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ON SOME SOUTH AFRICAN REPTILES OF THE SUBORDER THEROCEPHALIA PRESERVED IN THE AMERICAN MUSEUM OF NATURAL HISTORY

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In the Department of Vertebrate Palaeontology of The American Museum of Natural History there is a small collection of the remains of thirteen therocephalian reptiles, which were purchased from Dr. R. Broom in 1913. Only two of these specimens are represented by fairly good skulls; all the others are fragmentary and consist chiefly of weathered snouts, which show some features of the dentition.

All these forms are from the Lower Beaufort Beds; six genera are from the *Tapinocephalus* zone, four from the *Endothiodon* zone, and one presumably comes from the base of the *Cistecephalus* zone.

Three families of the suborder Therocephalia are represented; these are:—one genus of the *Ictidosuchidae*, two genera of the *Scalopsauridae* and eight from the composite family *Pristerognathidae*.

Family **PRISTEROGNATHIDAE**

***Alopecodon priscus* Broom**

BROOM, R., 1908, Ann. So. Afr. Mus., p. 361.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 64.

BOONSTRA, L. D., 1933, Ann. So. Afr. Mus., p. 216.

REFERRED SPECIMEN.—Amer. Mus. No. 5569, Fraserburg Road, Prince Albert District; *Tapinocephalus* zone.

This specimen is a very badly weathered fragment, which shows only some features of the dentition. There are remains of a total of fifteen incisors, with a space for an additional tooth between two teeth on the left premaxilla; there thus appear to be eight incisors on each side; the two posterior teeth differ somewhat in direction from the anterior ones and may represent two small canines; the posterior incisors are smaller than the anterior ones. The canine is of medium size. Remains of six small molars are preserved. In the lower jaw, the roots of one canine and three incisors are visible in the left dentary. The dental formula in

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this specimen would thus be, $\frac{I-8, C-1, M-6?}{I-3, C-1, M-?}$; for the type specimen in the South African Museum, Broom gave the formula, $\frac{I-7, C-2+1, M-8?}{I-7, C-?, M-?}$.

The number of teeth is thus not identical in the two specimens and the question arises as to whether this specimen can rightly be referred to *Alopecodon priscus*. I have, however, recently pointed out how bad the types of the various reputed species of *Alopecodon* are, and, in view of this, it is perhaps best to include this form in the original species *Alopecodon priscus*.

***Alopecognathus angusticeps* Broom**

(Figures 1 and 2)

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pt. II, p. 116.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 56.

TYPE.—Amer. Mus. No. 5559, Grootfontein, Beaufort West District; *Tapinocephalus* zone.

In 1915, Broom gave the dental formula, I-6, C-1, M-6, but he figured five incisors and seven molars; in 1932, he figured and described the formula as, I-6, C-1, M-8. I have ground down the left maxillary edge in order to expose the molars; there is now evidence of the existence of only five fairly small molars; behind the second molar there is a tip of a replacing tooth; the first molar lies 12 mm. posterior to the canine; the length of the series of five molars is 31 mm. On the right side, the crowns of four subequal molars are visible; anterior to the last tooth there is, however, a gap for another tooth, which would bring the total up to five. The canines are of medium size and have an oval cross-section. There are six subequal incisors, with a space of 12 mm. between the last incisor and the canine. The dental formula is thus, $\frac{I-6, C-1, M-5}{I-?, C-?, M-?}$.

This type specimen consists of a practically complete skull, but, being preserved in a very intractable matrix, it has not been found possible to expose the occiput and palate; and it was only after a long process of grinding and etching that some features of the dorsal and lateral surfaces were determined. The skull is slightly crushed from side to side, but, even after this is corrected, it still remains a very long and narrow skull. The orbit is relatively small and is situated in the posterior half of the skull; the snout is thus very long. The temporal opening is relatively large and the narrow parietal crest fairly high.

