THE CRANIAL MORPHOLOGY OF A NEW GENUS AND SPECIES OF ICTIDOSAURAN

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(With 7 figures in the text)

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INTRODUCTION

During 1924 the remains of a small reptile skull and a few postcranial remains (Broom's Ictidosaurian A. Nas. Museum C.249) were presented to the National Museum, Bloemfontein. The specimen was reported to have been found in the Cave Sandstone of Ladybrand, Orange Free State, but no data as to the exact locality were recorded. In 1926 the remains of a skull and fairly complete postcranial skeleton (Broom's Ictidosaurian B. Nas. Museum C.253) were discovered at a quarry in the Cave Sandstone of Ladybrand and purchased by the Museum for £1. The impression of an incomplete mandible and part of the maxilla and jugal were later discovered at the same quarry. This quarry lies on the N.W. outskirts of the town, but no particulars as to the exact position where they were found was ever recorded and no further specimens have been discovered at this quarry or anywhere else.

The importance of the first two specimens was realised by the late Dr. R. Broom who gave a preliminary account of them (Broom, 1929). He was unable to dissect the material, but claimed that both specimens (no mention of the impression of the mandible has ever been made in print) belonged to the same species and that they were far the most mammal-like of the known therapsids. He considered the age of the specimens to be Rhaetic and placed the Ladybrand specimens together with *Karoomys*, *Pachygenelus* and *Trithele-don* in a new suborder, the Ictidosauria. He was of the opinion that the mammals arose from a member of this suborder.

Broom referred to these two specimens again in 1932. In this account he expressed the view that they belonged to the same genus but differed specifically, but as they were to have been named by Dr. van Hoepen, he only referred to them as Ictidosaurians A and B. No further investigation of the specimens was undertaken until recently.

In this paper a description of the skull of Ictidosaurian B has been given and the specimen has been named *Diarthrognathus broomi*. The generic name has been chosen to indicate the double articulation of the lower jaw with the skull. The remainder of the material will be described in later papers.

In the text-figures widely spaced cross-hatching has been employed to indicate the matrix filling the nasal capsule, narrowly spaced cross-hatching for broken bone surfaces, and stippling for the sandstone matrix still *in situ*.

I am deeply indebted to the National Museum and especially to the Director, Dr. A. C. Hoffman, for his constant encouragement and for permitting me to study this valuable material. Special thanks are due to Mr. F. R. Parrington for his help, encouragement and advice.

I wish to record my cordial thanks to the South African Council for Scientific and Industrial Research for a grant enabling me to study the Stormberg Series.

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DESCRIPTION OF THE SKULL OF *DIARTHROGNATHUS BROOMI*
gen. et sp. n.

Subclass **SYNAPSIDA**

Order *THERAPSIDA*

Suborder THERIODONTIA

Infraorder ICTIDOSAURIA

Family **Diarthrognathidae** fam. nov.

Genus *Diarthrognathus* gen. n.

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Genotype. *Diarthrognathus broomi* gen. et sp. n.

Generic description. An advanced mammal-like reptile in which both the reptilian and mammalian jaw articulations function together.

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DIARTHROGNATHUS BROOMI gen. et sp. nov.
(Figs. 1–7)

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(1) " Mammal-like reptile ". Broom. 1929, *Proc. Linn. Soc. N.S.W.* **53**, 688–694. Type locality : Ladybrand, Orange Free State, South Africa. Cave Sandstone. Upper Triassic.

(2) Ictidosaurian B. Broom, 1932, *The mammal-like reptiles of South Africa and the origin of mammals*. H. F. & G. Witherby, London.

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General

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The remains of *Diarthrognathus broomi* were exposed by the splitting of a sandstone block. Unfortunately only one half of the block was acquired by the museum and consequently a large part of the animal was lost. The preserved portion consists of the posterior half of the skull and the greater part of an articulated postcranial skeleton. In dorsal view the skull is complete as far forward as the anterior region of the frontals. From this point the line of fracture passes obliquely backwards and downwards to the anterior region of the pterygoids. Only those portions of the mandibles and postdentary bones behind this line are preserved. Considering the small size of the

animal, the preservation is remarkably good. The identification of sutures is extremely difficult because the specimen is small and the surface is covered with a mosaic of fine cracks.

The specimen was dissected as far as possible without seriously endangering it with the aid of a sharp needle and stereo-binocular microscope.

In view of the importance of the material, drawings have been given of the material as preserved in addition to reconstructed drawings. Drawings of the material were obtained by photographing the material in colour with the aid of a long focal length lens (to minimise parallax) and tracing the projected image of the colour transparencies.

Parietal (Figs. 1 & 3)

An outstanding feature of the parietals (P) is their length ; they reach forward to within a short distance of the lacrimals. A median suture does not appear to be present. In dorsal view the lateral edges of the parietals are slightly concave. Posteriorly the parietals flare out laterally to establish contact with the squamosals (S.Q.) but no sutures between these bones are visible. The posterior edges of the parietals are drawn upwards to form a sharp lambdoidal crest which is continued laterally by the posterior edges of the squamosals. A pronounced sagittal crest (S.C.) stretches forward from the posterior border of the parietals to beyond the mid-point of these bones. Posteriorly this crest is high but it loses height progressively in an anterior direction. There is no evidence of either a pineal foramen, or of postorbital bones.

In lateral view it can be seen that the edge of the parietal establishes contact with the periotic (P.O.) and epipterygoid (E.P.). A similar relationship is present in cynodonts.

Relative to the size of the skull the parietals are broad.

Frontal (Figs. 1 & 3)

The anterior border of the frontals (F.) are damaged, but it is probable that the greater part of these bones are preserved. The skull roof formed by the parietal is practically horizontal, but the level of the skull table falls away rapidly in an anterior direction in the region of the frontals.

In dorsal view the two frontals form a broad triangular table with the apex of the triangle directed backwards. A median suture between the two bones is visible. The central portion of the table is slightly concave. There is no indication of a pre-frontal and this bone has presumably been lost or considerably reduced.

In contrast to the condition found in typical therapsids, the frontal of *Diarthrognathus* extends downwards to form an inner wall to the orbit as it does in mammals and tritylodontids. The orbital flange of the frontal appears to meet the lacrimal (L.) and palatine (PAL.). A slender process of the frontal appears to extend backwards below the parietal to establish contact with the antero-dorsal edge of the epipterygoid. A similar relationship was described by Parrington (1946 a) in *Thrinaxodon*.

Fig. 2.—*Diarthrognathus broomi* gen. et sp. nov. Ventral view of the preserved portion of the skull. × 3. (Key to lettering, p. 216).
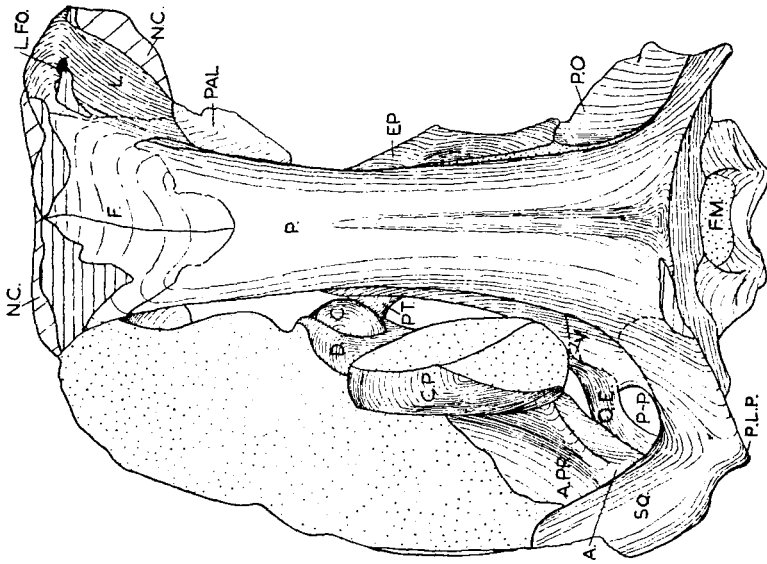
Fig. 1.—*Diarthrognathus broomi* gen. et sp. nov. Dorsal view of the preserved portion of the skull with the right lower jaw and zygomatic arch removed. × 3. (Key to lettering, p. 216.)
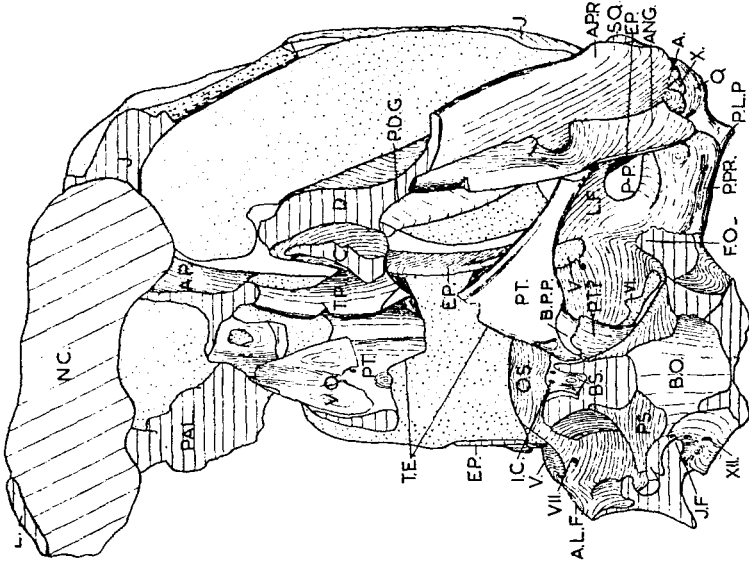
Squamosal (Figs. 1–4)

The posterior portion of the left squamosal is well preserved whereas only the anterior part of the right squamosal is well preserved. It was therefore, possible to reconstruct this bone (Figs. 6 and 7). The anterior and posterior terminations of the right zygomatic arch are badly damaged. During preparation this arch, together with the right mandible, was removed from the skull, and this enabled a dissection of the lateral wall of the cranium and inner surface of the mandible.

