

ON SOME SMALL THEROCEPHALIANS

By A. S. BRINK

ABSTRACT

The snout of a new specimen of *Akidnognathus parvus* is described in detail from serial sections at .5mm. intervals. Special reference is made to the structure of the septomaxillary and its possible morphological significance. It is suggested that its peculiar arrangement is relatable to a readaptation in the mode of smelling in mammal-like Reptiles. Additional descriptions deal with new specimens assignable to *Ictidostoma hemburyi*, *Ictidosuchops intermedius*, *Ictidosuchops bauroides* and *Ictidosuchoides longiceps*. All descriptions are accompanied by adequate figures. The new information adds little to existing views on the relationship of the families Ictidosuchidae and Scaloposauridae.

INTRODUCTION

An interest in the peculiar arrangement of the septomaxillary in Therapsids, especially with a view to its possible relationship to the organs of Jacobson and the change from the reptilian to the mammalian mode of smelling, has induced the author to grind serially the snout of a small Therocephalian in which these bones are well preserved. The intention was, and still is, to grind serially and graphically reconstruct in wax as many Therapsid specimens as possible, representing a cross-section of this fauna, with the object of creating a broad and clear comparative anatomical picture to which certain physiological considerations can be related.

It was in due course appreciated that there are not enough small duplicate specimens available, fit for serial grinding, with well preserved septomaxillaries, and at the same time also representing each major type of mammal-like reptile. Besides, at the very outset this task proved to be too ambitious for a single research project and the subject should better be dealt with in a series of phases. Each specimen, after serial grinding, presents itself as a subject for a substantial descriptive paper, more so when it draws attention to several other specimens which had previously suffered some neglect.

These are the circumstances which led to the presentation of this paper. The specimen serially sectioned is described first, with some emphasis on the septomaxillary and casual reference to some speculative views which the author holds about its peculiar nature. Thereafter descriptions follow of several other Therocephalians of similar size — not necessarily of close affinity.