The maxilla is large and, dorsally, stretches very nearly to the median line. The septomaxilla is fairly small, particularly that part lying posteriorly to the septomaxillary foramen. The prefrontal is large

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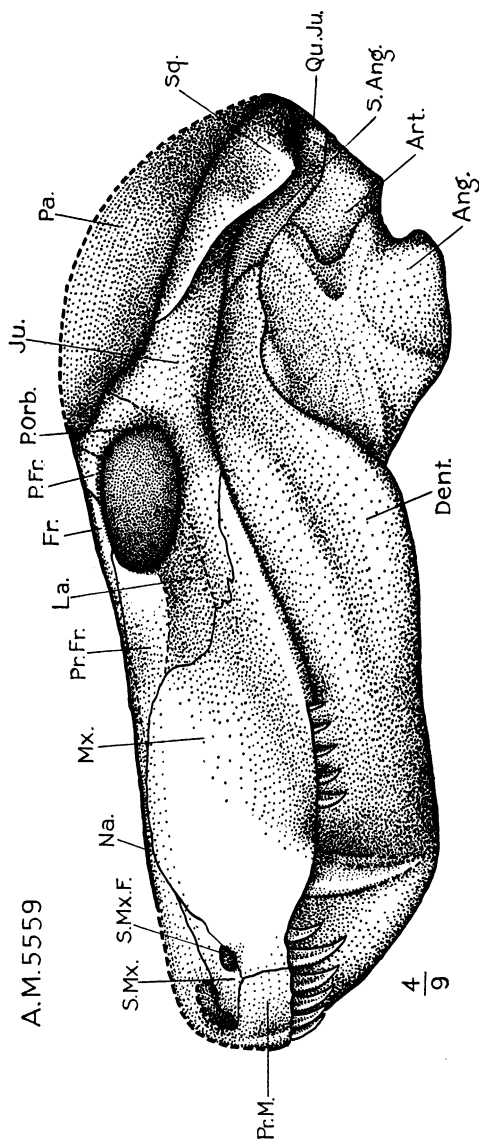


Fig. 1. *Alopecognathus angusticeps*. Lateral view of the type skull, Amer. Mus. No. 5559. $\times \frac{4}{9}$. $\bar{1}$

Ang.	=angular.	Pal.	=palatine.
Art.	=articular.	P.Fr.	=postfrontal.
B.Oc.	=basioccipital.	P.Orb.	=postorbital.
Dent.	=dentary.	Pr.Fr.	=prefrontal.
Est.Pter.	=ectopterygoid.	Pr.Mx.	=premaxilla.
Fr.	=frontal.	Pr.V.	=prevomer.
I.	=upper incisors.	Pter.	=pterygoid.
I.P.V.	=interpterygoid vacuity.	Qu.Ju.	=quadratejugal.
Ju.	=jugal.	S.Mx.	=septomaxilla.
L.	=lacrimal.	S.Mx.F.	=septomaxillary foramen.
L.C.	=lower canine.	Sq.	=squamosal.
Mx.	=maxilla.	S.Ang.	=surangular.
Na.	=nasal.	U.C.	=upper canines.
Pa.	=parietal.		

and forms a rather prominent preorbital thickening, which overhangs a preorbital depression, whose surface is formed by the lacrymal. The nasals are very long but narrow; anteriorly and posteriorly they swell

