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A RE-EVALUATION OF THE GENUS *TROPIDOSTOMA* SEELEY

by

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ABSTRACT

The type specimens of *Cteniosaurus platyceps* Broom, *Dicynodon acutirostris* Broom, and *Dicynodon validus* Broom were re-examined and were found to be very similar in a number of features rarely encountered in other Anomodontia. The skull of the type of *Cteniosaurus platyceps* is described in some detail. It is concluded that the above species must be considered to be junior synonyms of *Tropidostoma microtrema* (Seeley).

INTRODUCTION

The genus *Cteniosaurus* was first introduced by Broom (1935, pp. 66–67, Fig. 7) to accommodate forms resembling *Tropidostoma microtrema* (Seeley) with more "molars" which are serrated both in front and behind. Since the appearance of the first descriptions no further work has been done on the genus and no other specimens have been referred to it to the author's knowledge.

While examining the type specimens of anomodontia in the Transvaal Museum, Pretoria, the author came across the type material of *Cteniosaurus platyceps* Broom. This was completely unprepared and in the condition in which it was collected in the field and subsequently described by Broom in 1935. No preparation whatever had been done on the specimens.

It was decided to subject the specimens to preparation in order to ascertain the affinities of the genus within the Endothiodontidae and to study the cranial morphology of the genus in greater detail. The type specimens of *Dicynodon acutirostris* Broom and *Dicynodon validus* Broom were prepared for comparison.

Later the author had the opportunity to study the type material of *Tropidostoma microtrema* (Seeley) as well as a large number of other specimens referred to this species in the British Museum (Natural History).

The morphological description is based on the following:

MATERIAL

Catalogue No.	Diagnosis	Locality
T.M. 249	Skull lacking left zygomatic arch. Holotype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 383	Anterior half of skull. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 384	Posterior half of skull. Paratype of *Cteniosaurus platyceps* Broom. It is possible that it belongs to the same skull as T.M. 383.	Leeukloof, Beaufort West
T.M. 385	Crushed skull lacking quadrates and tip of the snout. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 387	Crushed skull lacking occiput and zygomatic arches. Paratype of *Cteniosaurus platyceps* Broom.	Leeukloof, Beaufort West
T.M. 250	Laterally crushed anterior half of skull. Holotype of *Dicynodon acutirostris* Broom.	Leeukloof, Beaufort West
T.M. 252	Distorted anterior half of skull and mandible. Holotype of *Dicynodon validus* Broom.	Leeukloof, Beaufort West

TECHNIQUE

Preparation was done by the conventional mechanical methods. The more detailed preparation was done with a dental mallet. The matrix does not react with hydrochloric or acetic acid precluding the use of acid preparation.

The drawings are based mainly on the holotype of *Cteniosaurus platyceps* Broom, additional information was obtained from the rest of the material.

THE SKULL

The skull is fairly short and broad and appears very much like *Oudenodon baini* Owen on superficial examination (Plate V). The intertemporal region is wider than in most other Anomodontia. The external nares are small and placed high up in the snout. The dorsal part of the premaxilla on the surface of the snout extends far posteriorly, unlike the condition in most other *Cistecephalus* Zone dicynodonts.

The palatines form a very important part of the secondary palate and are as extensive as in *Compsodon helmoedi* van Hoepen.

THE SNOUT AND SKULL-ROOF

The premaxillae (Figs. 1, 2 and 3) are completely fused and tend to separate the nasals anteriorly extending posteriorly to the level of the posterior margins of the external nares. This latter feature is rare in *Cistecephalus* Zone dicynodonts. There is a prominent median and two less

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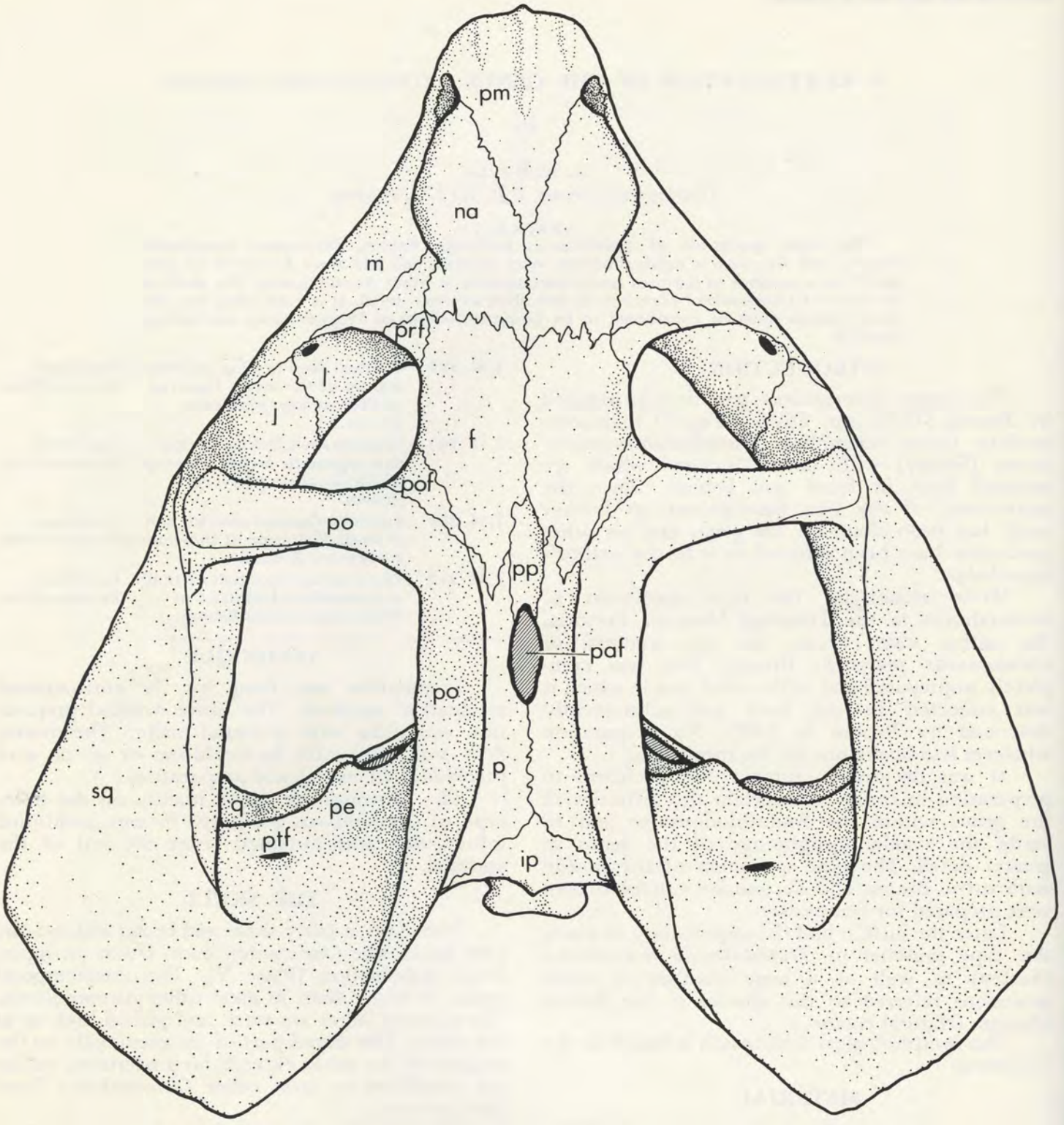