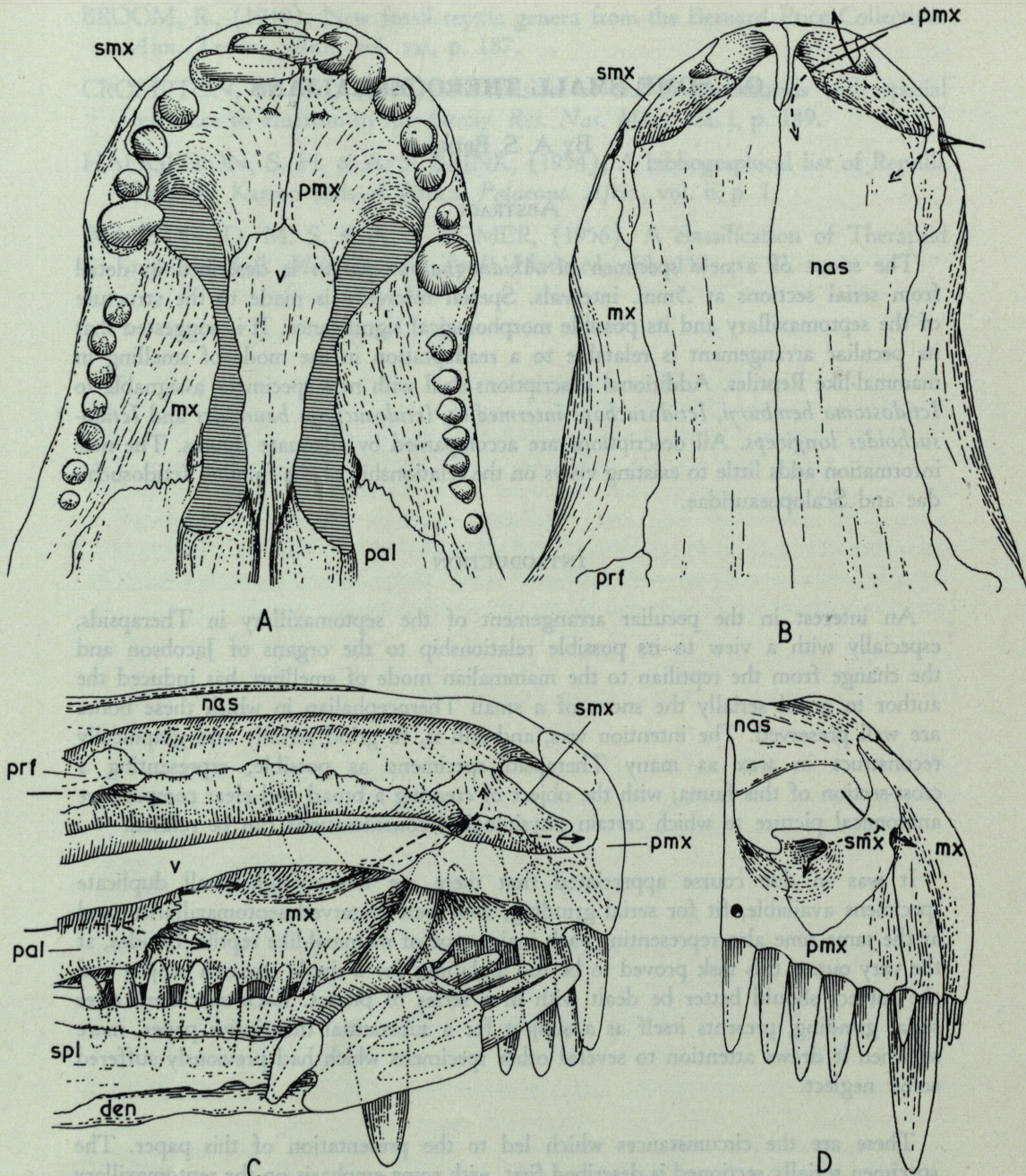


Figure 36

A, Palatal; B, Dorsal; C, Sagittal and D, Anterior views of the snout of *Akidnognathus parvus*, graphically reconstructed from a complete series of parallel sections at .5 mm. intervals. Twice natural size. For abbreviations see end of article.

Akidnognathus parvus Haughton
(Figures 36 and 37)

1918 HAUGHTON, S. H., *Ann. S. Afr. Mus.*, XII, p. 192, figs. 51, 52.

1932 BROOM, R., *Mammal-like Reptiles*, p. 64, figs. 20C, D.

Type: Skull in the South African Museum, Cape Town (No. 4021), from *Cistecephalus*-zone beds on the farm Zuurpoort in the Graaff-Reinet District.

Present specimen: Snout, serially sectioned, represented by a cast, a detailed wax model four times natural size and a complete series of section figures, in the Bernard Price Institute (No. 340) from the *Cistecephalus*-zone, near the *Endothiodon*-zone contact, on the Graaff-Reinet Commonage (Collector: Mr. B. J. Kitching).

The process of grinding was undertaken with the aid of the Croft Parallel Grinder. The specimen was embedded uncleaned in calistone and secured to the specimen holder with bee's wax. Section intervals are consistently .5mm., and every section was drawn with the aid of an Opague 1000 Delineascope (standard episcope of the American Optical Company). The episcope was secured to a stable horizontal bench surface at a distance from the "screen" calculated to project images at exactly 4 times natural size, with lens settings and focus fixed. The platform was made to drop lower than the design permits by securing the supports to left and right wooden strips of desired thickness and by removing the cross bar at the back on which the platform catches when it is desired to leave it in the open position.

A receptacle constructed of $\frac{1}{4}$ " masonite was bolted on to the platform. It was accurately constructed to receive the specimen holder, taken from the Croft Parallel Grinder, always in the same position. On raising the platform, the ground surface of the specimen was consistently from the first to the last section brought up against the glass pressure plate and it was thus ensured, with focus, lens setting and elevation fixed, that a standard 4 times natural size projection was obtained on a stable drawing board "screen", erected in the vertical plane. Moreover, successive projections proved to coincide exceptionally accurately as a result of the limitations of movement in the process to an absolute minimum. The only movement was bringing the specimen with holder from the Croft Grinder to the projector, but it fitted into the projector as accurately as in the grinder. The design of the platform elevating mechanism ensured the most accurate positioning against the glass pressure plate that could be desired. On the drawing board, standard sized paper with two standard holes were positioned over two fixed pegs, these holes having served as the base line for both graphical figuring and wax reconstruction. No base line indicator was associated with the specimen itself.

This procedure is exceptionally simple and easy to handle, without prejudicing accuracy. In fact, the procedure proved to be so accurate that hardly any ziz-zag difficulties were encountered in either figuring or reconstructing. The only disadvantage was tracing in the vertical plane. This could have been overcome by introducing a mirror, but it was considered that it would also introduce a certain measure of inaccuracy.

Grinding was performed with a standard No. 0 carborundum powder on a zinc plate. Each section was coloured with Alizarine Red and covered, when dry, with a thin coat of dilute glyptal cement, which had the effect of giving the surface a very glossy finish as though it had received the finest possible polish. This brought out all the details, especially colour contrasts, so clearly that detailed study under the binocular microscope proved to be hardly necessary. The projected image in total darkness (with the projector outside the dark room) was as clear as could be desired, even at only four times natural size.

The wax model was constructed with the aid of standard 1 mm. thick high stability "Modelling Wax" plates, an Amalgated Dental Product, "a specially toughened wax with wide temperature range particularly suitable for tropical climates".

Only the left half of the snout was reconstructed in wax (except for the vomer which is complete) to allow for a better study of the nasal cavity and to assist in preparing figure 36c.