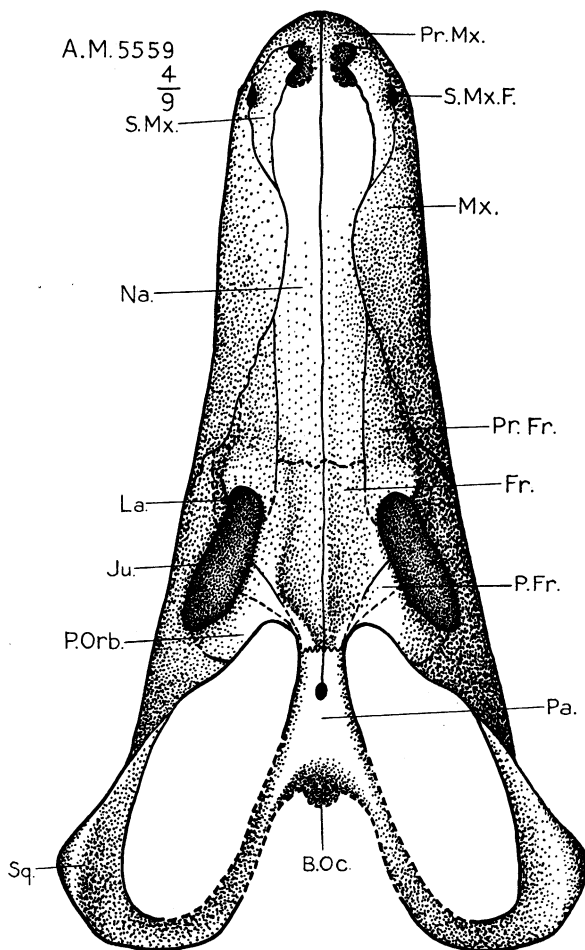


Fig. 2. *Alopecognathus angusticeps*. Dorsal view of the type skull, Amer. Mus. No. 5559. $\times \frac{4}{9}$.

out somewhat. The frontals are short and together present a cruciform dorsal surface; they enter the orbital border. Due to the nature of the matrix, it has not been possible to determine the limits of the postfrontal and postorbital; the postfrontal can, however, be only a small element.

The mandibular symphysis slopes sharply backwards; the outer surface of the angular is large and carries a number of ridges, which form the distinctive pattern met with in practically all therocephalians. The relations of the articular, quadrate and quadratojugal appear to be as in *Scymnosaurus watsoni*.

The long snout, high parietal crest, few molar teeth, and the details of the arrangement of the bones of the lateral and dorsal surfaces indicate that *Alopecognathus* is undoubtedly closely related with the generalized pristerognathid therocephalians, *Scymnosaurus* and *Pristerognathus*.

The chief skull measurements are:

Premaxilla to pineal foramen	210 mm.
Premaxilla to the anterior orbital border	140
Length of the lower jaw	240
Width across the squamosals	135?
Interorbital width	35
Intertemporal width	10
Width of the snout over the canines	55
Height of the snout at the canines	50

***Alopecorhinus parvidens* Broom**

BROOM, R., 1912, Proc. Zool. Soc., p. 864.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 57.

TYPE.—Amer. Mus. No. 5503, Beaufort West Commonage; *Endothiodon* zone.

This type consists of a very fragmentary part of the snout; the left dentary is nearly complete; the symphysial portion of the right dentary and parts of the two maxillae are also present. On the right side, remains of three small incisors are visible; there appears to be space for a total of six; the canine is of medium size and is rounded in section; a diastema is followed by the remains of the crowns of seven small molars. There are four lower incisors, the fourth lying interior to the line of the other three; the lower canine is small and is rounded in section.

Broom's (1932) reconstruction of the left side is poor; the lower border of the dentary curves evenly upwards in the direction of the coronoid process; behind the canine the maxilla is concave; the mandibular symphysis is long and low; the snout was presumably broad and low. The dental formula is $\frac{I-6?, C-1, M-7}{I-4, C-1, M-?}$.

As this specimen shows little more than some features of the teeth, it appears unlikely that it will ever be possible to identify new finds as definitely of this species. Thus the "species" is simply another name which encumbers scientific literature, without adding to our knowledge of the Therocephalia.

Cynariognathus platyrhinus Broom

BROOM, R., 1912, Proc. Zool. Soc., p. 863.

BROOM, R., 1915, Phil. Trans. Roy. Soc. London, p. 47.

BROOM, R., 1931, Rec. Albany Mus., p. 161.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 57.

BOONSTRA, L. D., 1934, Ann. So. Afr. Mus., p. 216.

TYPE.—Amer. Mus. No. 5502, Grootfontein, Beaufort West District; *Tapinocephalus* zone.