The zygomatic arch, consisting of the jugal (J.) and squamosal, is slender. The squamosal extends forwards as a thin plate of bone overlying the jugal (Fig. 3). Posterior to the jugal the squamosal, when viewed from above, has the form of a wide, horizontally orientated, convex plate. Laterally to this
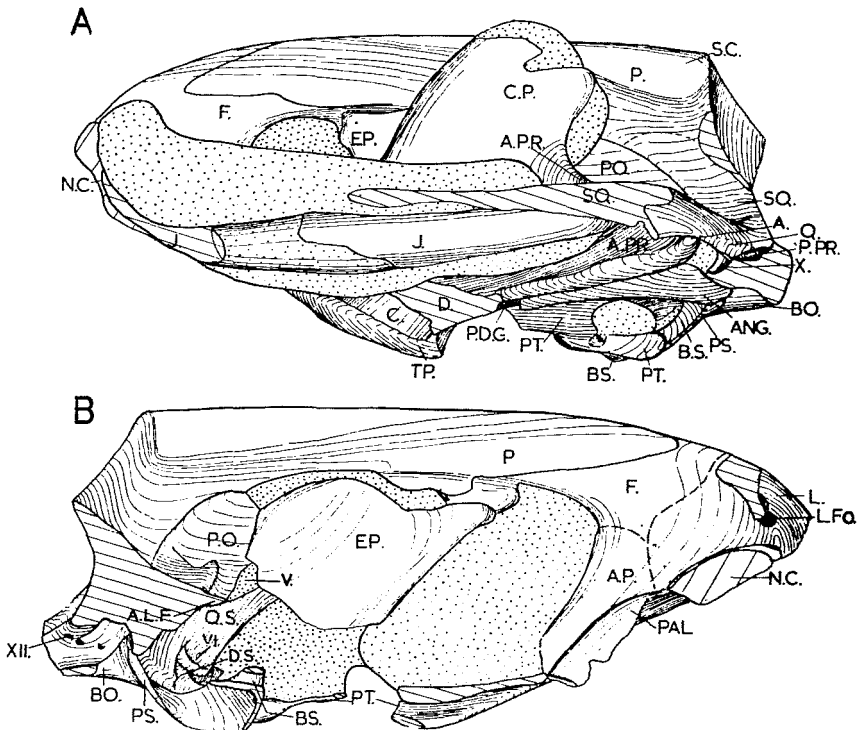

Fig. 3.—*Diarthrognathus broomi* gen. et sp. nov. A, lateral view of the left side of the preserved portion of the skull and B, right side with lower jaw and zygomatic arch removed. Both × 3. (Key to lettering, p. 216).

plate the squamosal extends inwards as a broad flange to meet the parietal. Unfortunately no suture could be observed between these bones. The posterior edge of the squamosal is drawn upwards to form the lateral extension of the lambdoidal crest. This crest terminates laterally as a distinct postero-laterally directed process (P.L.P.) separated by a small indentation from the convex horizontally orientated plate of the squamosal. The ventral

surface of the squamosal below the postero-laterally directed process is flat, horizontal and abutts against the lateral surface of the paroccipital process (P.PR., Fig. 2). The outer posterior edge of the squamosal is drawn downwards to form a sharp ridge. Internally to this ridge the bone is markedly concave ; the wide, horizontally orientated plate, visible in dorsal view, forming the roof of this concavity. The posterior region of the articular process of the dentary (A.PR.), articulates with this glenoid cavity of the squamosal. Broom (1932) claimed that there was no contact between the dentary and the squamosal, but this contact is quite clear. In Fig. 6B the mandible has been
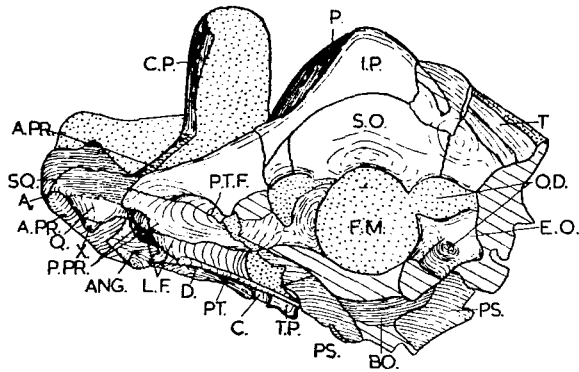

Fig. 4.—*Diarthrognathus broomi* gen. et sp. nov. Occipital view. × 3. (Key to lettering, p. 216).

removed to illustrate the form of this cavity. In typical therapsids the squamosal above the quadrate has the form of a vertically orientated plate, but in *Diarthrognathus* this region of the squamosal extends forwards to form the roof to the glenoid cavity. This relationship is best seen in occipital view (Fig. 4).

The postero-ventral border of the squamosal adjacent to the paroccipital process supports a small quadrate (Q.) which is preserved on both sides of the skull. The form of this bone and the nature of the jaw articulation are described on page 198.

Jugal (Figs. 3 & 5)

The entire right jugal is preserved except for its anterior end ; the left is badly damaged, but an impression of the missing portions is preserved in the matrix. A marked feature of the jugal is its great length. The posterior part of the bone is a vertically orientated sheet of bone and in an anterior direction the bone gradually becomes retangular in transverse section. The anterior edge of the jugal appears to meet the lateral border of the lacrimal. A shallow V-shaped depression (A.M.) is visible upon the antero-ventral surface of the jugal and probably indicates the position of the suture between the jugal and the maxilla. Unfortunately no part of the maxilla is preserved in this specimen.

Antero-medial wall of the orbit

A significant difference in the skull structure of mammals and typical therapsids is the presence in the former of a median wall to the orbit formed by the lacrimal, frontal, alisphenoid (epipterygoid) and palatine. Although this wall is not as complete in *Diarthrognathus* as in mammals, it is further developed than in therapsids, with the possible exception of the tritylodontids.

The wall to the orbit is shown in Fig. 3B. A flange of the palatine (A.P.) extends upwards to meet the downwardly directed flange of the frontals. The anterior edges of both these flanges appear to meet the lacrimal (L.) although no sutures separating the three bones could be observed. A large foramen within the lateral wall of the skull lies behind the frontal and palatine flanges. The lacrimal is large and forms a narrow anterior floor to the orbit. Unfortunately the lateral edge of this bone is damaged. As a result of the reduction or disappearance of the prefrontal the lacrimal appears to be situated fairly high in the skull ; its dorsal border is confluent with the dorsal surface of the skull. The left lacrimal could not be exposed without endangering the specimen.

There is evidence of at least one lacrimal foramen (L.F.O.) but a second is probably present alongside the first. Anterior to the lacrimal foramen the lacrimal forms part of the lateral wall of the snout, but as a result of damage to the skull it is not possible to determine how far forward it extended.

Exoccipital and Basioccipital   (Figs. 2 & 6B)

The posterior edge of the basioccipital (BO.) is damaged, but the preserved section is slender in transverse section and it is therefore unlikely that this bone terminated posteriorly in an occipital condyle. A basioccipital condyle would not be expected in such an advanced form. Although the posterior surface of the exoccipitals (EO.) are damaged they are sufficiently substantial to have supported condyles.

No suture is visible between the basioccipital and basisphenoid. In ventral view the basioccipital is fairly broad and convex. A clear suture between the basioccipital and exoccipital is visible on the right. Three foramina for the hypoglossal nerves (XII.) penetrate the lateral surface of the right exoccipital. On the right the posterior portion of the periotic is almost completely destroyed, whereas on the left the exoccipital is badly damaged, but the periotic fairly well preserved. Consequently it is rather difficult to establish the relationship between the exoccipital and the periotic. The medial surface of the right exoccipital, lateral to the first and second hypoglossal foramina is sharply indented. This has been interpreted as the medial portion of the jugular foramen (J.F.). It would appear therefore, that the jugular canal is bordered anteriorly and laterally by the periotic and by the exoccipital medially and posteriorly (Fig. 6B).

The exoccipital forms the lateral border to the foramen magnum (F.M.) but it could not be ascertained to what extent it contributes to the formation of the floor. A shallow depression (O.D.) is visible in the exoccipital lateral to the foramen magnum ; probably for musculature attachment.

Basisphenoid and Parasphenoid   (Figs. 2, 3B & 6B)

Unfortunately the ventral surface of the basisphenoid (BS.) is badly damaged. The preserved antero-ventral border of this bone appears to be undamaged, and no medial ossification anterior to this bone is present. The presphenoid which would be expected in this position has either been lost or remained cartilaginous. Immediately behind the anterior border of the basisphenoid two small foramina (I.C.) are visible on the ventral surface. These are probably the foramina for the internal carotids or at least the remnants of these foramina ; these arteries may have entered the skull further laterally. A low medial ridge is present upon the basisphenoid immediately behind the two carotid foramina, but the posterior extent of this ridge could not be determined due to damage to the ventral surface of the basisphenoid. It could not be ascertained whether this ridge is formed exclusively by the basisphenoid or whether the parasphenoid (P.S.) contributes as well.

Two shallow concavities are visible in the antero-lateral surfaces of the basisphenoid. The thickened ventral edges of the pterygoids (P.T.) fit into these concavities. A clear suture between the two bones is visible. Dorsal to this contact two thin, broad flanges of the basisphenoid, the basipterygoid processes (B.P.P.), extend in an antero-lateral direction above the pterygoids. Presumably the epipterygoids meet the lateral edges of the basipterygoid processes, but this point could not be confirmed in *Diarthrognathus*. Similar basipterygoid processes have been described by Watson (1931) and Crompton (1955) in scaloposaurids. In *Diarthrognathus* the pterygoids are fairly widely separated in the region of the basipterygoid articulation. It is difficult to determine how far the pterygoid extends backwards beyond the basipterygoid articulation. A narrow fractured strip passes through the pterygoid lateral to the basipterygoid articulation and separates the anterior portion of the pterygoid from a small bone (PT.?) lying alongside the basisphenoid.

This ossification may be interpreted as part of the pterygoid as reconstructed, Fig. 6B, or as part of the basisphenoid. The anterior region of this ossification has a fairly flat horizontal ventral surface and in a posterior direction the bone twists to form a practically vertically orientated sheet of bone with its medial border meeting the ventro-lateral edge of the parasphenoid. In lateral view (Fig. 3A) this posterior ossification appears to overlap the basisphenoid and terminates posteriorly with a crescent-shaped edge. Unfortunately this suture could only be observed on the left.

As preserved the parasphenoid (PS.) consists of two isolated pieces of bone lying upon the ventral surface of the basisphenoid. The lateral edges of these plates are drawn downwards to form prominent crescent-shaped ridges which terminate a short distance below what has been interpreted as the fenestra ovalis (F.O.). Unfortunately the medial edges of the parasphenoidal plates are badly preserved and as a result of damage to the palate in this region it is not possible to state whether the two plates are fused in the mid-line and continued forwards by a parasphenoidal rostrum. Of importance however, is the establishment of the fact that in an advanced form such as *Diarthrognathus* the parasphenoid has the same relationship to the basisphenoid

as is found in other mammal-like reptiles. There is no basis for Broom's (1929) reconstruction of this form in which the vomer is drawn halfway between the basisphenoid and the nasal region. The view of Parrington & Westoll (1940) that the parasphenoid is reduced or lost in mammals is in the light of this new evidence far more acceptable. The dorsal surface of the basisphenoid has been exposed by the loss of the greater part of the right pterygoid. In lateral view (Fig. 3B) it appears that the anterior portion of the basisphenoid is fairly thick dorso-ventrally, but that in a posterior direction the bone thins progressively. A prominent feature of the dorsal surface of the basisphenoid is a short process which projects dorsally from the anterior region of this bone. In anterior view this process is triangular in shape with the apex situated dorsally. The dorsal surface of this process is damaged and oval in section. It is probable that this process was continuous with the presphenoid or cartilaginous interorbital septum. Posterior to the dorsal process the basisphenoid is markedly concave. This concavity has been interpreted as the pituitary fossa. It would appear that the carotid foramina open into this fossa. The posterior border of the pituitary fossa is formed by a broad sheet of bone extending upwards from the dorsal surface of the basisphenoid. This appears to be an ossification of the dorsum sellae (D.S.). The dorsum sellae is continued upwards by an ossification which has been interpreted as an ossification of the pila antotica (see pp. 195).