When it was decided to subject the present specimen to serial grinding, the possibility was considered that it might turn out to be the type of a new form of Therocephalian, in spite of the fact that superficially it showed great likeness to another, much smaller specimen (which could subsequently be identified as an *Ictidosuchops baurioides*). As progress was made with the grinding, it became increasingly clear that it was quite a different form, but nothing could be done to avoid the possible situation where a type specimen would subsequently be represented by a wax model. Fortunately, however, after the specimen had been graphically figured and reconstructed in wax, it was discovered that it represents the form *Akidnognathus parvus*.

Identification is based on the following features:

- (1) The dental formula is $i5, c2, pc7$ as in the type.
- (2) The incisors are substantially larger than the post-canine teeth.
- (3) The fifth incisor is smaller than the other four, superficially quite near in size to the anterior canine, and there is a distinct diastema between these two teeth.
- (4) The seventh post-canine tooth either side is situated at a level forward of the posterior borders of the internal nares.
- (5) The palatal foramen on the palatine-maxillary suture is approximately at the level of the 5th post-canine tooth.

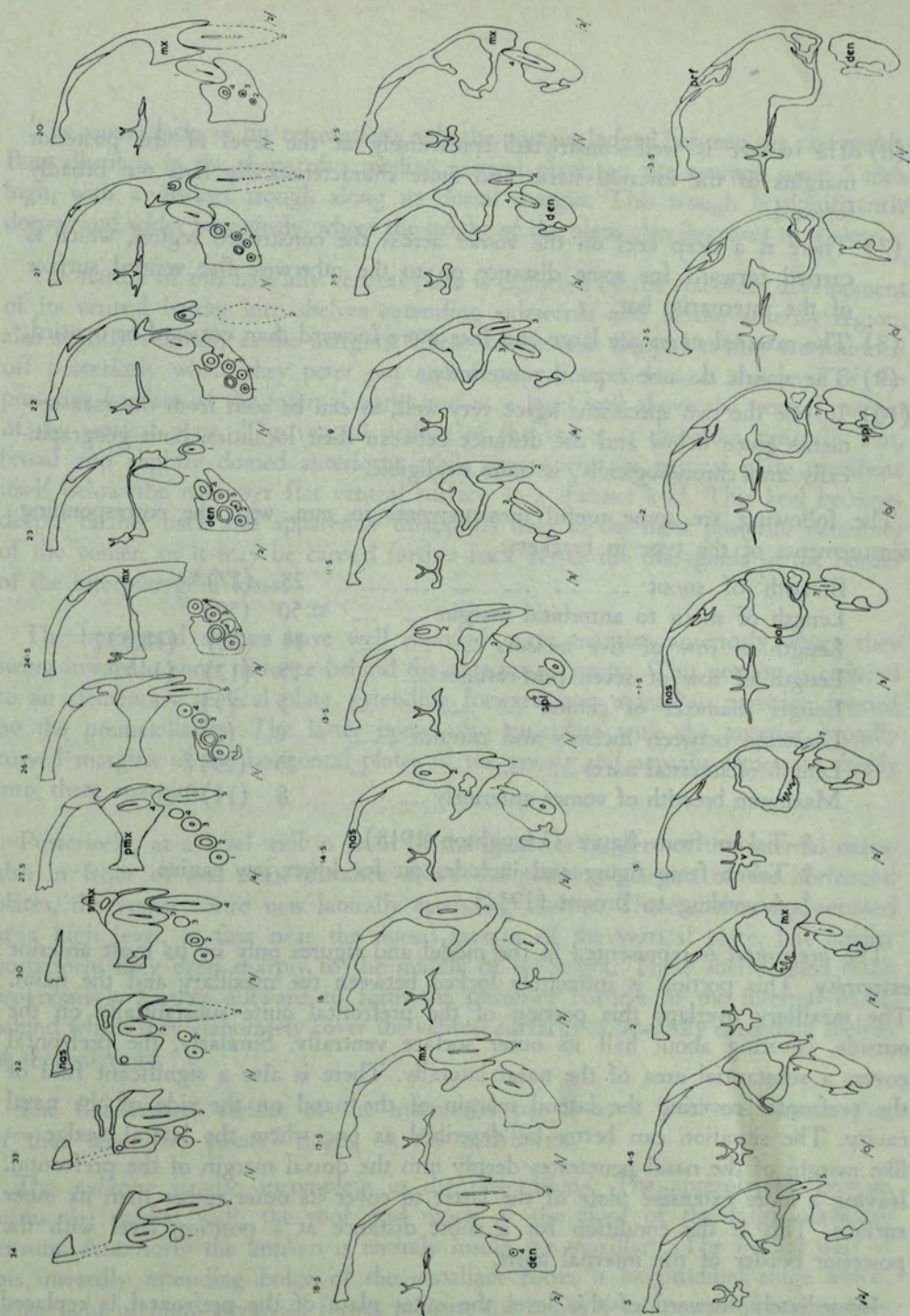


Figure 37

Series of sections following in order from left to right through the snout of *Akidnognathus parvus*.
Natural size.