Fig. 1 Reconstruction of the dorsal view of *Tropidostoma microtrema* (Seeley) (about natural size). Abbreviations in this and subsequent figures after Romer "Osteology of the Reptiles".

prominent lateral external longitudinal ridges on the antero-dorsal surface of the snout.

On the palatal surface the premaxillae exhibit the usual two anterior and one posterior median palatal ridges. Posteriorly the premaxillae are in sutural contact with the palatines and the vomer anterior to the anterior margins of the choanal slits. Laterally they form straight sutures with the maxillae.

The septomaxillae lie in depressions surrounding the nares externi, which they bound ventrally and posteriorly. They form sutures with the premaxillae, maxillae and lachrymals.

The maxillae (Figs. 1, 2 and 3) are the only tooth-bearing elements in the skull. They constitute an important part of the sides of the snout and form prominent caniniform processes that bore tusks in some specimens. One of the

paratypes, T.M. 383, displays a large socket on its right caniniform process. The occurrence of post-canines is highly variable in the type material. The holotype of *Cteniosaurus* and specimen T.M. 383 show no trace of post-canines in the maxillae. Specimen T.M. 387 has a single large root of a post-canine on the alveolar margin posterior to the caniniform process. Specimen T.M. 385 has post-canines on each maxilla. In this specimen the post-canines are placed medial to the alveolar border on the palatal part of the maxilla postero-medial to the caniniform process. On the right side there are two post-canines and a socket of a third. On the left there is one post-canine and a socket of a second. In this specimen the post-canines are arranged in clusters and not in rows. A similar range of variation was observed in the British Museum specimens of *Tropidostoma microtrema* (Seeley). In the anterior part of the zygomatic arch, the maxilla extends posteriorly to the level of the postorbital arch.

The nasals form the posterior halves of the dorsal margins of the nares externi where they are thickened to form small nasal bosses. Anteriorly they are separated by the posterior dorsal process of the premaxillae. This development of the premaxillae results in relatively short nasal bones.

The prefrontals (Figs. 1 and 2) are slightly thickened, but do not form such prominent bosses as in *Oudenodon*.

The frontals form the dorsal margins of the orbits where they are slightly raised but not to the same extent as in *Oudenodon*.

The postfrontals (Fig. 1) separate the frontals from the parietals, seemingly as, superficial, triangular-shaped bones, visible on the dorsal surface.

The preparietal (Fig. 1) is a small lanceolate bone that constitutes the anterior margin of the parietal foramen. The shape of this bone is highly variable in the type series. It is long and narrow in the holotype and very broad in specimen T.M. 385. In specimen T.M. 383 the preparietal is situated entirely in front of the parietal foramen and does not take part in the formation of the anterior margin of the parietal foramen.

The postorbitals extend posteriorly to meet the squamosals at the posteromedial corners of the temporal fossae.

The parietals form two longitudinal plates posterior to the parietal foramen on their ventral sides. These plates are fused with the expanded dorsal extremities of the epipterygoids.

The interparietal (Figs. 1 and 4) is visible in the dorsal view of all the types except T.M. 384.

The jugals (Figs. 1, 2 and 3) form the medial parts of the zygomatic arches and extend posteriorly to near the posterior margins of the temporal fossae.

The squamosals (Figs. 1, 2, 3 and 4) extend anteriorly to the level of the middle of the orbits.

The tabulars (Fig. 4) are small plate-like bones that lie on the sides of the interparietal and overlap the squamosals.