This type consists of an incomplete, weathered snout; it is of a medium-sized skull; the snout is low and broad; the relations of the septomaxilla and septomaxillary foramen are correctly figured by Broom (1932). In the upper jaw, roots of three incisors are preserved on the right side; there is sufficient space for an additional two. On the left side there are roots of three incisors, a fragment of one anterior to these and a space for another. There thus appear to be five incisors in each premaxilla; the incisors increase in size in anterior direction, so that there would not be space for a total of six as maintained by Broom; on the right side the last incisor but one has a posterior edge, which may be serrated. The upper canines are fairly large and are rounded in section; no evidence of serrations is preserved. Remains of eight molars are preserved in the left maxilla; they are close-set and decrease in size in posterior direction; no evidence of serrations is preserved. In the lower jaw, the incisors are hidden by the upper jaw; in the right dentary, one canine, followed, without diastema, by remains of eight molars, is visible. The dental formula is thus: $\frac{I-8?, C-1, M-8}{I-3, C-1, M-8}$. Of the palate, nothing can be determined with any degree of certainty. The specimen in the British Museum (No. R4097) recently redescribed by me appears, in the light of the above facts, to be correctly identified as of this species.

"Ictidosaurus angusticeps" Broom

BROOM, R., 1903, Ann. So. Afr. Mus., p. 151.

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pt. II, p. 118.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 60.

REFERRED SPECIMEN.—Amer. Mus. No. 5527, Beaufort West; *Endothiodon* zone.

This laterally crushed snout shows the following characters: a deep square mandibular symphysis; in the upper jaw, the roots of seven molars, visible on both sides; one very long slender canine; four fair-sized incisors on both sides, with posteriorly an additional small tooth, which appears to be implanted in the premaxilla; in the lower jaw, four incisors in both dentaries. The dental formula is thus: $\frac{I-4 \text{ or } 5, C-1, M-7}{I-4, C-1, M-?}$; for

the type Broom gave the formula: $\frac{I-5+1, C-1+1, M-8}{I-3, C-1, M-9}$. If the nature of the dentition alone constitutes a valid criterion, then this specimen cannot be included in the species *Ictidosaurus angusticeps*. It is, in fact, doubtful if this snout is that of a therocephalian at all; the square mentum suggests that it is a gorgonopsian, but, with the exception of *Lycaenodon longiceps*, no gorgonopsian has so large a number of molars. I regard this fragment as unidentifiable and do not propose to distinguish it by a new name from *Ictidosaurus angusticeps*.

Scylacoides ferox Broom

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pl. II, p. 119.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 57.

TYPE.—Amer. Mus. No. 5558, Beaufort West; ?*Tapinocephalus* zone.

This type consists of a crushed snout, without the dentaries; the left side is imperfectly preserved, and Broom's figure (1932) is probably a fairly correct reconstruction. On grinding down the dentigerous border, the teeth roots were rendered visible; five small uncrowded incisors are present on both sides; the single canine on each side is fairly large and is oval in cross-section; the roots of five small molars are visible. The dental formula is thus: I-5, C-1, M-5. The palate is badly stripped, so that no details of its structure can be determined with certainty; there appears to be no suborbital vacuity; it appears probable that the pre-momers underlie the palatines. The former fact would point to this form being a gorgonopsian; the latter, to its being a therocephalian. No other diagnostic characters can be determined, so that it is impossible to state in which of these suborders this snout belongs. That one cannot even determine the suborder again stresses the absolute futility of creating new so-called "species" on such bad material.

Scylacosaurus sclateri Broom

(Figure 3)

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pt. II, p. 120.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 62.

BOONSTRA, L. D., 1934, Ann. So. Afr. Mus., p. 219.

REFERRED SPECIMEN.—Amer. Mus. No. 5560, Beaufort West; ?*Tapinocephalus* zone.