Legend: Numbers above section figures are the levels in mm., 37 mm. being the level where first contact was made with the premaxillaries and grinding having been ceased at -3.5 mm. Numbers below and between section figures, between strokes, indicate, for easier interpretation, the number of sections at .5 mm. intervals that have been left out of the series in this illustration. Numbers accompanying teeth indicate their place in their respective incisor, canine and post-canine series.

For abbreviations see end of article.

- (6) The vomer is well constricted transversely at the level of the posterior margins of the internal nares and quite characteristically fans out broadly forward.
- (7) There is a deep keel on the vomer across the constricted region, which is carried forward for some distance on to the otherwise flat ventral surface of the internarial bar.
- (8) The external nares are large and face more forward than outward or upward.
- (9) The nasals do not expand posteriorly.
- (10) In size the two specimens agree very well, as can be seen from the measurements given below and the distance between their localities, both geographically and chronologically, is quite negligible.

The following are some useful measurements in mm. with the corresponding measurements of the type in brackets:

Breadth of snout	28	(27)*	
Length of snout to antorbital margin	±50	(50)	
Length of row of five incisors	14	(22)	(18.5)†
Length of row of seven post-canines	15	(12)	(14)‡
Longer diameter of canine	5	(5)	
Diastema between incisors and canines	2	(2)	
Length of internal nares	25	(29)†	
Maximum breadth of vomer anteriorly	8	(11)*	

* Taken from figure (Haughton 1918).

† Taken from figure and includes pit for lower jaw canine.

‡ According to Broom (1932).

The *prefrontal* is represented in the model and figures only by its most anterior extremity. This portion is intimately locked between the maxillary and the nasal. The maxillary overlaps this portion of the prefrontal quite substantially on the outside, covering about half its outer surface ventrally. Similarly, the prefrontal covers a substantial area of the nasal laterally. There is also a significant fold of the prefrontal covering the lateral margin of the nasal on the side of the nasal cavity. The situation can better be described as one where the lateral wedge — like margin of the nasal penetrates deeply into the dorsal margin of the prefrontal, leaving a more extensive plate of the latter to cover its outer rather than its inner surface. This is the condition for a short distance at a position level with the posterior border of the internal naris.

Immediately forward of this level the outer plate of the prefrontal is replaced by a similar fold of the maxillary, while on the side of the nasal cavity the inner plate becomes more extensive as it forms, in addition, the dorsal margin and roof of the foramen linking the nasal cavity with the vacuity accommodating the lachrymal duct. Shortly forward of this opening the prefrontal terminates.

The *vomer* lacks in the restorations only the portion lodged between the pterygoids. Basically it is in the shape of a median vertical plate, on the average some 5 mm. high, with a distinct trough along its dorsal margin. This trough is significantly deeper and wider posteriorly, where the height of the plate also increases to 6 mm.

The nature of this basically vertical plate is distorted by the elaborate development of its ventral border into shelves extending sideways and in the anterior region, also slightly ventrally at the margins. These margins are sharp, but they are rounded off posteriorly where they peter out and disappear as shelves at the level of the posterior borders of the internal nares and at a level well above the ventral margin of the vertical plate. The ventral surface of the vomer is therefore generally flat, broad and slightly domed anteriorly, while posteriorly the vertical plate manifests itself below the narrower flat ventral surface as a distinct keel. This keel becomes deeper farther back and apparently disappears only in the most posterior extremity of the vomer, or it may be carried farther back across the pterygoids to the border of the interpterygoid fossa.

The horizontal shelves have well rounded outer margins anteriorly where they swing inward a short distance behind the anterior extremity. This portion is reduced to an elementary vertical plate, extending forward over a median partition formed by the premaxillaries. The latter bones also articulate with the anterior broadly curved margins of the horizontal plates of the vomer and actually penetrate deeply into these margins.

Posteriorly, at a level well in front of the posterior borders of the internal nares, also in front of and some distance above the petering margins of the horizontal plates, the vomer forms new laterally extending shelves. These shelves are situated at a high level, at first near the dorsal margin of the vertical plate, but farther posteriorly they drop sharply to the middle of its height. These shelves also reach progressively farther outward to form the posterior borders of the internal nares, behind which they elaborately cover the ventral surfaces of inwardly extending shelves of the palatines.

The flat ventral surface of the internarial bar is at a level well above that of the "secondary palate" ridges on the maxillaries.

The *palatine* is also incomplete in the restorations. The anterolateral portion forms the medial wall, the roof and much of the floor of the large maxillary antrum. Anteriorly the antrum is entirely inside the maxillary. The medial wall of this inwardly extending bulge of the maxillary forms a longitudinal ridge which, in the light of more advanced forms, indicate the initial development of a secondary palate. This ridge is not carried back distinctly on to the palatine. Immediately below the ridge, still in the maxillary, is the palatine foramen, bordered posteriorly by the palatine. Haughton (1918) figures these foramina as situated more entirely inside the palatines, but the palatine-maxillary suture is so elaborately interdigitated

in this region that such a variation can quite likely occur within the same species. Otherwise, a slight under- or overdevelopment in the process of cleaning could also be responsible for presenting this difference.