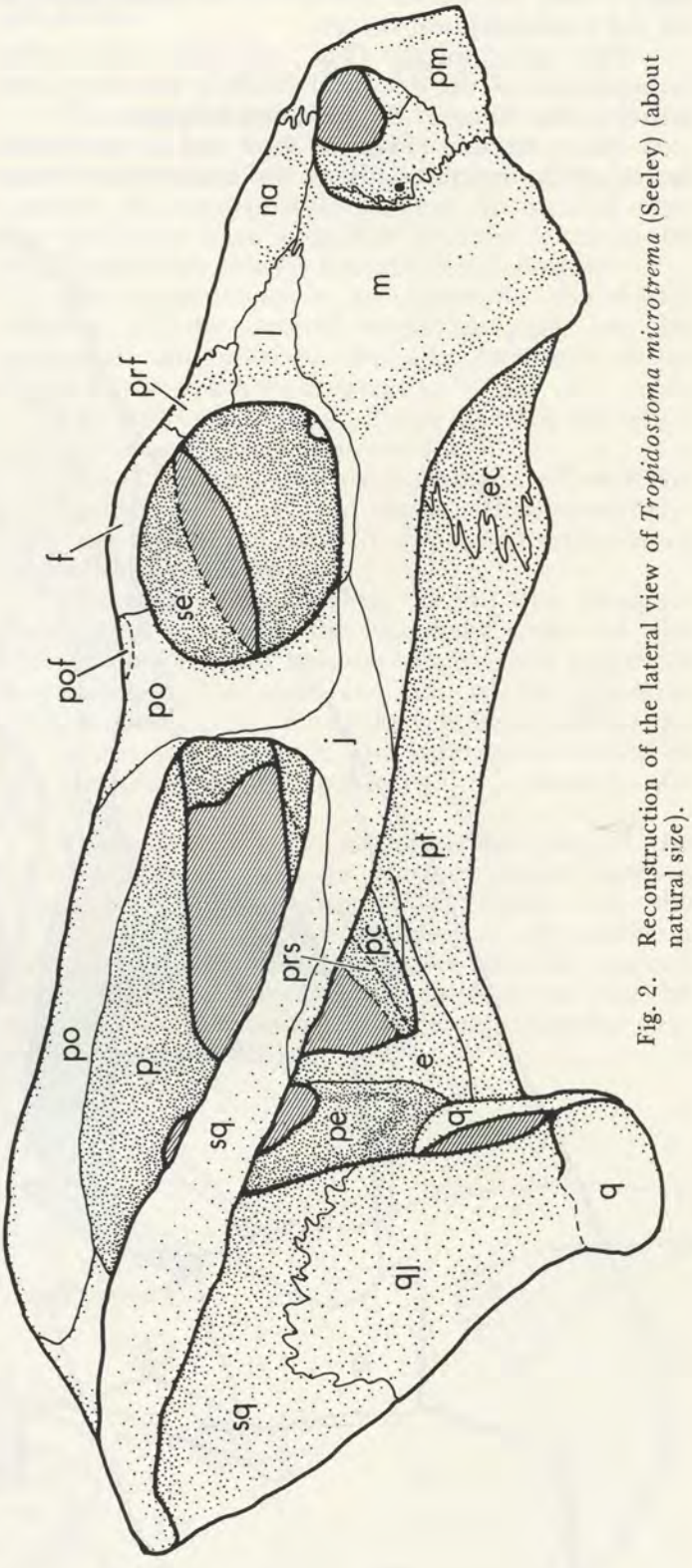

Fig. 2. Reconstruction of the lateral view of *Tropidostoma microtrema* (Seeley) (about natural size).

THE OCCIPITAL AND OTIC REGIONS

These regions do not show any unusual specialisations and the structure does not differ appreciably from any of the other medium-sized anomodonts of the *Cistecephalus* Zone.

The supraoccipital (Fig. 4) extends between the post-temporal fossae and constitutes the dorsal half of the margins of the foramen magnum. It only forms the dorsal halves of the medial margins of the post-temporal fossae.

The exoccipitals (Fig. 4) form the lateral tuberosities of the occipital condyle and meet each other in the floor of the foramen magnum.

The periotics (Figs. 1, 2, 3 and 4) constitute most of the lateral walls of the brain-case. On the occipital surface the periotics form the greater part of the medial and the ventral margins of the post-temporal fossae. The paroccipital processes that extend laterally to meet the squamosals in the suspensoria are fairly massive. Where the distal extremity of the paroccipital process meets the squamosal, a ridge is formed. This ridge is termed the tympanic process by Cox (1959, p. 9) and the opisthotic process by Barry (1967, p. 145). There are very prominent venous grooves on the antero-