Pterygoid, Palatine and Vomer (Figs. 2, 3B & 6B)

Only the left pterygoid is fairly well preserved and sufficient is present to enable this bone to be reconstructed. Posterior to the transverse process (T.P.) the pterygoid is triradiate in form. One ramus is directed towards the basisphenoid (pterygoid flange), one towards the quadrate (quadrate ramus) and one towards the anterior region of the pterygoid (anterior ramus). In ventral view the pterygoid flange has the form of a skewed triangular plate the apex of which is directed backwards alongside the basisphenoid (see above). The lateral edge of the plate is fairly thin and it becomes thicker in a medial direction to terminate with a broad medial edge abutting against the basisphenoid. The medial edge of the pterygoid flange anterior to the basisphenoid is genuine and has not been formed as a result of damage to the specimen. This together with information from the anterior part of the pterygoid, indicates that a large interpterygoid vacuity (I.V.) was present. This vacuity is of importance in determining the affinities of Diarthrognathus.

The quadrate ramus is slender. As in Thrinaxodon this ramus does not appear to meet the quadrate, but terminates posteriorly upon the ventral edge of the quadrate ramus of the epipterygoid antero-medial to the pterygo-paroccipital foramen. In lateral view the quadrate ramus of the pterygoid is fairly substantial and the quadrate ramus of the epipterygoid overlaps it lightly. The anterior ramus has been partially destroyed, but may be reconstructed with confidence.

The postero-medial edge of the anterior part of the pterygoid is a well-preseved true edge which extends obliquely backwards and outwards. In the reconstruction of the palate (Fig. 6B) it has been continued backwards to meet

the medial edge of the pterygoid flange to form part of the lateral of the large interpterygoid vacuity (I.V.). A small tuberosity is present on the ventral surface of the pterygoid immediately in front of the interpterygoid vacuity. The anterior portion of the pterygoid is extended laterally by a short stout process (T.P.) to meet the medial surface of the coronoid (C.). On the basis of comparative anatomy this process would appear to be the transverse process of the pterygoid.

The ventro-lateral edge of the transverse process is drawn downwards and inwards to form a trough. The fleshy palate was presumably supported by the ventral edges of this trough. If this is correct, the pterygoids form the roof and side walls of the internal choanae. A well-pronounced ridge extends forwards upon the ventral surface of the pterygoid and terminates behind the posterior border of the vomer. In Fig. 7B the lateral surface of the transverse process is illustrated. It is deep dorso-ventrally and its outer surface which meets the coronoid is triangular in form. This relationship was confirmed on the right (Fig. 5B) where a small part of the transverse process of the pterygoid is preserved in contact with the coronoid. The outer surface of the transverse process slopes lightly inwards in a ventral direction, the result being that the lower jaws are firmly buttressed when apposed to the upper. The posterior surface of the transverse process is slightly concave. As a result of extensive damage to the pterygoid during the splitting of the sandstone block, it is impossible to determine the position of the pterygo-palatine suture ; neither could it be ascertained whether the transversum was present.

Damage to the anterior region of the palate has made the identification of the vomer (VO.) difficult. The structure which has been identified as the vomer may be a portion of the pterygoid. The vomer appears to consist of a broad arrow-shaped plate of bone lying upon the pterygoids. Two flanges are directed posteriorly and in an anterior direction the bone narrows rapidly. The central portion of the vomer is depressed by a narrow longitudinal groove.

The ventral surfaces of the palatines have been destroyed but they presumably contributed to the formation of the secondary palate. A flange of bone (A.P.) which extends upwards to form part of the lateral wall of the orbit and a small shelf of bone lying adjacent to this flange are the only portions of the palatine which are well preserved. Unfortunately the ventral surface and lateral edge of this shelf have been badly damaged. A deep depression, visible from above (Fig. 1) separates the dorsal flange of the palatine from the lateral shelf. The contribution of the palatine to the lateral wall of the obit and part of the floor of the orbit represents an advance in a mammalian direction.

As a result of the splitting of the sandstone block a section (N.C.) through the posterior portion of the nasal capsule has been obtained (Fig. 1). The matrix within this portion of the nasal capsule is a soft yellowish to white fine homogeneous deposit, completely devoid of any sand grains. It is readily distinguishable from the coarse sandstone matrix in which the entire skull is embedded. The nasal capsule matrix is roughly kidney-shaped in section and its anterior and lateral edges meet the frontals and lacrimals. The

section through the skull has exposed the cranial cavity between the ascending rami of the palatines. This space is filled with a coarse sandstone matrix. The ventral portion of the matrix was removed. A sharp line of demarcation separates the sandstone matrix of the cranial cavity from the soft matrix of the nasal capsule within the nasal, but no ossified septum could be observed between these two entities. From the limited dissection that could be undertaken in this region it appears that the posterior surface of the nasal capsule matrix slopes forwards in a dorsal direction to terminate immediately behind the preserved anterior edge of the frontals.

As there is no ossification between the cranial cavity and the nasal capsule, some explanation must be offered for the sharp demarcating line between the two cavities. A possible explanation is that the posterior wall of the nasal capsule was cartilaginous. It would be expected that sand grains would enter the nasal capsule through the external nostrils and come to lie against the anterior surface of the posterior wall of the nasal capsule. Sand grains entering the cranial cavity would come to lie against the posterior surface of the posterior wall of the nasal capsule. If after the consolidation of the sand grains the posterior cartilaginous wall to the nasal capsule disintegrated, an unoccupied space would remain within the skull. It would be expected that finely suspended material would permeate through the sandstone matrix and be deposited in this space. This deposit would be a replica of the posterior wall to the nasal capsule. If a large single olfactory foramen had been present in *Diarthrognathus*, as is found in living reptiles, sandstone matrix indicating the position of these foramina would be expected.

However, the fine matrix found in the posterior region of the nasal capsule forms a complete seal between the cranial cavity and the nasal capsule, indicating that no such single foramen was present. It is reasonable to assume that a cartilaginous cribiform plate as found in embryonic mammals was present. The small olfactory foramina penetrating this plate would presumably be too small to allow the transmission of sand particles. If special attention were to be paid to the nature of the matrix during the preparation of therapsid skulls much useful information as to the nature of the cartilaginous structures in these forms could possibly be obtained. In a specimen of the cynodont *Thrinaxodon* a similar phenomenon was encountered; the matrix of the nasal capsule was pure calcite in contrast to the calcareous mudstone in which the rest of the skull was embedded.

In most mammals the antero-dorsal edge of the cribiform plate terminates below the anterior edge of the frontals. On the basis of this relationship it appears likely that the frontals are nearly completely preserved.

Periotic, Pleurosphenoid, Epipterygoid and Sphenoid (Figs. 1–4, 6 & 7)

No sutures are visible dividing the periotic into opisthotic and prootic. The paroccipital process (P.PR.) is preserved only on the left. This process terminates laterally as a broad horizontally orientated sheet of bone ; the postero-lateral region apposed to the squamosal and the antero-lateral edge meeting the quadrate (Q.). A similar contact between the paroccipital process and the quadrate has been described in scaloposaurids (Watson, 1931 and

Crompton, 1955). The ventral surface of the paroccipital process is slightly concave ; this concavity is trough-shaped and terminates medially adjacent to a badly damaged depression in the periotic. This depression has been interpreted as the fenestra ovalis (F.O.). Unfortunately neither stapes is preserved, but they probably rested in depressions in the paroccipital processes. The paroccipital process forms the ventral border to a deep depression (P.T.F.) in the occiput (Fig. 4). Despite extensive damage to this region of the occiput it appears that this depression is bordered laterally by the squamosal, dorsally by the tabular and medially by the periotic and on the basis of this relationship appears to be homologous with the post-temporal fossa. In ventral view (Fig. 2) the anterior border of the paroccipital process is separated from the more anteriorly situated portion of the periotic by a shallow step. A similar step was described by Parrington (1946) in *Thrinaxodon* and was claimed to co-incide with the suture between the prootic and opisthotic.

The fenestra ovalis, although not well defined, appears to be exclusively bordered by the periotic as in mammals. This foramen is situated far more dorsally relative to the ventral surface of the basisphenoid than in either cynodonts or bauriamorphs.

Lateral to the foramen ovale a broad fan-shaped flange (lateral flange, L.F.) of the periotic passes outwards and downwards to terminate against the medial face of the quadrate ramus of the epipterygoid and the dorso-medial edge of the quadrate ramus of the pterygoid. The postero-lateral region of this flange is drawn backwards towards the periotic immediately anterior to the antero-lateral corner of the paroccipital process to all but form a slender lateral border to the large pterygo-paroccipital foramen (P–P.). Fragments of broken bone on the inner surface of the epipterygoid appear to indicate that the postero-lateral edge of the periotic flange was continued backwards to form a continuous lateral border to the pterygo-paroccipital foramen. In dorsal view (Fig. 1A) the lateral border of the pterygo-paroccipital foramen appears to be formed by the quadrate ramus of the epipterygoid because the dorsal edge of this ramus is turned slightly inwards to obscure the lateral edge of the posterior projection of the lateral flange of the periotic. The anterior border of the periotic flange is continued forward as a short process alongside the inner surface of the epipterygoid. The right lateral flange of the periotic has been destroyed.

Two broad plates of bone (O.S.) extend upwards and forwards from the dorsal surface of the basisphenoid behind the pituitary fossa, and from the periotics. A shallow step separates these plates from the ossified dorsum sellae. Posteriorly the two plates are separated by a narrow median gap, connecting the cranial cavity with the pituitary fossa, and anteriorly the two plates meet in the mid-line, with a low ridge indicating the point of fusion. At the base of these plates, immediately above the dorsum sellae, a marked depression (VI, Fig. 3B), is visible on the right and a damaged depression on the left. This depression has been interpreted as the foramen for the abducent nerve. The plates described above form the ventral border to the incisure prootica (V, Figs. 2 & 3B). A small foramen (VII.) is visible on either side

of the skull in these plates near the ventral edge of the incisura prootica. This foramen has been interpreted as the foramen for the facial nerve.

In the ontogeny of the vertebrate skull (Goodrich, 1930, De Beer, 1937) the pila antotica connects the dorsum sellae (crista sellaris, acrochordal plate) with the orbital cartilage. The orbital cartilages usually fuse in the mid-line to form the planum supraseptale which forms a floor to the anterior portion of the cranial cavity. The pila antotica is pierced by the canal for the abducent nerve. The pila antotica forms the antero-ventral border to the incisura prootica and the posterior and dorsal border of this incisura is formed by the otic capsule and the taenia marginalis posterior. Extending forwards from the anterior surface of the otic capsule to the base of the pila antotica is the prefacial commissure which separates the foramen for the facial nerve from the incisura prootica.