This specimen was first described by Broom under the name *Scylacorhinus falkenbachii*. It consists of the anterior half of a skull from which most of the dorsal surface has been weathered away. The teeth are, however, clearly shown. The dental formula is as given by Broom, I-7, C-1+1, M-8. Anterior to the large canine, there are thus eight teeth,

as in *Scylacosaurus*; in describing the skull of *Scylacosaurus* in the British Museum, I thought that the posterior three precanine teeth were probably implanted in the maxilla, but the evidence was not very conclusive, due to the amount of overlap of the maxilla over the premaxilla; whether these posterior precanine teeth are canines or incisors must, I

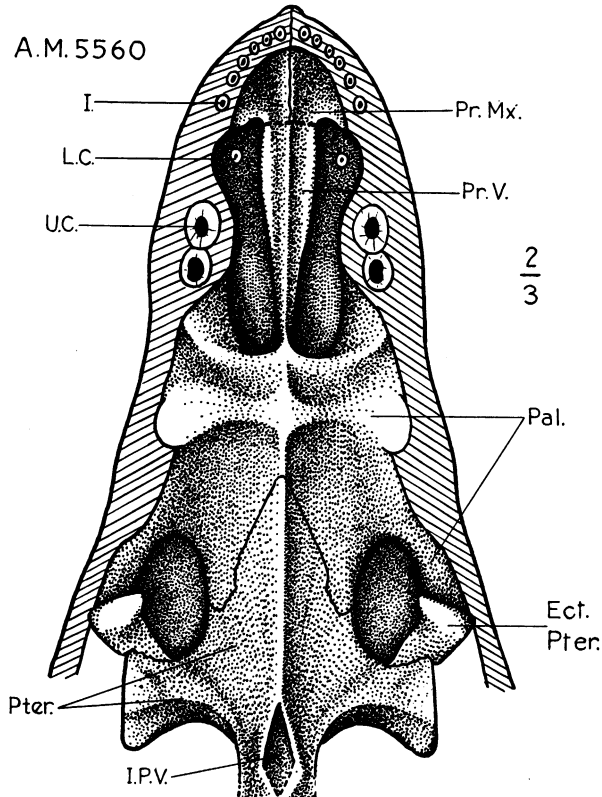


Fig 3. *Scylacosaurus sclateri*. Dorsal view of the anterior two-thirds of the palate, Amer. Mus. No. 5560. $\times \frac{2}{3}$.

think, remain uncertain, and therefore the slight differences in the arrangement of these teeth in these two forms should not be taken to imply generic differences. In all other characters—general form, size, nature of the maxillaries, dentaries and the mandibular symphysis, the dentigerous ridges on the pterygoids and the details of the palatal structure, as described below—the two skulls are in close agreement. I

propose, therefore, that the name *Scylacorhinus falkenbachii* be considered a synonym of *Scylacosaurus sclateri*.

I have been able to expose the dorsal surface of the palate (Fig. 3); this is the first time that this structure can be studied from this view in any therocephalian. The anterior two-thirds of the palate is formed by the usual four elements—paired prevomers, palatines, ectopterygoids and pterygoids. The prevomers have the usual spatulate shape; their posterior ends underlie the palatines; on their dorsal surface a thin, but high, median keel is developed; this is confluent with a median ridge on the palatines. In dorsal view, the palatine shows a very interesting structure; its posterior two-thirds is represented by a thin sheet of bone, whose median and posterior edges overlie the prevomer and pterygoid, and form the antero-medial edge of the large suborbital foramen; the important feature, however, is situated on the anterior third; here two thickened ridges form two transverse girders, medially confluent with the median longitudinal ridge and laterally abutting against the maxilla.