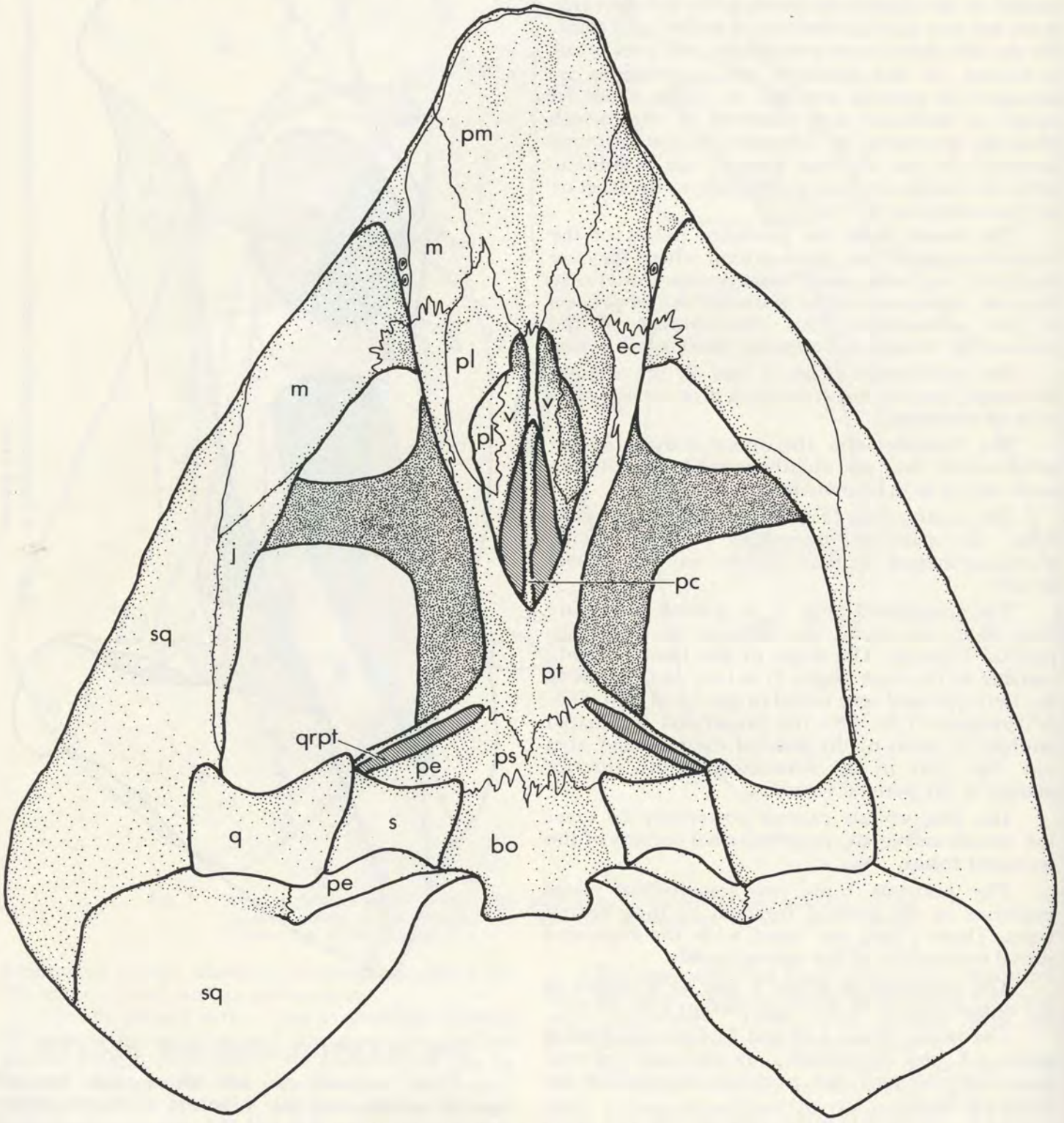

Fig. 3. Reconstruction of the ventral view of *Tropidostoma microtrema* (Seeley) (about natural size).

lateral face of the periotic. These grooves connect the post-temporal fossae with the pterygo-quadrate foramina ventrally and the notch between the supraoccipital and the periotic dorsally. The periotic appears to form most of the margins of the fenestrae ovales. The fenestrae are small and circular and are situated at the posterior extremity of a flat surface for articulation with the stapes.

The basioccipital (Figs. 3 and 4) is indistinguishably fused with the basisphenoid. Sutures between the basisphenoid and the periotics can be seen ventral to the jugular foramina. Anteriorly the basioccipital is overlapped by the parasphenoid which covers the basioccipital basisphenoid contact.

The proximal end of the stapes is larger than the distal end. The distal ends are closely appressed to the quadrates.

THE BASIS CRANII

The basisphenoid cannot be studied satisfactorily in the material at hand as little of it can be seen in a prepared specimen. Ventrally it is covered by the parasphenoid and the pterygoids and dorsolaterally by the periotics. The exact relationship of the cultriform process to the vomer and the elements of the sphenethmoid region are uncertain due to the crushing of all the specimens, but the cultriform process appears to reach the level of the posterior part of the nasal cavity.

The sphenethmoid (Fig. 2) consists of two separate ossifications. The posterior element consists of a thin vertical plate of bone that stands on the dorsal surface of the cultriform process dorsal to the interpterygoid vacuity. The anterior element consists of a vertical median plate that divides dorsally to form two wings that lie against the frontals. There is general agreement that the wings are the orbitosphenoids. The median vertical part is termed the presphenoid by Agnew (1958, p. 94) and septosphenoid by Boonstra (1968, p. 260) and Barry (1967, p. 149). No foramina for the passage of the optical nerves were seen in the orbitosphenoids.

THE PALATE

The quadrates (Fig. 1, 2, 3 and 4) of *Cteniosaurus* are very similar to those of *Oudenodon baini* Owen. As in the latter genus the lateral condyle is more prominent that the medial one. The quadrates have a smaller articular facet on the dorsal processes than is found in *Oudenodon*.

The quadratojugals are fused to the dorsal surfaces of the lateral condylar parts of the quadrates and extend dorsally to form interdigitated sutures with the jugals.

The pterygoids (Figs. 2 and 3) have the usual configuration found in Anomodontia.

The ectopterygoids are interdigitated with the pterygoids posteriorly and the maxillae anteriorly. They are of similar size to the ectopterygoids of *Oudenodon baini* Owen.

The epipterygoids (Fig. 2) are thin elongate plates that connect the quadrate rami of the pterygoids with the ventral longitudinal plates of the parietals. The quadrate rami of the epipterygoids do not extend along the quadrate rami of the pterygoids and are short. The anterior extremity of the foot-plate of the epipterygoid is fused to the basisphenoid.

The palatines form an important part of the secondary palate and are more extensive than in most other anomodontia. They form both the lateral and the anterior margins of the anterior choanal slits and have extensive sutural contact with the premaxillae. Near the posterior end of the choanal slits the palatines develop tubercles that project ventromedially.