In modern reptiles the pila antotica remains cartilaginous, in therapsid reptiles it ossifies and in most mammals it disintegrates in the advanced onto-genetic stages. An ossified pila antotica has been identified in cynodonts (Parrington, 1946 a) and in scaloposaurids (Crompton, 1955 a). Olson (1944) refers to the ossified pila antotica as the antero-ventral process of the periotic. It is probable that an ossification of the orbital cartilage (planum supraseptale) forms the orbitosphenoid and an ossification of the remnants of the inter-orbital septum, the presphenoid. This question has been fully discussed by Olson (1944).

Although the proportions in *Diarthrognathus* are different from those found in modern reptiles it appears that the strip of bone lying antero-medially to the foramen for the facial nerve must be interpreted as an ossification of the prefacial commissure.

The broad plates extending forwards from the dorsum sellae which fuse anteriorly in the mid-line and form the ventral border to the incisura prootica must be considered composite structures. It appears that the connection between the pila antotica and the orbital cartilage has remained and the whole structure ossified to form a single ossification. That part of this ossi-fication which lies behind an imaginary line extending backwards, downwards and inwards from the anterior region of the incisura prootica to the anterior region of the gap between the two ossifications above the pituitary fossa must be considered to be the pleurosphenoid (ossification of the pila antotica) and the fused portions of these plates anterior to this line as the orbitosphenoids (O.S.) (ossification of the planum supraseptale). Unfortunately it was not possible to determine the anterior extent of the orbitosphenoids as the removal of the matrix in this region would have seriously endangered the specimen.

The dorsal border to the incisura prootica is formed by a broad plate of bone extending forwards from the prootic (P.O., Fig. 3B). This process has been identified by Olson (1944) as the antero-dorsal process of the periotic and probably represents an ossification of the taenia marginalis. The lateral flange of the periotic (L.F., Fig. 2) arises from the prootic as a horizontal sheet of bone immediately behind the posterior corner of the incisura prootica. In ventral view (Fig. 2) its antero-medial edge appears to form part of the border of the incisura prootica whereas in reality it lies lateral to this incisura.

On the right the lateral flange of the periotic has been lost but its area of attachment (A.L.F. Fig. 3B) to the prootic immediately behind the incisura prootica is visible.

The epipterygoid (E.P.) is well preserved on the left but it is difficult to illustrate because the lower jaw and zygomatic arch are still in position (Fig. 3A). On the right the epipterygoid has been exposed by the removal of the right lower jaw ; unfortunately the ventral portion has been destroyed. The dorsal portion of the epipterygoid has the form of an extremely broad plate of bone. The dorsal border has been damaged on the right, but on the left it can be seen that it meets the parietal with a long suture. The antero-dorsal edge of the epipterygoid meets the posterior extension of the frontals. The anterior border of the epipterygoid slopes gently backwards in a ventral direction and is drawn outwards to form a distinct ridge with the result that the outer surface of the bone is slightly concave. On the left where the pterygoid is complete the epipterygoid continues downwards to meet the pterygoid (Fig. 7B).

A large vacuity is present within the lateral wall of the orbit. This vacuity is bordered posteriorly by the anterior wall of the epipterygoid, dorsally by the frontals, anteriorly by the ascending plates of the palatines and ventrally by the pterygoids. The matrix within this vacuity was removed as far as the mid-line of the skull, but no indication of any ossification was found. The optic nerve presumably emerged through this vacuity. The posterior edge of the epipterygoid overlaps the periotic above the incisura prootica. The posterior border of the epipterygoid in the region of the incisura prootica is slightly indented. On the left it can be observed that below this incisura the epipterygoid extends backwards towards the quadrate (quadrate ramus). The trigeminal foramen (V.) (Fig. 7B) is thus bordered postero-dorsally by the ventral edge of the dorsal component of the periotic (this edge also forms the postero-dorsal border to the incisura prootica), and anteriorly and ventrally by the epipterygoid. A wide space, the cavum epiptericum, which lodges the ganglion Gasseri lies between the ossified pila antotica and the epipterygoid.

Although difficult to ascertain, it appears that the quadrate ramus of the epipterygoid meets the antero-medial edge of the quadrate. In dorsal view the quadrate ramus of the epipterygoid continues backwards below the squamosal towards the quadrate. A small piece of bone, identified as part of the epipterygoid, is apposed to the medial surface of the right quadrate. (Fig. 5A).

It would be interesting to discover whether the lateral edges of the orbito-sphenoids project upwards to meet the ventral surface of the parietal and thus excluding the epipterygoids from forming any part of the true side wall to the cranial cavity or whether the epipterygoids do partially contribute to the formation of the side wall. In lateral view (Fig. 3B) it can be seen that a large gap separates the antero-ventral surface of the orbitosphenoid from the dorsal surface of the basisphenoid and pterygoids. The ventral surfaces of the exposed portions of the orbitosphenoids are directed upwards and forwards. Further anteriorly they presumably lie parallel to the dorsal surface of the skull. The wide gap between the orbitosphenoid on the one

hand and the basisphenoid and bones of the palate on the other was presumably bridged by an interorbital septum. It is impossible to determine whether this was a cartilaginous septum or whether it was ossified and was lost before fossilization. However it does indicate that a deep interorbital septum or presphenoid was present. An interorbital septum appears to be present in all the known therapsids. Consequently in the advanced therapsid *Diarthrognathus* the suppression of the interorbital septum or presphenoid from a vertically orientated sheet of bone to a horizontally orientated bone forming part of the skull base as it does in mammals, has not yet been initiated. The brain of *Diarthrognathus* therefore occupies a relatively small volume of the available space within the skull and this aspect is truly reptilian.

The Occiput   (Figs. 4 & 7C)

The occiput of the skull may be divided up into three regions ; a central and two lateral (Fig. 4). The central portion is roughly triangular with the apex being formed by the junction of the sagittal and lambdoidal crests and the base by the basioccipital, exoccipitals and paroccipital processes. The lateral regions consist of two wings formed by the squamosals supporting the quadrates. In therapsids in general the squamosal above the quadrate is a deep bone which is hollowed in advanced cynodonts to lodge the external auditory meatus (Parrington, 1955). The extent of development of the external auditory meatus varies in different therapsid families. In *Diarthrognathus* the squamosal when viewed from behind is, in comparison with other therapsids, compressed dorso-ventrally. The course of the auditory meatus cannot be determined. It may have been lodged in the indentation between the postero-lateral process of the squamosal and the more lateral component of this bone.

Numerous fine cracks and areas of extensive damage to the occipital surface of the skull make the interpretation of this region extremely difficult. A faint, and in parts ill-defined, suture running horizontally above the supra-occipital (S.O.) appears to indicate the presence of an interparietal (I.P.). No suture between this bone and the parietal could be observed, but there is an indication of a suture between the interparietal and what has been identified as the tabular (T.). On the edge of the lambdoidal crest on the right it is possible to distinguish a clear suture between the squamosal and the tabular. It is impossible to ascertain the exact form of the tabular.

The post-temporal fossa or depression has been described above in the section dealing with the periotic.

The form and shape of the foramen magnum (F.M.) is clear from the figures and does not require description. The supraoccipital is slightly hollowed because its ventral edge above the foramen magnum is drawn outwards to form a thick rounded edge. Lateral to the foramen magnum there are deep depressions (O.D.) in the occiput, the floors of which are still covered with matrix. Unfortunately the depth of these depressions could not be ascertained without endangering the specimen. No suture dividing the exoccipital from the paroccipital and supraoccipital could be identified. A small oval depression is visible in the right exoccipital and there are faint indications of it on

the left. These depressions in the occiput alongside the foramen magnum may possibly be interpreted as areas for muscle attachment.

The Quadrate (Figs. 2, 3A, 5, 6B & 7)

Both quadrates (Q.) are fairly well preserved but no dividing suture between the quadrate and the squamosal could be distinguished. The faint ridge upon the posterior edge of the squamosal (Fig. 4) may indicate the border between these two bones. In occipital view the ventral border of the quadrate is S-shaped. On the left a small piece of bone (X.) is preserved in contact with this ventral edge. This is most probably a fragment of the articular which has been lost on this side of the skull.

In ventral view (Figs. 2 & 5B) the quadrate has a semi-circular posterior border which is drawn downwards to form a high ridge. Anterior to this ridge the articular surface of the quadrate is markedly concave. This is important as in all known therapsids including *Bienotherium* and *Oligokyphus* the articular face of the quadrate is either flat or convex, but never concave. This feature will be returned to when discussing the nature of the articulation of the lower jaw with the skull.

The antero-medial surface of the quadrate appears to meet the lateral surface of the paroccipital process and anterior to this point the antero-medial face of the quadrate appears to establish contact with the posterior termination of the quadrate ramus of the epipterygoid. This relationship is difficult to establish on the left as the region is obscured by the displaced angular. On the right however, a small fragment of bone (EP., Fig. 5A) is preserved against the medial surface of the quadrate; this appears to be a part of the epiptery-goid. The antero-medial portion of the quadrate is drawn downwards and outwards to grip the dorsal convex surface of the articular. As both lower jaws are in position it could not be established how far the quadrate extends forwards upon the ventral surface of the squamosal above the articular. On the right (Fig. 5B) part of the articular process of the dentary is absent and it can be observed that the articular surface of the quadrate is continuous with the articular face of the squamosal. In the reconstructed drawing of the palate (Fig. 6B) the lower jaw has been removed to illustrate this feature.

The lower jaw (Figs. 1–7)

Only the posterior portions of the dentaries (D.) are preserved; the entire dentigerous region and the angle of the jaw having been lost. However, several extremely important facts may be established from what remains. Both lower jaws appear to be preserved in their correct position relative to the remainder of the skull.

