jugal canal
cm	— crista muscularis	fcht	— chorda tympani foramen	la	— lachrymal
d	— dentary	fm	— foramen magnum	mx	— maxilla

n	— nasal	prh	— hamate process of prearticular	sacc	— sulcus accessorius
p	— parietal	prprc	— precondylar process	smand	— sulcus mandibularis
pal	— palatine	prptc	— postcondylar process	soral	— sulcus oralis
pc	— precoronoid	ps	— parasphenoid	sp	— splenial
pf	— postfrontal	pt	— pterygoid	sq	— squamosal
pmx	— premaxilla	ptf	— post-temporal fossa	stp	— supratemporal
por	— postorbital	q	— quadrate	sul	— supraorbital canal
pp	— postparietal	qj	— quadratojugal	t	— tabular
pra	— prearticular	rp	— retroarticular process	tr	— trough for depressor mandibulae muscle
prf	— prefrontal	sa	— surangular	v	— vomer