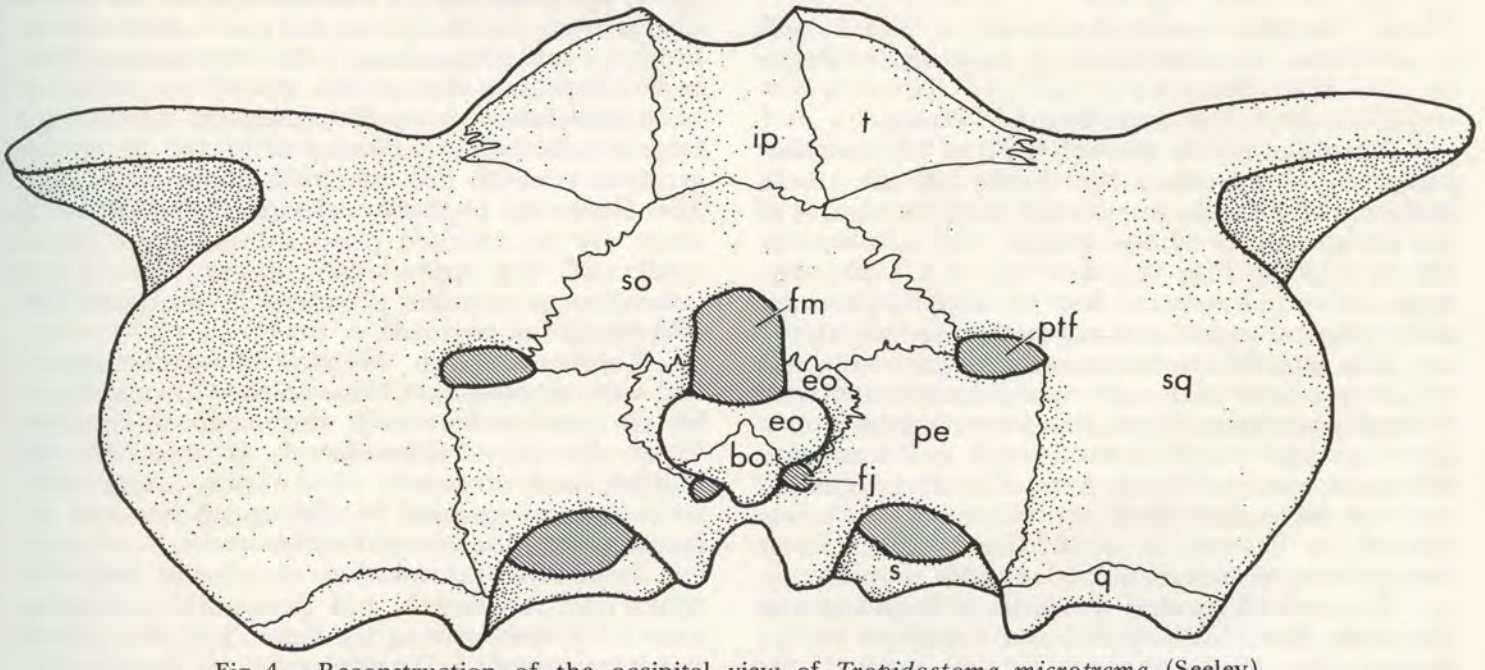

Fig. 4. Reconstruction of the occipital view of *Tropidostoma microtrema* (Seeley) (about natural size).

The suture between the vomers and the premaxilla (Fig. 3) occurs at the level of the anterior margins of the choanal slits. The interpterygoid vacuity is long and extends anteriorly for two thirds of the length of the choanal depression. The margins of the vacuity are raised to a greater extent than in *Daptocephalus.*

THE LOWER JAW

Broom (1953, p. 67) described some "molars" found in the lower jaw of the holotype. Unfortunately, the parts of the specimen containing the teeth are lost. Part of the ramus of a mandible lies against the occipital surface of the holotype. Unfortunately, it is so weathered that no features can be distinguished. There is no other lower jaw material available at present.

COMPARISON OF THE SKULL WITH *TROPIDOSTOMA MICROTREMA* (SEELEY)

(Plates I and II)

Dicynodon microtrema Seeley (1889, pp. 228–232, Pl. 11)
Dicynodon (Tropidostoma) duni Seeley (1889, pp. 232–236, Pl. 12)
Tropidostoma microtrema (Seeley) (Broom, 1915, pp. 355–361, Figs. 3–4)
Tropidostoma microtrema (Seeley) (Broom, 1932, pp. 209–211, Fig. 69C–D)
Tropidostoma microtrema (Seeley) (van Hoepen 1934, pp. 71–74, Fig. 9)
Tropidostoma microtrema (Seeley) (Broili and Schröder, 1935, pp. 239–241, Fig. 9)
Tropidostoma microtrema (Seeley) (Watson, 1948, pp. 855–857, Figs. 13–14)
Tropidostoma microtrema (Seeley) (Haughton and Brink, 1954, p. 67)
Tropidostoma microtrema (Seeley) (Watson, 1960, pp. 131–308, Fig. 10)
Type: Occipital part of a skull in the British Museum (Natural History), London. Catalogue No. 868. (Plate I)
Type Locality: Tafelberg, Beaufort West.

Examination of the holotype of *Cteniosaurus platyceps* shows that the bones of the dorsal surface of the skull agree closely with the figures of the dorsal surface of the skull of *Tropidostoma* by Broom (1915, Fig. 3 and 1932, Fig. 69D). The type of *Cteniosaurus* has a slightly broader intertemporal region and a more pointed snout.

The lateral view of the snout of the holotype of *Cteniosaurus platyceps* agrees remarkably with Watson's specimen (1948, Fig. 9) of *Tropidostoma.* The high placement of the nostril in the snout is the most notable feature here. The dorsal view of the specimen described by Watson (1948) was figured by Pearson in 1924 (Fig. 8). This figure shows the structure of the floor of the nasal cavity.