The coronoid process (C.P.) is exceptionally large and is formed by a thin sheet of bone the apex of which is directed slightly posteriorly (Fig. 5). The anterior border of the left coronoid process has been deflected inwards but this is probably the result of pressure subsequent to death (Fig. 1). The medial surface of the antero-ventral region of the coronoid process is thickened to form a buttress against which the coronoid (C.) is apposed. Unfortunately the ventral portions of the coronoids are not preserved. A simple suture is
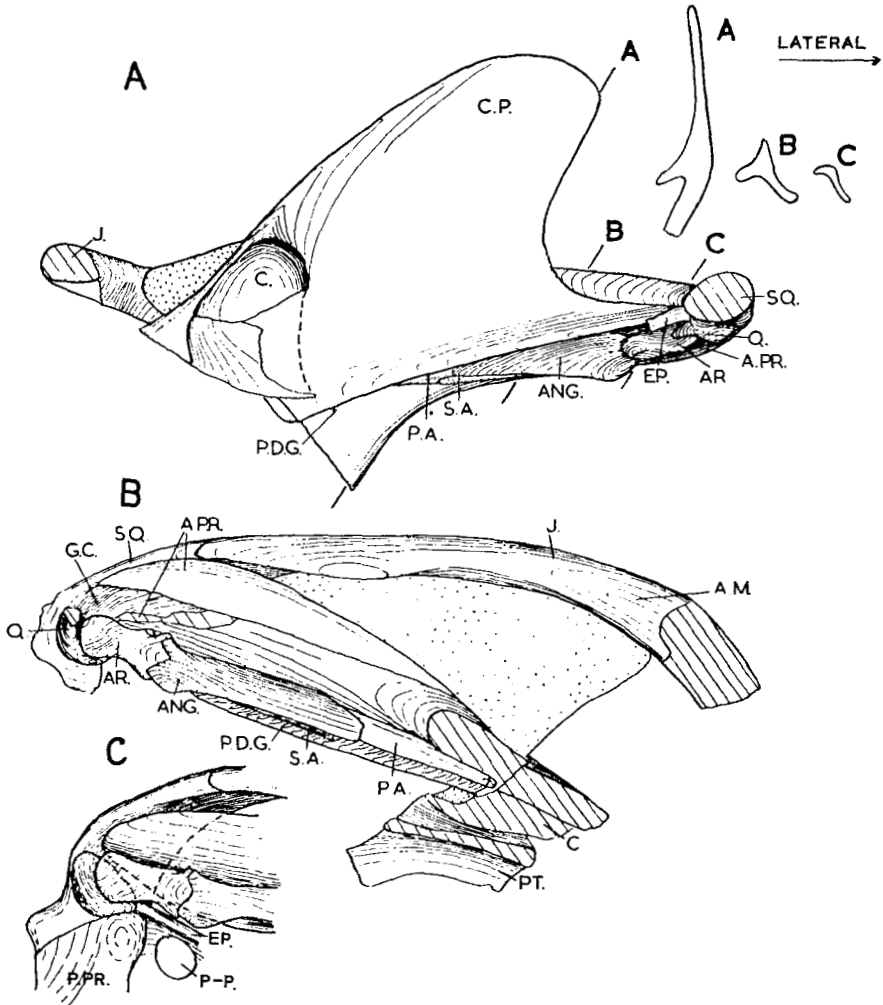
Fig. 5.—*Diathrognathus broomi* gen. et sp. nov. A, inner view of the preserved portion of the
right lower jaw and three sections through the articular process of the dentary, B, ventral
view of the lower jaw and C, reconstruction of the jaw articulation.   All × 3.   (Key to
lettering, p. 216).

visible between the preserved portions of the coronoids and the buttress of the
coronoid process on both sides of the skull.   The posterior and dorsal edges
of the coronoids are thick and the bone thins in an anterior and ventral
direction.   The anterior edge is parallel for a short distance with the anterior
border of the dentary.   The medial surface of the coronoid is flattened to
meet the triangular lateral surface of the transverse process of the pterygoid.
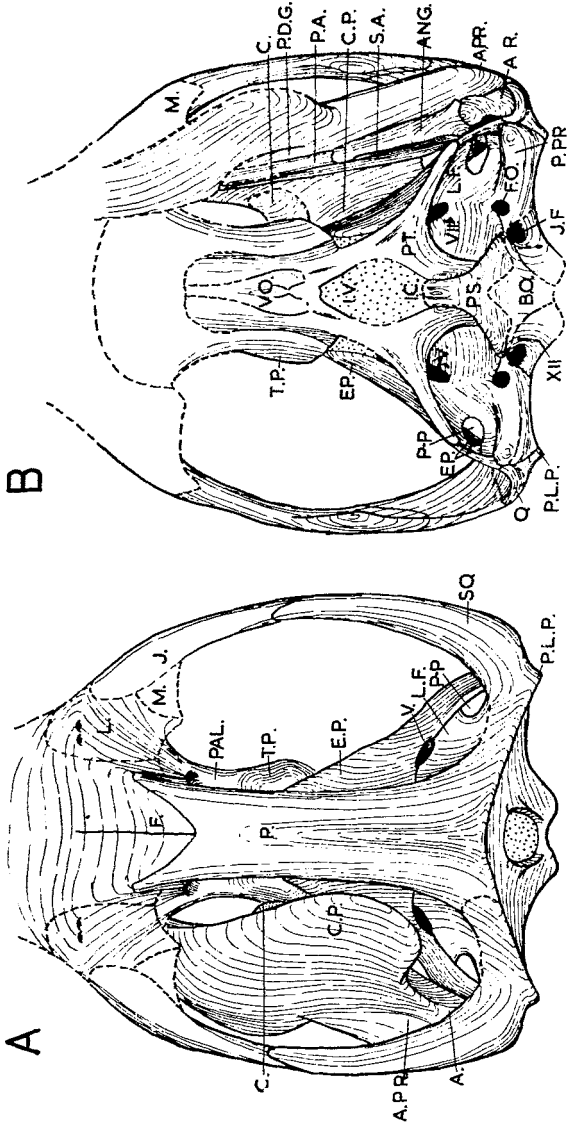This contact was observed on both sides of the skull.   A horizontal section

Fig. 6.—*Diarthrognathus broomi* gen. et sp. nov. Reconstruction of preserved portion of the skull. A, dorsal and B, ventral. Both × 2. (Key to lettering, p. 216).
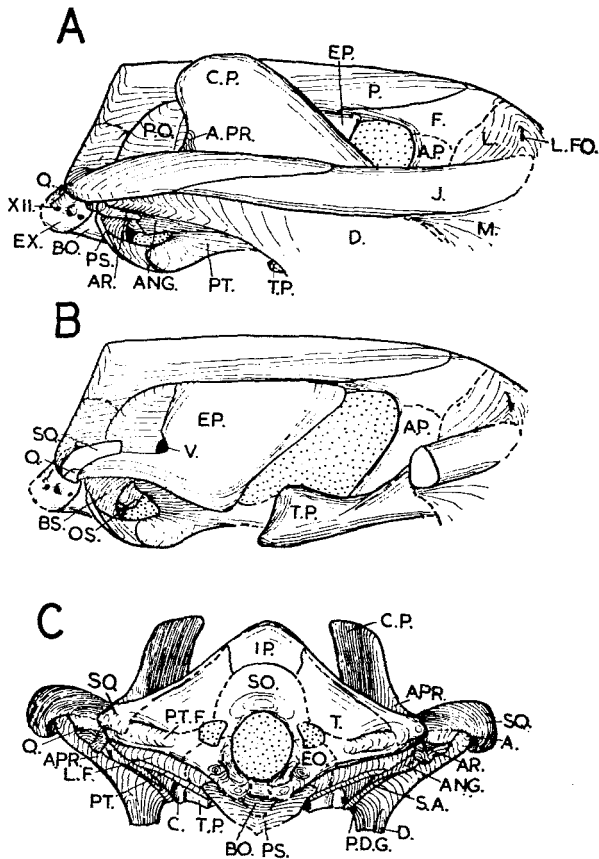
Fig. 7.—*Diarthrognathus broomi* gen. et sp, nov.   Reconstruction of preserved portion of the skull.   A, lateral, B, lateral with lower jaw and zygomatic arch removed and C, occipital. All × 2.   (Key to lettering, p. 216).

through the coronoid adjacent to its contact with the pterygoid was obtained by the splitting of the sandstone block in which the skull was embedded (Fig. 1).   In this section the curved lateral border of the coronoid fits into a shallow depression on the medial face of the dentary.   A boss of bone on the medial surface of the dentary has been described in *Bienotherium* (Watson, 1942 and Young, 1947), Broom's Ictidosaurian A (Broom, 1932 and Watson, 1942) and in *Oligokyphus* (Kuhne, 1949) but these authors never considered it to be a coronoid.   Gregory (1951) indicated that the boss in *Bienotherium* was possibly a coronoid.   The bosses found in *Diarthrognathus broomi* are clearly coronoids and there is evidence of sutures in the identical position in Broom's Ictidosaurian A.

In therapsids (with the exception of advanced cynodonts) the posterior border of the dentary slopes gently forwards in a ventral direction from the

apex of the coronoid process. The postdentary bones project backwards toward the quadrate beyond the posterior border of the dentary.   In *Diarthrognathus* a fairly long and stout articular process (A.PR.) projects backwards from the main body of the dentary to establish contact with the ventral surface of the squamosal. In view of the fact that the form of this process and its relationship to the dentary are difficult to describe, three schematic transverse sections through the dentary and articular process have been given in Fig. 5. The positions of these sections are indicated by the parallel lines annotated A, B and C in Fig. 5A. The postdentary bones are not shown in these sections. In the advanced cynodont *Protacmon* (Watson, 1951), a thin sheet of bone lying laterally to the postdentary bones projects posteriorly from the main body of the dentary but in contrast to the conditions existing in *Diarthrognathus* does not establish contact with the squamosal neither is it broadened latero-medially. In dorsal view the articular process in *Diarthrognathus* (Fig. 1) is broad and it passes backwards below the anterior edge of the squamosal. The dorsal surface of the articular process (A., Fig. 1) immediately in front of the squa-mosal contact is convex. More anteriorly a small ridge arises from the dorsal surface of the articular process ; it extends forwards and is continuous with the narrow posterior edge of the coronoid process.

Medial to this ridge a shelf of bone extends outwards and downwards (Fig. 5, sections A, B and C) from the articular process. This shelf forms the dorso-medial roof to the postdentary groove (P.D.G.). Lateral to this ridge a broad shelf extends outwards and downwards (sections B and C) to form the dorso-lateral roof to the postdentary groove. In Figs. 2 and 5B the post-dentary groove formed by these two shelves is illustrated. It is a deep groove below the articular process and continues forward below the coronoid process and lodges the postdentary bones. Unfortunately the anterior extent of this groove could not be determined as the dentary is incomplete.

A small portion of the dentary which extends downwards below the articular process of the dentary and the postdentary groove towards the angle of the jaw is preserved. It has the form of a thick plate and its posterior border is roughly in line with the posterior border of the coronoid process. This region forms the lateral wall to the anterior region of the postdentary groove. The narrow posterior edge of the broad shelf of bone forming the dorso-lateral wall to the postdentary groove (Fig. 5A, section C) articulates with the anterior wall of the glenoid cavity (G.C.) formed by the squamosal. On the right (Fig. 5B) damage to this region has exposed a section through the articular process at one of the points of contact   This articulation between the dentary and the squamosal lies adjacent to the articulation between the articular (AR.) and quadrate. Dorsal to this point it appears that the articular face of the dentary curves inwards and expands slightly. The expanded portion (A, Fig. 1) is visible in dorsal view. Consequently no articular condyle of the type which is found in mammals is present in *Diarthrognathus* but nevertheless a definite articulation between the dentary and the squamosum has been established in this form.

In support of the claim that the articulation of the dentary with the squamo-sal is natural and not an artifact produced as a result of pressure subsequent to

death, forcing the dentaries backwards, are the following considerations : the dentary was preserved in contact with the squamosal on both sides of the skull, identical relations being found ; the coronoids are in contact with the transverse processes of the pterygoids, a contact which would be lost if the dentaries were moved sufficiently forward to enable the dentaries to lose contact with the squamosals ; the dentary has a clear articular process ; and the squamosals, in contrast to all other known therapsids with the possible exception of *Oligokyphus*, form a clear glenoid cavity.