Another foramen is situated directly above in the roof of the antrum, also in the maxillary and bordered posteriorly by the palatine. The palatine reaches farthest forward between these two foramina.

Dorsally on the roof of the antrum the palatine is met halfway by a shelf of the maxillary. This shelf is restored farther back to allow the palatine to form the whole of the roof. However, at the very level of the posterior border of the internal naris the palatine falls away from the maxillary, leaving a wide opening between the antrum and the nasal cavity. At this level it very abruptly sends a shelf inward to the vomer, the latter covering its ventral surface extensively. Exactly on the posterior border of the internal naris the palatine extension is not in the shape of an horizontal shelf; the margin is turned sharply upward to form a distinct vertical wall some 3 mm. high, extending transversely. The dorsal free margin of this wall is continuous with the border, formed by the palatine, of the wide opening between the antrum and the nasal cavity.

This vertical transverse wall served for the insertion of the anterior oblique muscles of the eye.

Along the floor of the maxillary antrum the palatine elaborately clasps the maxillary between extensive thin plates.

The *nasal* lacks its posterior extremity, but enough is preserved to show that, as in the type, it does not expand noticeably at the level of the anterior end of the prefrontal. This is a rather general Bauriamorph, or more particularly a Scaloposaurid characteristic.

The outer face of the downward inclined wedge-like lateral margin of the nasal is extensively covered by the prefrontal behind, the maxillary in the middle and the septomaxillary in front. Only the prefrontal endeavours to cover the nasal margin on the inside as well.

There is a distinct ridge running longitudinally some 5 mm. from the skull midline on the ventral surface of the nasal. This ridge evidently marks at least the initial development of a fronto-nasal ethmo-turbinal.

The *maxillary* is broadly depressed on the outside in the region above the roots of the cheek teeth and behind the slight bulge of the canine root. This depression does not affect the alveolar margin so that the snout is not constricted in dorsal view.

The maxillary carries a small canine in front on the border of the excavation for the lower jaw canine. The main canine is a large tooth and the sections show no indication, either left or right, of replacement — not even as far as elementary toothbuds are concerned. Behind the canine there are seven cheek teeth, subequal in size. On the right the fifth had been lost before fossilization, but quite likely after death, leaving an empty socket with no tooth bud. None of the cheek teeth show signs of recent or impending replacement.

All the cheek teeth are smaller than the incisors. The seventh cheek tooth is the smallest and equal in size to the anterior canine.

The elementary "secondary palate" ridge on the lingual aspect of the maxillary becomes progressively more crested forward of the palatal foramen and at the level of the canine, where the general inner face of the maxillary bulges markedly across the root, the crest becomes a distinct shelf, but turned upward to form a deep alcove. This deep hollow leads forward and upward to a foramen communicating with the outside surface of the snout. The crest of this upward inclined shelf also forms the anterior margin of the internal naris as it swings inward and backward to the vomer at a level immediately behind the tip of the lower jaw canine where the latter is in normal closed position. This portion of the border is formed by the premaxillary.

The *premaxillary* carries five teeth. The first four are quite large, but the fifth is reduced and the exposed crown is near in size to that of the first canine. When the roots are also compared, however, the fifth incisor is still substantially larger.

All the incisors (and the post-canine teeth) are directed straight down (excluding the last cheek tooth which leans with the crown backwards). The incisor roots curve slightly backwards in their sockets, the rather short root of the first tooth doing so somewhat more conspicuously. (Both canines either side project forward slightly.)

The premaxillary elaborately overlaps the maxillary on the side of the excavation for the lower jaw canine. Here, for some distance, it joins the maxillary in forming the upward turned crest, that is, the maxillary-premaxillary suture extends along the summit of the crest. Farther forward the premaxillary brings the crest inward to form the anterior border of the internal naris. More medially the premaxillary extends backward as a thin tapering projection cutting quite deeply into the border of the anterior rounded margin of the horizontal portion of the vomer. On the midline the premaxillary very suddenly attains substantial height as it builds, with its fellow of the opposite side, a median crest dorsally, continuous with the vertical plate of the vomer. The groove in the dorsal margin of the latter bone is not continued on to the premaxillary crest.

The premaxillary characteristically builds anteriorly, with its fellow of the opposite side, an internarial bridge which extends upward and subsequently backward, penetrating between the anterior ends of the nasals.