The palatal view of the skull of *Tropidostoma* has been figured by all the above authors except Seeley. One of the most striking features of the palatal view is the long interpterygoid vacuity with its raised margins. Such structure of the interpterygoid vacuity is rare among anomodonts. The vacuity of the specimen figured by Watson (1948, Fig. 13) is relatively shorter than in the specimens figured by the other authors. The length of the vacuity is variable in the types of *Cteniosaurus.* In specimen T.M. 383 it is almost as short as in Watson's specimen. The British Museum specimens from Tafelberg, Beaufort West show a similar range of variation.

Another very noticeable feature is the large part that the palatines play in the formation of the secondary palates of both *Cteniosaurus* and *Tropidostoma.* The palatines usually form the anterior margins of the anterior choanal slits in *Cteniosaurus.* This feature is, however, subject to some variation. In specimen T.M. 383 the anterior margin of the left choanal slit is formed by the premaxilla while the one on the right side is bounded by the palatine. A similar condition is figured by Broili and Schröder (1935, Fig. 9) in a specimen identified as *Tropidostoma microtrema.* In the specimen of *Tropidostoma* figured by Watson (1948, Fig. 13) the palatines appear to form the anterior margins of the anterior choanal slits. In the palate figured by Broom (1915, Fig. 3 and 1932, Fig. 69D) there is extensive contact between the palatines and premaxilla, but the palatines do not form the anterior margins of the choanal slits.

The ectopterygoids of both genera are extensively developed to meet the jugals on the medial sides of the anterior roots of the zygomatic arches.

The dentition is highly variable in the type series of *Cteniosaurus platyceps* as has been shown in the first part of this paper in the section dealing with the maxilla. The dentition of *Tropidostoma* is also highly variable and the post-canines are absent in mature specimens (Broom, 1915, p. 358 and 1932, pp. 209–211). This could also be the case in *Cteniosaurus* as there are no post-canines in the holotype and in specimen T.M. 383. Broom (1935, p. 67) expresses the opinion that *Cteniosaurus* can be distinguished from *Tropidostoma* by having a large number of molars and in having the molars serrated on both the anterior and posterior edges. This statement probably refers to the lower jaw, as there are no serrated post-canines in any of the skulls of the type series. There is only one unbroken post-canine preserved in specimen T.M. 385 which is unserrated.

Toerien (1953, p. 75) showed that the number and structure of post-canine teeth is too variable to be of taxonomic use in the Endothiodontidae. From the above discussion it is clear that the number and structure of the post-canine teeth alone cannot be used to distinguish between the genera *Cteniosaurus* and *Tropidostoma.*

From the information obtainable from the types of *Cteniosaurus* and the published descriptions of *Tropidostoma,* specimen T.M. 383, one of the type series of *Cteniosaurus,* can be placed in either of the two genera because the left palatine

does not form the anterior margin of the left anterior choanal slit while the right one does!

The evidence at present available to the author points to close affinity between the two species. It is therefore desirable to place both species in the same genus i.e. *Tropidostoma.*

Although the present facts do not permit a distinction being made between the two species, there is still insufficient information at hand to prove conclusively that they are synonyms. Studies on the variation of additional specimens from both the type localities are necessary to decide this point. Present evidence however suggests that the name *Cteniosaurus platyceps* Broom is a junior synonym of *Tropidostoma microtrema* (Seeley).

COMPARISON OF THE SKULL WITH *DICYNODON ACUTIROSTRIS* BROOM
(Plate III)

Dicynodon acutirostris Broom (1935, pp. 71–72, Fig. 12)

Dicynodon acutirostris Broom (Haughton and Brink, 1954, p. 72)

Type: Anterior half of skull in the Transvaal Museum, Pretoria. Catalogue No. T.M. 250. (Plate III)

Type Locality: Leeukloof, Beaufort West.

The type is laterally compressed and the flange of the right maxilla is bent over the palatal surface. This was not evident in the unprepared state in which it was described originally. The snout was therefore broader than is shown in Broom's figure (1935, Fig. 12).

There is a striking similarity between the holotype of *Dicynodon acutirostris* and the type series of *Cteniosaurus platyceps*. This similarity is notable in both general shape and in a number of details that are of taxonomic importance and which are rare in other Anomodontia. It is also notable that the type locality of both these species is given as Leeufontein, Beaufort West.

The palatines of *Dicynodon acutirostris* form the anterior margins of the anterior choanal slits. As far as the author could ascertain this feature only occurs in this species, in *Cteniosaurus platyceps* and in *Compsodon helmoedi* van Hoepen.

Another uncommon feature that *Dicynodon acutirostris* has in common with the type series of *Cteniosaurus platyceps* is the long interpterygoid vacuity with raised margins.

Other unusual characters shared by the two species are the great posterior extent of the premaxilla on the dorsal surface of the skull, the presence of small nasal bosses situated behind the level of the middle of the nares externi, the presence of raised orbital margins, the presence of tubercles on the alveolar margins behind the caniniform processes, the fusion of the septomaxilla with the maxilla, the wide contact between the jugal and the ectopterygoid at the anterior root of the zygomatic arch, the dorsal position of the nares externi in the snout and the presence of tubercles on the medial surface of the palatine at the posterior extremity of the anterior choanal slits.

The characters enumerated above are of rare occurrence in other Anomodontia and indicate affinity between the two species. This view is strengthened by the fact that the type locality of both species is the same.

Broom (1935, p. 72) compared the type with various species of *Dicynodon* but not with *Cteniosaurus* described in the same paper. The reason for this is that the type of *Dicynodon acutirostris* is laterally crushed and therefore appears to have a much higher snout than any specimen in the type series. The resemblance between the types could only be noted after preparation. There is no sign of teeth in either the holotype of *Cteniosaurus platyceps* or that of *Dicynodon acutirostris*. As specimens of *Tropidostoma* tend to lose all post-canine teeth and are often tuskless (Broom, 1915, p. 358 and 1932 p. 211), the absence of teeth in a larger specimen is of no value as a distinguishing feature.