The postdentary bones are well preserved, but only on the right are they firmly lodged in the postdentary groove. Considering the size of these bones it is indeed remarkable to find them preserved in their correct position relative to the dentary and the quadrate. In ventral view the articular has a narrow semicircular posterior edge which articulates with the concave anterior face of the quadrate. The ventral surface of the posterior portion of the articular is flat to concave ; the medial and posterior border of this area being formed by a ridge which extends from the ventro-medial edge across the ventral surface of the articular. Anterior to this ridge a small process directed antero-medially and slightly upwards arises from the main body of the articular to meet the postero-dorsal surface of what has been identified as the angular (ANG.). The dorsal surface of the articular is convex and appears to articulate with the concave antero-ventral surface of the quadrate.

The angular consists of a long slender splint of bone. Its postero-ventral edge is continued backwards, downwards and inwards to form a small, inconspicuous lamina. A small plate of bone, presumably the surangular or prearticular is apposed to the dorso-medial surface of the angular and a clear suture between these two bones is visible along the ventral edge. Anteriorly the two bones appear to be fused. The anterior regions of both these bones are missing.

A thin splint of bone, presumably the splenial or prearticular (P.A.) lies above the angular and continues forwards in the postdentary groove beyond the anterior termination of the angular and surangular. The posterior extent of this bone could not be determined as it is overlain by the angular and surangular.

The double articulation

Mainly as the result of the researches of Carus (1818), Meckel (1820) and Reichert (1837) a theory was developed which claimed that the mammalian malleus, incus and stapes are homologous with the reptilian articular, quadrate and stapes respectively. This theory, commonly known as Reichert's theory, has been accepted and supported by a vast number of workers. The evidence for this theory has been comprehensively reviewed by Goodrich (1930).

Study of the structure of the mammal-like reptiles has shown that throughout the history of this group there has been a tendency to reduce the size of the postdentary bones and to increase the size of the dentary. In advanced therapsids (cynodonts, tritylodontids, etc.), it extends so far posteriorly that it all but establishes contact with the squamosal. The articulation of the dentary with the squamosal has long been accepted as a fundamental diagnostic

feature of mammals and Reichert's theory presupposes that at some stage of the development of mammals from reptiles the reptilian jaw articulation between the articular and the quadrate must have existed together with the articulation between the dentary and the squamosal. Only when a functional articulation is obtained between the dentary and squamosal can the reduced quadrates and articulars migrate inwards to form the mammalian malleus and incus. The stage in which both articulations exist side by side has been found to exist in *Diarthrognathus*. Parrington (1949) expressed the view that this type of articulation should be found in a transitional form.

The most important feature of the double articulation of *Diarthrognathus* is the form of the articulating surfaces of the quadrate and articular ; that of the quadrate being concave and the articular convex. In all known therapsids the quadrate is always convex to flat and the articular concave to flat.

In this connection it is interesting to note that in typical mammals the malleus (articular) has a convex articular surface which meets a concave articular face in the incus (quadrate), i.e. similar to the relationship found in *Diarthrognathus*.

The concave articular surface of the quadrate is continuous with the concave articular surface of the glenoid cavity formed by the squamosal. The articular surfaces of the articular and dentary lie against one another in the same plane.

Consequently articular and dentary form a composite single condyle which articulates with a composite single glenoid cavity formed by the quadrate and the squamosal. A reconstruction of the double articulation is shown in Fig. 5C.

TAXONOMIC POSITION AND RELATIONSHIPS

Taxonomic position

Before discussing the possible relationship between *Diarthrognathus* and the advanced therapsids, a summary of the mammalian and reptilian characteristics of the skull of *Diarthrognathus* will be given in order to determine whether this form should be classified as a mammal or reptile. Mammalian characteristics found in typical therapsids have not been listed. The following mammalian or advanced characteristics are present in *Diarthrognathus* :

1. A well developed articular process of the dentary articulates with a glenoid cavity in the squamosal.

2. The articular surface of the articular (malleus) is convex and that of the quadrate (incus) concave.

3. Both the frontals and the palatines contribute to the formation of the lateral wall of the orbit.

4. The transverse processes of the pterygoid are considerably reduced compared with typical therapsids.

5. A cribiform cartilaginous mesethmoid was probably present.

6. The prefrontal and postorbital appear to have been lost.

7. The fenestra ovalis is completely surrounded by the periotic.

The following reptilian or primitive characteristics are present :

1. The lower jaw is a composite structure and articulates with the quadrate in addition to the squamoso-dentary articulation.

2. A coronoid is still present although it has lost contact with the postdentary bones.

3. The squamosal does not contribute to the true side wall of the cranial cavity.

4. The internal carotids penetrate the basisphenoid near the mid-line of the skull.

5. A large parasphenoid is present.

6. A large interpterygoid vacuity is present.

7. The pituitary fossa is exposed to the exterior through a large foramen.

8. The periotics are large and a massive paroccipital process is present.

9. It appears that a deep interorbital septum (cartilaginous or ossified) was present which separated the orbitosphenoids from the skull base. This indicates that the brain was reptilian in size compared with that of typical mammals and that the presphenoid (interorbital septum) has not yet been suppressed to form a horizontally orientated sheet of bone forming part of the skull base.

10. The epipterygoid although expanded is not penetrated by the branches of the trigeminal nerve.

11. A quadrate ramus of the epipterygoid meets the quadrate. This ramus supports the quadrate ramus of the pterygoid.

12. A tabular and post-temporal fossa are present.

An articulation between the dentary and the squamosal has long been accepted as one of the fundamental osteological features differentiating reptiles from mammals. However, in view of the composite nature of the lower jaw and the numerous other reptilian features present in the skull, *Diarthrognathus* is best classified as a reptile.

Relationships

The establishment of a relationship between *Diarthrognathus* and therapsids is difficult as a large time gap separates the relatively well-known fauna of the *Cynognathus* zone from that of the Cave Sandstone. Only fragmentary remains are known from the Red Beds and Molteno Beds, with the possible exception of the fauna from the Middle Triassic of Tanganyika, which is probably of Molteno age.

Three therapsid groups will be considered ; the Cynodontia. Bauriamorpha and Ictidosauria (all as classified by Watson, & Romer, 1956). It is not proposed at this stage to attempt to establish the relationship between *Diarthrognathus* and early mammals of the late Tirassic and Jurassic. These forms are known mainly from isolated teeth and jaws and consequently will be discussed in the paper dealing with Broom's Ictidosaurian A in which the teeth are well preserved. The mammalian finds reported by Kermack (1956) will be of the greatest importance in establishing a relationship between mammals and *Diarthrognathus*.

Cynodonts

In order to compare *Diarthrognathus* with cynodonts it is necessary to outline briefly the main trends of cynodont development from their first known appearance in the *Cistecephalus* zone in order to determine whether the features common to *Diarthrognathus* and cynodonts indicate a true relationship or are the result of convergence.

There has been considerable debate on the origin of cynodonts. Watson (1951) is of the opinion that they arose from gorgonopsids whereas Broom (1938), basing his conclusion on the appearance of early cynodonts, is of the

opinion that they arose from the therocephalians. The cynodonts have recently been classified by Haughton & Brink (1954), and Watson & Romer (1956). Primitive cynodonts have been placed in the family Procynosuchidae. Haughton & Brink (1954) have placed *Protocynodon* (Broom, 1949), *Silphedestes* (Brink, 1951) and *Silphedocynodon* (Brink, 1951) in this family, but Watson & Romer have placed them in the Bauriamorpha. They are certainly extremely scaloposaurid-like in appearance and their correct classification can only be determined when they have been further prepared. They are characterized by broad parietals and slender zygomatic arches. *Protocynosuchus* (Broom, 1938 b) is one of the better known of the primitive cynodonts. The zygomatic arch is slender, but the squamosal is fairly deep above the quadrate. The parietal has a pronounced sagittal crest, but the bone is fairly broad compared with later cynodonts. The secondary palate is incomplete and the occipital condyle only incipiently divided into two. A narrow interpterygoid vacuity is present in *Procynosuchus rubidgei*, but it is far narrower than that found in scaloposaurids. The epipterygoid is expanded and is firmly joined to the prootic. The quadrate ramus of this bone does not appear to reach the quadrate.

In *Levachia* (Broom, 1948) the zygomatic arch is slender and the squamosal deep above the quadrate. The parietals are compressed. Brink (1951) has shown that no interpterygoid vacuity is present. Primitive features present in this form are the absence of a coronoid process to the dentary ; the opening of the jugular canal is directed backwards and the paroccipital process appears to meet the quadrate. Unfortunately it is not known whether a lateral flange to the prootic is present in the Procynosuchidae ; this flange is known in all the remaining cynodonts. There is no evidence of an ossified spheneth-moid element in this family. The members of the family Thrinaxodontidae (Galesauridae) are more advanced than the Procynosuchidae and are known mainly from the *Cistecephalus* and *Lystrosaurus* zones. Other than different cranial proportions and differences in the shape of the teeth, the basic structure of the Thrinaxodontidae appears to be very similar. The best known member of the family is *Thrinaxodon* (Parrington, 1946 a). In this form the parietals are markedly constricted, the zygomatic arch is relatively deeper than in the Procynosuchidae, the squamosal is deep above the quadrate and an incipient external auditory meatus is present in this region, the secondary palate is complete, an interpterygoid vacuity is absent. The foramina for the internal carotid arteries lie near the midline of the basisphenoid, the occipital condyles are formed by the exoccipitals, the paroccipital process does not appear to meet the quadrate, the quadrate rami of the pterygoids meet the quadrate whereas those of the epipterygoid, although well developed, do not. A large periotic flange enclosing the pterygo-paroccipital foramen is present and a small ossified pila antotica or pleurosphenoid penetrated by the abducent nerve is present. Sections through the skull have been given by Broom (1938 a) Parrington (1940) and Olson (1944). Although Parrington and Olson found no indication of an ossified sphenethmoid element, Broom claimed the presence of a lightly calcified sphenethmoid element. The dentary is larger in the Thrinaxodontidae than in the Procynosuchidae.

The cynodonts of the *Cynognathus* zone with the exception of the survivors of the Thrinaxodontidae fall into two families ; the Diademodontidae and Cynognathidae. These families have been described by several authors and the following statements have been based mainly on the descriptions of Watson (1911), Broili & Schröder (1934, 1935) and Brink (1955). In these two families the trend of development visible in the earlier cynodonts have been carried further. The zygomatic arch is massive, the squamosal above the quadrate is deeply grooved to form the external auditory meatus, the parietal and cranial base is further constricted, the quadrate ramus of the pterygoid is absent, the pterygoid has a long sutural connection with the basisphenoid, the internal carotids enter the skull further laterally than they do in the earlier cynodonts. In the Diademodontidae the lateral border of the pterygo-paroccipital foramen is formed by the quadrate ramus of the epipterygoid except in *Protacmon* (Watson, 1920) where the quadrate ramus of the epiptery-goid is reduced as in some of the Cynogathidae, to transform this foramen into a deep notch. The dentary has increased in size in both families and has developed an angle to the jaw below the level of the postdentary bones. An incipient articular process is present in *Protacmon* (Watson, 1951), but it does not meet the squamosal. Small orbitosphenoids firmly attached to the antero-dorsal tip of the epipterygoid, frontals and parietals have been described by Brink (1955) in *Diademodon*. In *Diademodon* (Brink, 1955) and in an unidentified cynodont from East Africa (Parrington, 1946 a), the trigeminal foramen has been divided into two foramina.