The median ridge and these transverse girders are of interest when considering the palatal structure from an architectural point of view, viz., the whole of the primary palate is, in general, formed by thin sheet-like bones; these sheets of bone produce a lightening of the skull, but any resultant weakening is counteracted by the development of a system of girders admirably adapted for withstanding all the strains and stresses to which the palate is subjected. The pterygoid is also, in general, a sheet-like bone, but it likewise has a median dorsal ridge and a thickened lateral flange. A slit-like interpterygoidal vacuity separates the pterygoids at the level of the transverse flanges. The ectopterygoid is a V-shaped bone forming the lateral and part of the posterior border of the suborbital vacuity. The V-shape seems to be developed for mechanical reasons; with this aspect in view, it is interesting to note that the anterior limb of the ectopterygoid is overlain by a beam of the palatine, and that the other limb presses downward on the corner of the transverse pterygoidal flange; the ectopterygoid is thus locked and perfectly adapted to withstand any pressure tending to force the lateral pterygoidal flange upwards.

***Trochosaurus major* Broom**

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pt. II, p. 121.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 50.

BOONSTRA, L. D., 1934, Ann. So. Afr. Mus., p. 227.

TYPE.—Amer. Mus. No. 5543, Rietfontein, Prince Albert District; *Tapinocephalus* zone.

The type consists of a weathered and laterally compressed anterior two-thirds of a skull; much of the surface bone is weathered away, but on the right side some points of structure can be determined; the nasal is broader anteriorly than posteriorly; together the two frontals form a large cruciform bony surface, with a small entry on to the orbital border; the prefrontal and lacrymal are large; the maxilla is fairly deep.

The teeth are badly preserved; remnants of five incisors, with serrations, are preserved; on the left side, two erupted canines are visible; on the right, only one is erupted, but in the maxilla the root of another can be seen; in the right maxilla, two definite molar roots are visible, with an indefinite indication of another root. On the left dentary, four molars are visible and there appear to be three incisors. The dental formula is thus:
$$\begin{array}{c} \text{I-5, C-1 or 2, M-2 or 3} \\ \text{I-3, C-?, M-4+?} \end{array}$$

A full description of the dorsal, lateral, occipital and palatal surfaces, together with the outer view of the brain-case, of a specimen of this species in the British Museum has recently been given by me.

Family **ICTIDOSUCHIDAE**

Ictidosuchus primaevus Broom

BROOM, R., 1900, Ann. Mag. Nat. Hist., p. 314.

BROOM, R., 1901, Trans. So. Afr. Phil. Soc., p. 177.

BROOM, R., 1912, Anat. Anz., p. 628.

BROOM, R., 1915, Bull. Amer. Mus. Nat., Hist., XXV, Pt. II, p. 119.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 77.

TYPE.—Amer. Mus. No. 5529, Near Pearston, Cape Colony; *Endothiodon?* zone.

The material is very badly preserved; there is a right dentary with parts of seven teeth; in the maxilla the molar roots are very indistinct; four are distinct, but there may have been a total of seven or eight; the skull is broad over the squamosals, but the snout is narrow; the temporal openings are large; the orbits are medium-sized; there is a deep preorbital depression; the frontals are cruciform.

The left scapulo-coracoid is well preserved, except that the upper part of the scapular blade cannot be seen; Broom's original figure (1901) is very accurate.

The limb-bones are very fragmentary; the large entepicondylar foramen of the humerus is noteworthy; the shaft is long and slender.

Family **SCALOPOSAURIDAE****Ictidognathus parvidens** Broom

BROOM, R., 1911, Proc. Zool. Soc., p. 1078.

BROOM, R., 1914, Phil. Trans. Roy. Soc., London, p. 47.

WATSON, D. M. S., 1931, Proc. Zool. Soc., p. 1186.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 72.

TYPE.—Amer. Mus. No. 5522, Kuilspoort Nek; *Cistecephalus* zone.