The present evidence indicates that the name *Dicynodon acutirostris* should become a junior synonym of *Tropidostoma microtrema* (Seeley) when further material from the type locality is studied.

COMPARISON OF THE SKULL WITH *DICYNODON VALIDUS* BROOM
(Plate IV)

Dicynodon validus Broom 1935 (pp. 70–71, Fig. 11)

Dicynodon validus Broom (Haughton and Brink, 1954, p. 85)

Type: Anterior third of skull and lower jaw in the Transvaal Museum, Pretoria. Catalogue No. 252. (Plate IV)

Type Locality: Leeukloof, Beaufort West.

The holotype of this species is badly crushed and distorted. The enormous tusks are broken off, but a cast of the left tusk is preserved in the matrix. The skull is greatly deformed and a line drawn through the anterior margins of the orbits makes an angle of 30 degrees with the long axis of the skull. The intertemporal region is turned upwards. This was certainly not the case in the living animal as is evinced by a fracture at the point where the intertemporal bar turns dorsally. This fracture occurred prior to the lithification of the mudstone in which the specimen is preserved and was not visible when the specimen was originally described as it was covered by matrix. This upturning of the intertemporal bar was considered to be the main distinguishing feature of the new species by Broom (1935, p. 71).

Because of the deformation the specimen has undergone many of the sutures are obliterated. The palatal region is particularly difficult to interpret.

The specimen has a number of rare features that agree with the type series of *Cteniosaurus*

platyceps. The nares externi are small and placed high up in the snout. There are nasal bosses that are situated posterior to the level of the middle of the nares externi. The septomaxilla is fused to the other surrounding elements in a similar fashion. The dorsal margins of the orbits are slightly raised. The palatines appear to form the anterior margins of the anterior choanal slits, but there is some doubt about this interpretation because of the many cracks in this part of the skull.

The specimen differs from the type series of *Cteniosaurus platyceps* by being much larger than any specimen in the series, by having large tusks and a more robust build. It differs from the type of *Dicynodon acutirostris* by having tusks and being larger.

From the above it appears that the differences between the three species could be due to difference in size and consequently in age. The type of *Dicynodon validus* Broom is, however, such a poor specimen that no definite conclusion can be reached.

CONCLUSIONS

If one assumes that the holotype of *Cteniosaurus platyceps* Broom is a medium sized specimen, it appears that the types of *Dicynodon acutirostris* Broom and *Dicynodon validus* Broom are what one would expect a large individual of *Cteniosaurus platyceps* Broom to look like. When the specimens studied for this paper are arranged according to size the specimens have the appearance of being a growth series. As arranged, the series of skulls display a number of trends associated with an increase in size. Firstly, there is the tendency to a reduction in the number of post-canine teeth. Secondly, there is an increase in the size of the nasal bosses. Thirdly, the orbital margins tend to become more raised in the larger specimens and fourthly, there is a tendency for the bones in the snout to become more massive. By speculative extrapolation of the series of skulls to find a theoretical young specimen, one could arrive at a small skull with a wide intertemporal region, an oudenodont type of palate and a fair number of post-canine teeth. Such a specimen would conform to Toerien's (1953, p. 110) definition of the genus *Emydops*. It is, therefore, likely that a young specimen of *Tropidostoma microtrema* (Seeley), would be referred to some species of *Emydops*. A species of the latter genus, *Emydops microdon* (Broom) (1935, p. 382), has been described from Leeufontein. There are however no intermediate specimens between this species and the type series of *Tropidostoma platyceps* (Broom) and present evidence indicates that they are separate species.

The great similarity that exists between the species *Cteniosaurus platyceps* Broom, *Dicynodon acutirostris* Broom, *Dicynodon validus* Broom and *Tropidostoma microtrema* (Seeley) could mean that the resemblance between them is more then superficial and that they are synonyms.

The genus *Tropidostoma* can be derived from an *Emydops*-like form by an increase in size and in the extent of the palatine in the secondary palate and a decrease in the width of the intertemporal region. The skull of *Tripidostoma* shows some very advanced features such as a more extensive secondary palate than found in any other anomodont and the development of nasal bosses while retaining a primitive endothiodont dentition. The genus *Tropidostoma* cannot be regarded as a transition between the families Endothiodontidae and Cryptodontidae because of the secondary palate in this genus is even further developed than in the most advanced Cryptodontidae like *Oudenodon* and *Rhachiocephalus*. The genus *Tropidostoma* therefore appears to be a specialized side branch of a line of *Emydops*-like endothiodonts leading towards the Cryptodontidae.

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Plate I
Dorsal view of the type of *Tropidostoma microtrema* (Seeley).