There is a peculiar canal penetrating the premaxillary. This canal extends well above and inside the root of the first incisor. Anteriorly it runs sharply downward to open on the surface immediately in front of the root of this tooth, shortly above the alveolar border. Dorsally it has a second opening intimately on the side of the base of the internasal bridge. The canal continues backward and has a third opening in the roof of the mouth immediately behind the first incisor.

The premaxillary builds a substantial floor either side in the anterior part of the nasal cavity. This floor is generally flat, somewhat depressed centrally. The floor rises very slightly towards the anterior margin of the internal naris. On the side of the mouth cavity the well excavated pit to receive the lower jaw canine is obtained more as a result of a reduction in the thickness of the bone laterally than of a general elevation of this massive plate-like shelf.

This floor in the anterior part of the nasal cavity is given a depressed appearance largely on account of the substantial upheaval anteriorly across the incisor roots, forming the ventral border of the external naris. Across this upheaval extends the septomaxillary. The otherwise fairly level floor extends straight forward to the anterior face of the snout through a narrow gap between the internasal bridge and a shelf-like crest of the septomaxillary. The floor also extends backward medially to the internal naris as a shallow groove above the horizontal shelf of the vomer, and laterally as a more distinct groove to the deep hollow between the upturned "secondary palate" crest and the bulge of the canine root.

The *septomaxillary* extends as a thin plate across the high and wide ventral margin of the external naris. It covers a considerably greater area on the anterior slope of this upheaval, formed by the roots of the incisors, than on the posterior slope. Medially it is entirely on the anterior slope and laterally it folds over to a slight extent on to the posterior slope, from where it continues backward and upward as a wedge lodged intimately between the nasal and the maxillary.

Along the crest of the upheaval forming the ventral border of the external naris, the septomaxillary grows quite thick and is traversed by a canal. This canal opens forward and inward into a conspicuously depressed area on the anterior face of the septomaxillary, this hollow being greatly exaggerated by the sharpness of the crest above, leaning forward as a roof over the foramen in particular and the depression in general.

The canal opens laterally into the foramen through which the trough in the nasal cavity above the "secondary palate" ridge leads to the outer face of the snout, immediately on the side of the external naris.

The sides of the depression on the anterior face of the septomaxillary do not slope towards the foramen, but towards the notch between the septomaxillary crest and the premaxillary internasal bridge, leading inward on the floor of the nasal cavity.

The general structure of this region is most peculiar, more so on account of the fact that it is typical of all carnivorous Therapsids, from the earliest Gorgonopsian, through all the Therocephalia and Cynodontia, to the most advanced Bauriormorph. Quite conspicuous, too, is the fact that this peculiar arrangement is not characteristic of the herbivorous Dinocephalia and Anomodontia.

This arrangement has induced the author to consider to what extent it can be related to the organs of Jacobson and the function of smelling in animals where obviously a vast change must have occurred in this respect. These animals being transitional between reptiles and mammals must indicate how the change was effected from the reptilian way of smelling (basically by allowing the tongue to communicate directly with the organs of Jacobson) to the mammalian method of "sniffing". It is this interesting problem which induced the author to section the present specimen, but it was appreciated that a much broader picture is required before substantial conclusions can be formulated. The author intends, therefore, to section as many specimens as possible, representing the widest possible cross-section of Therapsids, to establish a detailed comparative anatomical picture on which more substantial views can be based. It was appreciated that this would be a lengthy and laborious task and that it would be advisable not to deal with the subject as a confined research project, but to report from time to time on results that are achieved. At this stage the author can only submit some speculative views, representing the line of thought on which this project is provisionally based.

At the outset it should be borne in mind that smelling is intimately associated with taste and that as far as the latter is concerned, the organs of Jacobson play a more definite and refined role than the taste papillae on the tongue. The tongue is also basically not intended to be a largely sensory taste organ, but a mechanical apparatus for assisting in the "manipulation" of food. It acquired a certain degree of taste sensitivity, but only to distinguish between major categories such as saltiness, sweetness, acidity and bitterness in their various degrees. The tongue must therefore decide immediately whether some particular food is consumable or not. The organs of Jacobson supplement by adding, through its ability to distinguish between the finer nuances in the field of odour, to an interpretation of the palatability of the food.

Smelling is therefore basically tasting and the organs of Jacobson are so conveniently situated in the roof of the mouth cavity or, otherwise, in the floor of the nasal cavity that they can detect odour either directly from the air inhaled or after it had become dissolved in the moisture of the mouth cavity.

In a reptile the detection of odour directly from the air inhaled is quite ineffective, firstly on account of the slow, irregular breathing and secondly on account of the dryness of the nasal passage. The organs of Jacobson are therefore directed toward the mouth cavity and in many forms the habit developed to allow the tongue to communicate directly with these organs. In many forms, too, the tongue is split and it is periodically projected from the mouth to allow odour to dissolve on its moist surface, after which it is retracted and passed through the internal nares to the organs of Jacobson.