In 1911, Broom gave the dental formula, $\frac{I-6, C-2, M-10}{I-6?, C-2, M-11?}$; in 1932, Broom gave the formula, $\frac{I-6?, C-2, M-11?}{I-4?, C-1, M-12}$; I find the formula to be: $\frac{I-6?, C-2, M-9+3?}{I-4?, C-1, M-12}$. After grinding, the roots of the teeth in the left dentary, of the right maxillary molars and of the left canines, became visible. The two canines in the left maxilla are of nearly equal size; in the right maxilla, the posterior one is large and the anterior one small. Posterior to the canines on the left side, there is a diastema followed by the roots of nine molars—the maxilla is then broken off. In the premaxilla, there is room for at least five incisors, but there may have been six. The mandibular molars follow immediately on the canine; this canine is smaller than either of the maxillary canines. The nine upper molars occupy a distance of 15 mm.; the twelve lower molars occupy 21 mm.

Very little of the snout structure can be determined; the septomaxilla is long and its foramen large. The snout is bulbous; posteriorly to this swelling, the surface is scooped out dorsally and laterally and then rises to form two prominent bosses on the prefrontal. The swollen nature of the snout of *Ictidognathus* is the only character wherein it resembles *Scaloposaurus*, where the maxillaries flare out anteriorly. Watson has already pointed out that, in its dentition, this form differs from *Scaloposaurus*, and, if it were not for the shape of the snout, I would agree with Watson that “there appears to be no sound reason for regarding this animal as a Scaloposaurid.”

Ictidostoma (Ictidognathus) hemburyi Broom

BROOM, R., 1912, Proc. Zool. Soc., p. 865.

BROOM, R., 1914, Phil. Trans. Roy. Soc. London, p. 47.

BROOM, R., 1915, Bull. Amer. Mus. Nat. Hist., XXV, Pt. II, p. 117.

BROOM, R., 1930, Phil. Trans. Roy. Soc. London, p. 371.

BROOM, R., 1931, Rec. Albany Mus., p. 161.

WATSON, D. M. S., 1931, Proc. Zool. Soc., p. 1186.

BROOM, R., 1932, Mammal-like Reptiles of South Africa, p. 72.

TYPE.—Amer. Mus. No. 5520, Beaufort West; *Endothiodon* zone.

This snout only shows some features of the dentition; there are five subequal incisors; the main canine is fairly small; immediately in front

of the canine there lies a very small tooth; the portion of the left maxilla preserved shows the roots of eight small molars; in the right maxilla, ten molar roots and a set of replacing teeth are visible. The dental formula thus is, I-5, C-1+1, M-10.

Topotype, Amer. Mus. No. 5521, Beaufort West; *Endothiodon* zone.

In this snout there are six small, long and slender incisors on either side; the canines are long and slender and rounded in cross-section; immediately anterior to these, there is a small tooth on either side; in the right maxilla, grinding has revealed only the roots of five molars. In the lower jaw, grinding has revealed four incisors, one canine and nine molars; the dental formula thus is:
$$\frac{I-6, C-1+1, M-5+?}{I-4, C-1, M-9+?}.$$

These two specimens again show only some features of the dentition. Amongst reptiles this is seldom a very reliable criterion. I doubt whether, in this case, it justifies distinguishing this form by name from *Ictidognathus*. In any case, it offers no conclusive testimony as to the affinities of this animal. For convenience, both *Ictidognathus* and *Ictidostoma* may provisionally be retained in the family Scaloposauridae, until their affinities are determined or until they prove indeterminable.

SUMMARY

1. A fairly good skull of the pristerognathid, *Alopecognathus angusticeps*, is figured in dorsal and lateral view and described; it is shown that this form is a fairly primitive therocephalian, related to *Pristerognathus* and *Scymnosaurus*.

2. In describing the palate of *Scylacosaurus sclateri*, I have drawn attention to the architectural arrangement of the constituent bones.

3. It is pointed out that there is very little evidence that *Ictidognathus* and *Ictidostoma* are scaloposaurids; this is in confirmation of Watson's opinion (1931).

In conclusion, my thanks are due to the officers of the Department of Vertebrate Palaeontology of The American Museum of Natural History for affording me the facilities I have enjoyed in my study of the material in their charge. To the University of Stellenbosch I am indebted for a small grant, which has enabled me to visit New York. The drawings which illustrate this paper have been done by my wife.