Cynodonts occur in the Middle Triassic of Tanganyika in beds which are probably of the same age as the Molteno Beds of South Africa. In one of the Tanganyika cynodonts, *Cricodon* (Crompton, 1955 b), a well developed post-dentary groove supporting reduced postdentary bones is present. This feature does not appear to have been developed to any marked extent in earlier cynodonts. It appears therefore that the cynodonts are characterised by the following trends of development :

1. Increase in the size of the dentary and development of a postdentary groove in the advanced forms.
2. Reduction in the size of the postdentary bones.
3. Increase in the depth of the zygomatic arch.
4. Increase in the depth of the squamosal above the quadrate, and the development in this bone of an external auditory meatus.
5. Increased lateral compression of the parietals.
6. Early obliteration of the interpterygoid vacuity.
7. Reduction and disappearance of the quadrate ramus of the pterygoid.
8. Increase in the length of the quadrate ramus of the epipterygoid and later reduction.
9. Development of a secondary palate.
10. Development of a double occipital condyle.
11. Loss of contact between the paroccipital process and the quadrate.
12. Early development of the lateral flange to the periotic.

There appears to be no marked trend to increase the degree of ossification of the sphenethmoid elements.

The large interpterygoid vacuity of *Diarthrognathus* appears to be a primitive characteristic and the absence of this feature in any of the known cynodonts

(only a remnant is present in some of the early cynodonts) appears to exclude any of the known cynodonts from being ancestral to *Diarthrognathus*.

It is, however, possible that an early and yet unknown cynodont in which a large interpterygoid vacuity, slender zygomatic arches and lateral flanges to the periotic were present, could have been ancestral to *Diarthrognathus*. Several of the trends of development in the cynodonts are certainly not towards *Diarthrognathus*, e.g. obliteration of the interpterygoid vacuity, increase in the depth of the zygomatic arch, reduction and disappearance of the quadrate rami of both the pterygoid and the epipterygoid, and the development of a deep external auditory meatus. The extremely wide pterygoid flange adjacent to the interpterygoid vacuity in *Diarthrognathus* is a characteristic not found in cynodonts and the nature of the basipterygoid articulation is different in both.

Despite the fact that cynodonts do not appear to be ancestral to *Diarthrognathus*, the similarities of some of the cranial structures is remarkable, e.g. the form of the epipterygoid, the periotic flange, the form of the dentary in the advanced cynodonts. Parallel evolution is a characteristic of the various therapsid groups and it appears likely that the similarities discussed above are a further example of this feature.

Bauriamorpha

Watson (1956) has included several forms in this infraorder which were formerly included in the Therocephalia. (Haughton & Brink, 1955). The Bauriamorpha are characterised by the retention of a primitive feature, viz. a large interpterygoid vacuity, which hints at a relationship between the Bauriamorpha and *Diarthrognathus*.

One of the most important families of the Bauriamorpha for the purpose of establishing a relationship with *Diarthrognathus* is the Scaloposauridae. This family extends from the *Tapinocephalus* zone to the *Lystrosaurus* zone and the phylogenetic trends within this family were determined by Watson (1931) and reviewed by Crompton (1955). The Scaloposauridae are characterised by several features found also in *Diarthrognathus* ; a slender zygomatic arch, shallow squamosal above the quadrate, broad parietals, large interpterygoid vacuity, basipterygoid articulation where known is similar to that of *Diarthrognathus*, broad ventral face to the ossified pila antotica forming a roof to the lateral opening of the pituitary fossa, well ossified sphenethmoid element (the ossified pila antotica and orbitosphenoid are not joined as they are in *Diarthrognathus*), the internal carotids enter the skull through two small foramina near the midline of the basisphenoid, and the paroccipital process has a broad contact with the quadrate. In addition to these similarities in skull structure, there is a tendency in the development of the Scaloposauridae to reduce the postorbital arcade, to loose the pineal foramen and to develop a secondary palate.

Several marked differences in the skull structure, however, differentiate the scaloposaurids from *Diarthrognathus*. A large suborbital vacuity is present in the scaloposaurids and there appears to be no evident tendency to reduce this vacuity in the development of the family. No such vacuity appears to

be present in *Diarthrognathus*. A suborbital vacuity is found in most thero-cephalians, but it has been reduced in one of the therocephalian families, the Whaitsiidae. Consequently it is not impossible that a similar development could have taken place in the descendants of the scaloposaurids. The epi-pterygoid is only mildly expanded in the scaloposaurids compared with *Diarthrog-nathus* and cynodonts, but more expanded than in the *Tapinocephalus* and *Endothiodon* zone therocephalians from which the scaloposaurids were most probably derived. A continued increase in the size of the epipterygoid is possible in the descendants of the scaloposaurids. The quadrate process of the epipterygoid is only rudimentary in the scaloposaurids. There is no evidence of a lateral flange to the periotic enclosing a pterygo-paroccipital process in scaloposaurids. This feature appears to be present only in *Diarthrognathus* and cynodonts. In an earlier paper (Crompton, 1955 a) it was concluded that the skull of one of the primitive scaloposaurids, *Ictido-suchops intermedius*, was kinetic. Even if the skull was not markedly kinetic, the two sections of the skull, viz. maxillary and occipital were not firmly joined indicating that the ancestors of the scaloposaurids probably had metakinetic skulls. It appears probable that the two sections of the cynodont skull are firmly cemented ; the tabular is suturally connected to the paroccipital process, the epipterygoid to the skull base, the epipterygoid to the parietal and the pterygoid to the parasphenoid and basisphenoid. It is not improbable that the lateral flange of the periotic was developed in order to help firmly join the two sections of the skull. Consequently it is possible that this feature could have developed in the descendants of the scaloposaurids if the skull ceased to be kinetic.

It appears that the similarities in skull structure in *Diarthrognathus* and the scaloposaurids are sufficient to indicate that the former could be derived from the latter. In addition it appears that the features which differentiate *Diarthrognathus* from the scaloposaurids, but which are common to *Diarthrog-nathus* and cynodonts, could have been independently acquired in the cynodonts and the line leading from the scaloposaurids to *Diarthrognathus*.

Watson (1956) has placed the advanced scaloposaurids in two families, the Ericiolacertidae and the Bauriidae. *Ericiolacerta* (Watson, 1931) is more advanced than the Scaloposauridae in that the secondary palate is completely formed and the postcanine teeth are more complicated. It is perhaps the closest known ancestral form to *Diarthrognathus*. The gomphodont teeth of of the Bauriidae appear to indicate that the members of this family are too highly specialized in this particular aspect to be considered ancestral to *Diarthrognathus*. *Bauria cynops* (Boonstra, 1938, Brink, 1955 and Crompton, 1955 a) is the best known member of the Bauriidae. The quadrate of this form is of particular interest. It consists of a simple broad wedge-shaped bone lying against the inner surface of the squamosal. Its medial edge is in contact with the paroccipital process. It is possible to derive the quadrate of *Diarth-rognathus* from this type of quadrate simply by hollowing the articular surface. A similarity between *Bauria* and *Diarthrognathus* is the presence in both of a sagittal crest.

The development of *Diarthrognathus* from a scaloposaurid of *Lystrosaurus* zone times would involve ; the loss of the prefrontals and postorbitals ; increase in the length of the parietal ; further expansion of the epipterygoid ; development of the quadrate ramus of the epipterygoid to reach the quadrate ; development of a periotic flange to enclose the pterygo-paroccipital foramen ; further increase in the size of the dentary and establishment of an articulation between this bone and the squamosal ; further reduction in the size of the postdentary bones ; development of a hollow articular surface to the quadrate ; reduction of the transverse process of the pterygoid ; development of a double occipital condyle (this condition has almost been reached by *Bauria* (Crompton, 1955 a)), and the disappearance of the suborbital vacuities.

The scaloposaurids are sufficiently unspecialized to be considered ancestral to *Diarthrognathus* and the trends outlined above in the descendants of scaloposaurids are quite possible. It is not impossible that forms showing these developments may be discovered in the thick deposits of the Red Beds, Molteno Beds, and *Cynognathus* zone beds. With the possible exception of the *Cynognathus* zone the other two beds have not been systematically searched. Until recently it was assumed that the Molteno Beds were practically barren, but the recent investigations of Dr. F. Ellenberger have shown this to be far from correct.

Ictidosauria

Broom (1929) proposed the suborder Ictidosauria for the reception of his Ictidosaurian A, and *Diarthrognathus broomi* (Ictidosaurian B) from the Cave Sandstone of Ladybrand. He also included *Karoomys*, *Pachygenelus* and *Tritheledon* in this suborder. In 1932 he also included *Lycorhinus*. Later von Huene (1933) added *Dromatherium, Microconodon* and *Tribolodon*. Young (1940) described *Bienotherium* as a mammal, but Watson (1942) pointed out that it was a reptile and placed it together with *Tritylodon* in the Ictidosauria. Watson was of the opinion that this suborder included highly specialized terminal forms. Romer (1945) added *Eozostrodon* and the Microleptidae to the Ictidosauria.

Parrington (1946 b) reviewed the known characteristics of the suborder and concluded that the only forms which should be included in the Ictidosauridae were the tritylodontids (*Tritylodon, Bienotherium* and *Oligokyphus*), *Tritheledon*, Broom's Ictidosaurian A and *Diarthrognathus*. Parrington pointed out that these forms had the following characteristics in common ; loss of prefrontal and postorbitals ; reduction of the postdentary bones ; ridge on the dentary to support these postdentary bones ; cheek teeth withdrawn on to the palate between the suborbital fossae. Parrington divided the Ictidosauridae into two groups, one containing the tritylodontids and the other *Tritheledon*, Broom's Ictidosaurian A and *Diarthrognathus*. He considered that the two groups could possibly have been derived independently from the cynodonts, but pointed out that very little was known of Broom's ictidosaurians.

Young (1947) stressed the marked differences between the specimens Broom had placed in this suborder. He raised the Ictidosauria to an order,

consisting of the following suborders ; Tritylodontoidea, Ictidosauroidea and Trithelodontoidea (*Pachygenelus*, *Tritheledon* and *Lycorhinus*).   Haughton & Brink (1954) included all the known South African forms which had from time to time been included in the Ictidosauria in the cynodonts.   No attempt was made to classify Broom's ictidosaurians.

Finally Watson & Romer (1956) classified the Ictidosauria as an infraorder of the Theriodontia and divided this infraorder into five families ; an un-named family for the Ladybrand specimens, Tritholodontidae, Tritylodontidae, Microleptidae and a family including the possible mammals of the Rhaetic. They are in agreement with Haughton and Brink that *Karoomys*, *Lycorhinus* and *Pachygenelus* are cynodonts.