In the mammal-like reptiles one major change contributed towards rendering this normal and basic way of tasting quite ineffective, that is, the development

of a secondary palate. As pointed out in a previous publication (Brink, 1956*) a secondary palate develops hand in hand with mastication, for three reasons:

- (1) To place the internal nares as far back as possible so as to allow the animal to breathe while masticating its food.
- (2) To prevent masticated food from passing into the nasal cavity.
- (3) To present a platform for the tongue to operate against in "handling" the masticated food.

It does not matter which one of these is taken as the principle function of the secondary palate. The major implication is that the communication between the tongue and the organs of Jacobson now becomes obstructed.

It would appear that the only alternative was for the organs of Jacobson to concentrate their attention directly to odours inhaled through the nasal cavity, thus changing their nature from taste to olfactory organs. This change could not be accomplished without involving a number of other significant adaptations.

The habit of mastication and the resultant development of a secondary palate cannot be regarded as having had a direct relatable effect upon the nature of the nasal cavity and breathing in general, other than that air now happens to pass for a longer distance through this cavity. To become effectively adapted for the function of smelling the nasal cavity had to undergo other changes, such as the extensive development of wet mucous tissues and additional elaborate ethmoturbinals to present the greatest possible surface for the inhaled air to pass over, so that the maximum amount of odour could be absorbed for detection. Mastication did, however, have a direct effect upon smelling in that it accelerated the general metabolism, which demanded an increased supply of oxygen, implying a faster rate of breathing, with or without reflections upon the significance of a diaphragm. This faster rate of breathing naturally facilitated the more effective absorption of odour in the nasal cavity and the diaphragm facilitated the phenomenon of deliberate "sniffing".

It should, however, be emphasised again that the major requirement for smelling is a wet nasal cavity with the greatest possible surface presented to the air passing through, and that this arrangement was not necessarily initiated as a direct consequence of the development of a secondary palate. The two developments cannot be interpreted as having occurred hand in hand, and it can virtually be taken for granted that some time passed between the stage when the organs of Jacobson had lost their communication with the mouth cavity and before they were amply re-adjusted to detect odour directly from the air "sniffed" through the elaborate nasal cavity. The peculiar nature of the septomaxillary must be indicative of an intermediate stage in this re-adaptation.

* *Palaeont. Afric.* iv, p. 77.

At the present stage of this investigation it appears that the characteristic depression on the anterior face of the septomaxillary lodged a gland which secreted a fluid used either for wetting the nostrils or for moistening the air to facilitate the absorption of odour. The shape of the depression suggests that here had been an effective communication directly between this gland and the organ of Jacobson while breathing might still have been at a slow tempo. The object was not to detect odour inside the nasal cavity, but on the outer surface of a wet nostril and upper lip. This would be the obvious arrangement for an animal that could not sniff, where it could detect odour in a breeze passing its nose. If the glands had an intimate relationship with the organs of Jacobson the latter may have been able to detect odour dissolved directly in the moisture of the nostrils and very effective "smelling" for the palatability of food could have been effected by bringing the nose in actual contact with it. Similarly, an occasional lick across the nostril while feeding may also have kept the organs of Jacobson effectively informed of the finer flavour of the food. The situation might even be interpreted as one where the organs of Jacobson, after losing their communication with the mouth, made a bold endeavour to re-establish communication along a different route, the only effective one being through the external nares, in the direction of the source of the odour and still within easy reach of the tongue.

The fairly large canal traversing the septomaxillary suggests a rich blood supply which provided the fluid secreted. In some Therapsid specimens a distinct groove leads from this depression back to the foramen on the side of the naris, which might indicate the effective venous drainage. The canal through the premaxillary with its opening into the depression, is evidently the approach of the nervous innervation, this nerve also sending a branch farther forward, apparently into the upper lip for greater general sensitivity.

Whatever the case might actually have been, at this stage it seems quite evident that in the Therapsids in general, the nasal cavity had not yet become adapted for smelling according to the mammalian arrangement. It is equally clear that some intermediate stage existed where the detection of odour was concentrated in a restricted locality, very far forward in the nasal cavity, perhaps more specifically in front of the nasal cavity in the external nostril. Subsequently all the other developments occurred which resulted in the adaptation of the entire nasal cavity to the function of detecting odour, as is the condition in mammals.

If this rather vague interpretation should eventually prove to be reasonably correct, answers will have to be found for a number of significant questions. First and foremost, the question will most definitely arise as to why this intermediate arrangement occurred only in the carnivorous Therapsids. Perhaps the herbivorous forms relied more on sight for the selection of their food. Perhaps their food had been so abundant that they were not required to search widely. Detection by smelling is quite definitely more important to a hunting carnivore than to a quietly grazing herbivore, although mammalian herbivores are quite dependent on odour for the

detection of approaching danger or in the selection of partners in the mating season. Nevertheless, herbivores might rely on hearing for the detection of approaching danger while odour in the mating season might be of less importance to a gregarious herbivore than to a lone marauding carnivore.