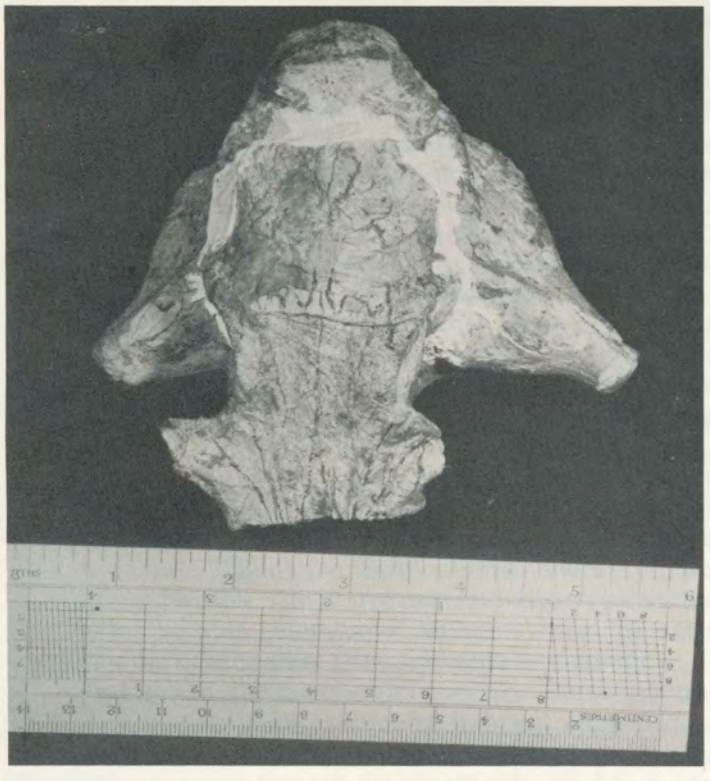

Plate II
Dorsal view of the snout of *Tropidostoma microtrema* B.M.N.H. 860.

Plate III
Dorsal view of the type of *Dicynodon acutirostris* Broom.

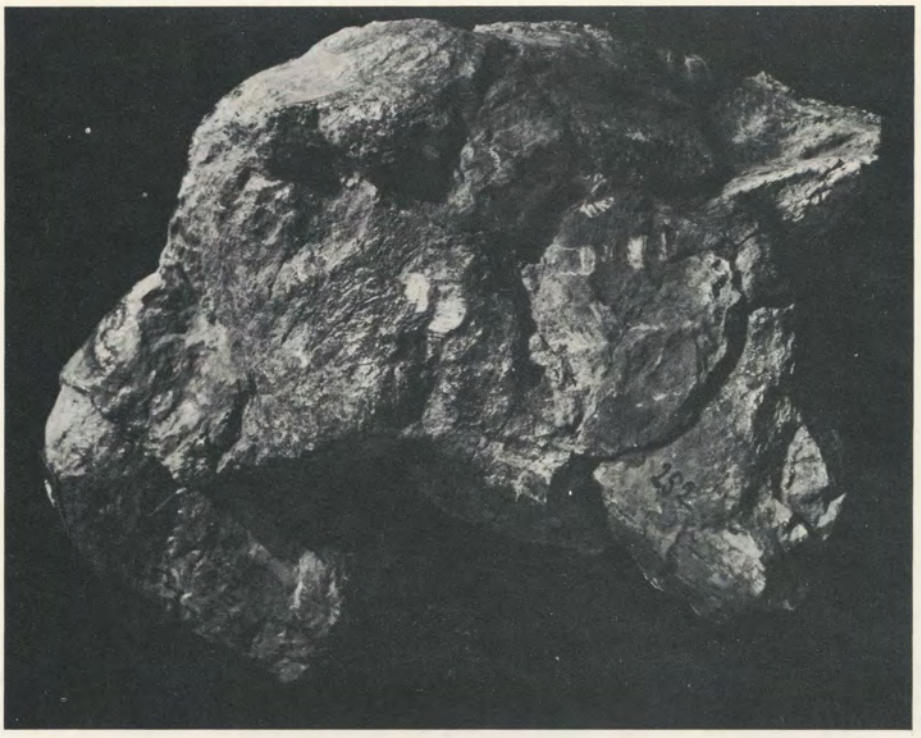

Plate IV
Lateral view of the type of *Dicynodon validus* Broom max. length of skull 172 mm.

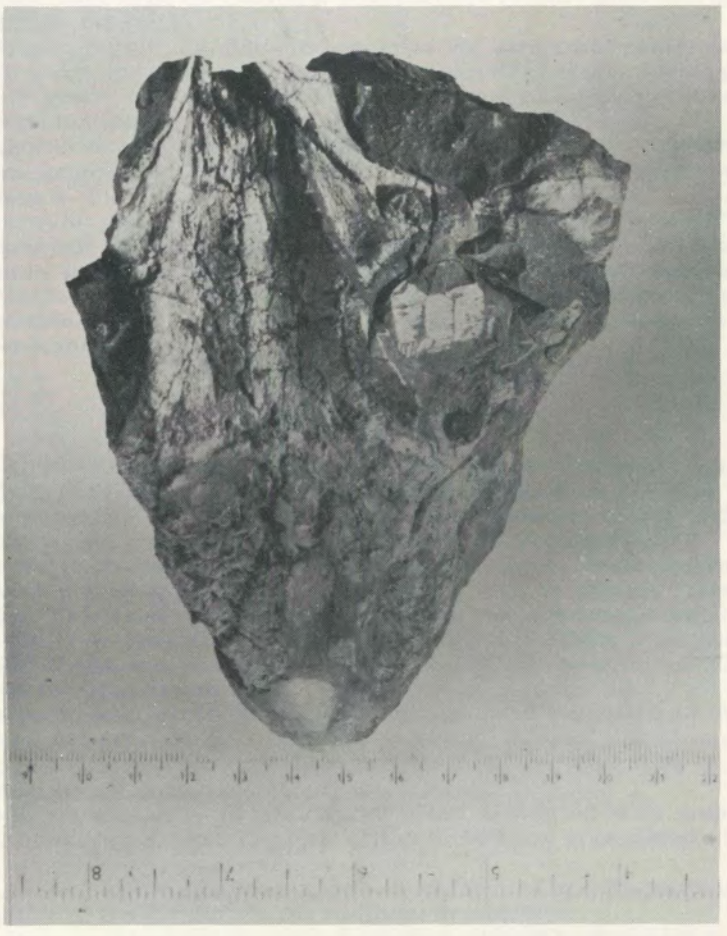

Plate V
Dorsal view of the type of *Cteniosaurus platyceps* Broom max. length of skull 190 mm.