In view of the fact that *Diarthrognathus* is known only from the posterior portion of the skull (postcranial skeleton still to be described) it is not the intention of this paper to attempt to reclassify the Ictidosauria.   This will be done when the remainder of the Ladybrand material has been described. The only members of the Ictidosauria with which *Diarthrognathus* can be successfully compared are the Tritylodontidae, for it is only in this family that the posterior portion of the skull is preserved.

The following features are common to the skulls of *Diarthrognathus* and the tritylondontids :

1. Prefrontal and postorbital absent.
2. Pineal foramen missing.
3. Broad frontals.
4. Broad nasals.
5. Frontal contributes to the formation of the side wall of the orbit.
6. Long parietal supporting a sagittal crest.
7. Teeth withdrawn on to the palate between the suborbital fossae.
8. Transverse process of the pterygoid considerably reduced.
9. Expanded epipterygoid.
10. Lateral flange of the periotic almost enclosing a pterygo-paroccipital foramen.
Reduction of the quadrate ramus of the epipterygoid in *Oligokyphus* (Kühne, 1949) has transformed this foramen into a notch.
11. Fenestra ovalis completely surrounded by the periotic.
12. Coronoid on the inner surface of the dentary.   Watson (1942) and Young (1947) have interpreted this as a boss of the dentary and not as a coronoid.
13. Groove in the dentary to support the reduced postdentary bones.
14. Angle to the dentary below the level of the postdentary bones.

Despite these striking similarities there are several fundamental differences :

Diarthrognathus	Tritylodontids
1. Slender zygomatic arch.	Deep zygomatic arch in *Bienotherium*, shallow in *Oligokyphus*.
2. No visible external auditory meatus.	Well developed external auditory meatus in *Bienotherium*, less well developed in *Oligokyphus*.
3. Broad parietals.	Parietals constricted.
4. Teeth do not extend backwards to near the posterior border of the transverse process of the pterygoid.	Teeth extend backwards to near the posterior border of the transverse process of the pterygoid.
5. Large interpterygoid vacuity.	No interpterygoid vacuity.

6. Epipterygoid narrow contact with the skull base.

Epipterygoid broad contact with the skull base.

7. Long quadrate ramus of the pterygoid.

No quadrate ramus to the pterygoid.

8. Lower jaw articulates with glenoid cavity in squamosal.

Lower jaw does not articulate with the squamosal, although a non-functional glenoid fossa appears to be present in *Oligokyphus*.

9. Hollow articular surface to quadrate.

Convex articular surface to quadrate in *Oligokyphus*; condition in *Bienotherium* unknown.

10. Quadrate supported by the anterior face of squamosal.

Quadrate in *Oligokyphus* supported by the posterior surface of the squamosal. Condition uncertain in *Bienotherium*, but appears to be anterior surface.

Broom's Ictidosaurian A is obviously closely related to *Diarthrognathus* and in the former the teeth are only slightly specialized in contrast to the highly specialized teeth of the tritylodontids where the incisors are reduced, the canines lost and the cheek teeth considerably widened to support several cusps. The common features to the skulls of *Diarthrognathus* and tritylodontids (numbers 4, 9, 10, 12, 13 and 14) are also found in several cynodonts. All the features which differentiate the tritylodontids from *Diarthrognathus*, with the exception of numbers 4 and 10, are present in some of the cynodonts. Both Watson (1942) and Kühne (1949) have pointed out the similarities in the skull structure of the tritylodontids and the cynodonts and have concluded that the former were derived from the latter. Most of the trends of development found in cynodonts appear to be in a tritylodontid direction. This view appears to be substantiated by the dentition of advanced cynodonts. In both *Aleodon* (Crompton, 1955) and *Pachygenelus* (Watson, 1933) the number of lower incisors has been reduced to two on either side indicating a relationship with the tritylodontids. Kühne (1949) has pointed out that there was probably no replacement of the post-canine teeth in *Olikokyphus* and that the anterior cheek tooth could be lost without replacement. In the advanced cynodont *Scalenodon* (Crompton, 1955 b) from Tanganyika there is no evidence of tooth replacement of the postcanine teeth in a series of twelve specimens with the exception of ninth and tenth postcanine teeth, whereas the incisors and canines are replaced several times. In this form the first postcanine tooth also appears to be lost without being replaced.

It has been pointed out above that it is not possible to derive *Diarthrognathus* from any of the known cynodonts and especially not the *Cynognathus* zone cynodonts (*Diademodon*, *Cynognathus*, etc.). It was concluded that the scaloposaurids were more likely ancestors. It appears that the tritylodontids were derived from the cynodonts. If this is the case, the similarities in the skulls of *Diarthrognathus* and the tritylodontids e.g. loss of prefrontals, postorbitals and pineal foramen, frontals contributing to the side wall of the orbits, teeth drawn on to the palate, expanded epipterygoid, lateral flange to the periotic and groove in dentary for the postdentary bone appear to be the result of parallel evolution and do not indicate a true relationship between the two groups.

The suborder Ictidosauria was created by Broom (1929) primarily for the reception of the two Ladybrand specimens and if one of these, *Diarthrognathus*

broomi, was derived from the scaloposaurids it follows that forms derived from the cynodonts should not be included in the Ictidosauria. It is proposed, therefore, that the tritylodontids should be removed from the Ictidosauria and placed either in a family of the Cynodontia or in a new infraorder.

DIARTHROGNATHUS A POSSIBLE MAMMALIAN ANCESTOR

It is difficult to compare *Diarthrognathus* with the earliest known mammals from the Triassic and Lower Jurassic since these mammals are known mainly from fragments consisting chiefly of teeth which are not preserved in the described specimen of *Diarthrognathus*. It will be possible to undertake such a comparison when the teeth of Broom's Ictidosaurian A have been described. It appears that this specimen belongs to the genus *Diarthrognathus* but it is possibly a different species.

One of the fundamental diagnostic characteristics of mammals is an articulation between the dentary and the squamosal. As this feature is known only in mammals and *Diarthrognathus*, the latter must in this respect be considered closer to mammals than are any of the other mammal-like reptiles. Although the advanced cynodonts and the tritylodontids have mammalian features not found in *Diarthrognathus*, e.g. the absence of an interpterygoid vacuity, these forms appear to be too highly specialized to be ancestral to mammals. *Diarthrognathus* possesses one of the fundamental features of mammals and in addition to this there appear to be no specializations in the skull structure which would preclude this form from being ancestral to mammals.

As to whether *Diarthrognathus* is ancestral to mammals depends primarily on the age of the Cave Sandstone. Du Toit (1954) considers these deposits to be older than the Rhaetic. True mammals have been reported from the Rhaetic of Switzerland and England. If these are the oldest mammals and the dating of the Cave Sandstone is correct, *Diarthrognathus* could possibly have been ancestral to mammals. It is possible however, that *Diarthrognathus* lived contemporaneously with mammals and rather than being ancestral to them was a surviving member of the group from which mammals arose. The importance of *Diarthrognathus* is that it appears to be very closely related to mammals and it adds considerably to our knowledge as to how the gap between mammals and reptiles was bridged. Of special importance is the fact that it indicates how the change over from a reptilian to a mammalian jaw articulation was achieved.

SUMMARY AND CONCLUSIONS

1. The skull of *Diarthrognathus broomi*, gen. et sp. nov. (Broom's Ictidosaurian B) has been prepared and described.

2. It was shown that in this form the dentary articulates with the squamosal alongside the reduced articulation between the quadrate and the articular. It was shown that this double articulation was possible because a single functional glenoid cavity was formed by both the quadrate and the squamosal.

3. A summary of the reptilian and mammalian characteristics of *Diarthrognathus* have been given. It was shown that a mosaic of reptilian and

mammalian characteristics were present in this form. Despite the articulation between the dentary and the squamosal it is concluded that this form should be classified as a reptile.

4. It is concluded that *Diarthrognathus* was the most mammal-like of the known therapsids and that if the Cave Sandstones in which this form was found are older than the Rhaetic mammals of Europe, *Diarthrognathus* could possibly be ancestral to some of the mammals. There appear to be no specializations in the skull structure to preclude it from this position.

5. The presence of a parasphenoid in *Diarthrognathus* in the reptilian position below the basisphenoid and not where it was figured by Broom (1929), half way between the nasal region and the basisphenoid, supports the theory of Parrington & Westoll (1940) that the mammalian vomer is not homologous with the reptilian parasphenoid.

6. It is concluded that *Diarthrognathus* could not have been derived from any known cynodont and that the features common to the skulls of *Diarthrognathus* and cynodonts are the result of parallel evolution.

7. It is concluded that *Diarthrognathus* might well have evolved from a scaloposaurid.

8. It is concluded that if the tritylodontids were derived from the cynodonts (there appears to be sufficient evidence to support the contention) and *Diarthrognathus* from the scaloposaurids, then the tritylodontids should be removed from the Ictidosauria as this infraorder was established primarily for Broom's Ictidosaurian A and *Diarthrognathus*.

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KEY TO LETTERING OF THE FIGURES

A.	Point of contact between the dentary and squamosal.
A.L.F.	Area of attachment of the lateral flange of the periotic.
A.M.	Area of attachment of the maxilla to the jugal.
ANG.	Angular.
A.P.	Ascending process.
A.PR.	Articular process.
ART.	Articular.
BO.	Basioccipital.
B.P.P.	Basipterygoid process.
BS.	Basisphenoid.
C.	Coronoid.
C.P.	Coronoid process.
D.	Dentary.
D.S.	Dorsum sellae.
EP.	Epipterygoid.
F.	Frontal.
F.M.	Foramen magnum.
F.O.	Fenestra ovalis.
G.C.	Glenoid cavity of the squamosal.
I.C.	Foramen for the internal carotid arteries.
IP.	Interparietal.
J.	Jugal.
J.F.	Jugular foramen.
L.	Lacrimal.
L.F.	Lateral flange of the periotic.
L.FO.	Lacrimal foramen.
N.C.	Nasal capsule
O.D.	Occipital depressions.
OS.	Orbitosphenoid.
P.	Parietal.
PA.	Prearticular.
PAL.	Palatine.
P.D.G.	Postdentary groove.
P.L.P.	Postero-lateral process of the squamosal.
PO.	Postorbital.
P–P.	Pterygo-paroccipital foramen.
P.PR.	Paroccipital process.
PS.	Parasphenoid.
PT.	Pterygoid.
P.T.F.	Post-temporal fossa.
Q.	Quadrate.
Q.E.	Quadrate ramus of the epipterygoid.
SA.	Surangular.
S.C.	Sagittal crest.
SO.	Supraoccipital.
SQ.	Squamosal.
T.	Tabular.
T.E.	True Edge.
T.P.	Transverse process.
V.	Foramen for trigeminal nerve.
VI.	Foramen for abducent nerve.
VII.	Foramen for facial nerve.
VO.	Vomer.
X.	Unidentified fragment of bone.
XII.	Foramen for the hypoglossal nerves.