A second significant question that arises even at this stage is why all carnivorous Therapsids are characterized by this peculiar septomaxillary arrangement, from early forms which had typically reptilian palates and could taste in the typical reptilian manner, to advanced Cynodonts and Bauriamorphs with long established secondary palates and nasal cavities evidently quite near in structure to that of mammals. Perhaps soft secondary palates featured in early forms long before a bony secondary palate appeared on the scene. Even in the present specimen the "secondary palate" ridges on the maxillaries are so obviously directed towards the sharp edges of the horizontal palatal plate of the vomer, the latter in turn reaching towards the maxillary ridges, that the conclusion of a soft palate having effectively confined the internal nares to a level near or even behind the bony posterior borders seems quite unavoidable. In the present specimen as in the majority of Therocephalians and to a lesser extent perhaps the Gorgonopsians as well, such a soft partition separating the mouth cavity from the nasal cavity could already have induced these animals to devise a different method for the detection of odour. In the advanced forms the nasal cavities might have achieved the mammalian structure, but the nostril arrangement had apparently been found quite effective enough for its retention. Even modern mammals find wet nostrils advantageous for some particular reason. It is also likely that even after the mammalian nasal cavity arrangement had been well established, the septomaxillary gland could have been retained for the sole purpose of additionally moistening the inhaled air, in animals now breathing substantially fast in an arid environment. It is quite evident that the Cynodonts had supplemented the septomaxillary gland in this role with maxillary glands, so serious was the danger of losing too great an amount of water through evaporation directly from the blood in the lungs.

Another question to be clearly elucidated bears upon the circumstance that the septomaxillary arrangement is apparently very standard in structure throughout the carnivorous Therapsids, from the giant Gorgonopsians to the most delicate Scaloposaurid. This circumstance may serve to emphasize the significance to these animals of this peculiar arrangement, whatever it may in actual fact prove to be.

The *dentary* is very straight anteriorly, with virtually no curving upward of the symphyseal region. There are four very long incisors directed almost straight forward. They have all recently replaced their predecessors, remnants of which are still to be seen in the sockets. The canine is directed very markedly forward. There are seven post-canine teeth.

The *spenial* has suffered some damage both sides. Its structure as displayed in figure 36C may, therefore, be somewhat incorrect.

Ictidostoma hemburyi (Broom)
(Figure 38)

- 1912 BROOM, R., (*Ictidognathus hemburyi*) *Proc. zool. Soc.*, p. 865; pl. XCI, 10, 11.
 1914 BROOM, R., (*Ictidognathus hemburyi*) *Phil. Trans.*, B206, p. 47; pl. VI, 76.
 1915 BROOM, R., (*Ictidognathus hemburyi*) *Bull. Amer. Mus. nat. Hist.*, XXV, p. 117.
 1930 BROOM, R., (*Ictidognathus hemburyi*) *Phil. Trans.*, B 218, p. 371, pl. XXXIV, 39.
 1931 WATSON, D. M. S., (*Ictidognathus hemburyi*) *Proc. zool. Soc.*, p. 1186.
 1931 BROOM, R., *Rec. Albany Mus.*, IV, p. 161.
 1932 BROOM, R., *Mammal-like Reptiles*, p. 72, fig. 22c, d.
 1935 BOONSTRA, L. D., (*Ictidognathus hemburyi*) *Amer. Mus. Novit.*, 771, p. 11.

Type: Middle and snout portion of skull with mandibles in good preservation, from apparently high in the *Endothiodon* zone at Beaufort West, now No. 5520 in the American Museum of Natural History, New York.

Present specimen: Complete skull with right mandible in situ, left dislocated, posterior region not well preserved, from *Cistecephalus*-zone beds, about 2 miles northwest of Richmond in a river bed alongside the De Aar road. It is numbered 341 in the collection of the Bernard Price Institute.

The present specimen is referred here to the poorly described *Ictidostoma hemburyi* on two unsatisfactory features; size and dental arrangement. Although existing figures and descriptions portray very little in the line of structure it is still fairly evident that in size and shape the present specimen compares very favourably with the type. It is, in fact, of exactly the same size and the shape of the snout is strikingly similar, especially where it is sharply pointed, and the external nares are inclined to face more outward than forward. The nasals also do not expand posteriorly. For size comparison the following measurements in mm. are useful, those in brackets being the equivalents in the type:

From tip of snout to anterior borders of orbits	42	(42)
Antero-posterior diameter of orbit	20	(18)
Interorbital width	21	(19)
Breadth of snout across canines	28	(27)
Diameter of large canine	4	(3.5)
Row of 8 postcanine teeth	19	(17)
Row of six incisors	12	(10)
From tip of snout to pineal	71	
From tip of snout to occipital border	88	
Approximate total length of skull	100	
Intertemporal width	10	
Approximate total breadth of skull	67	

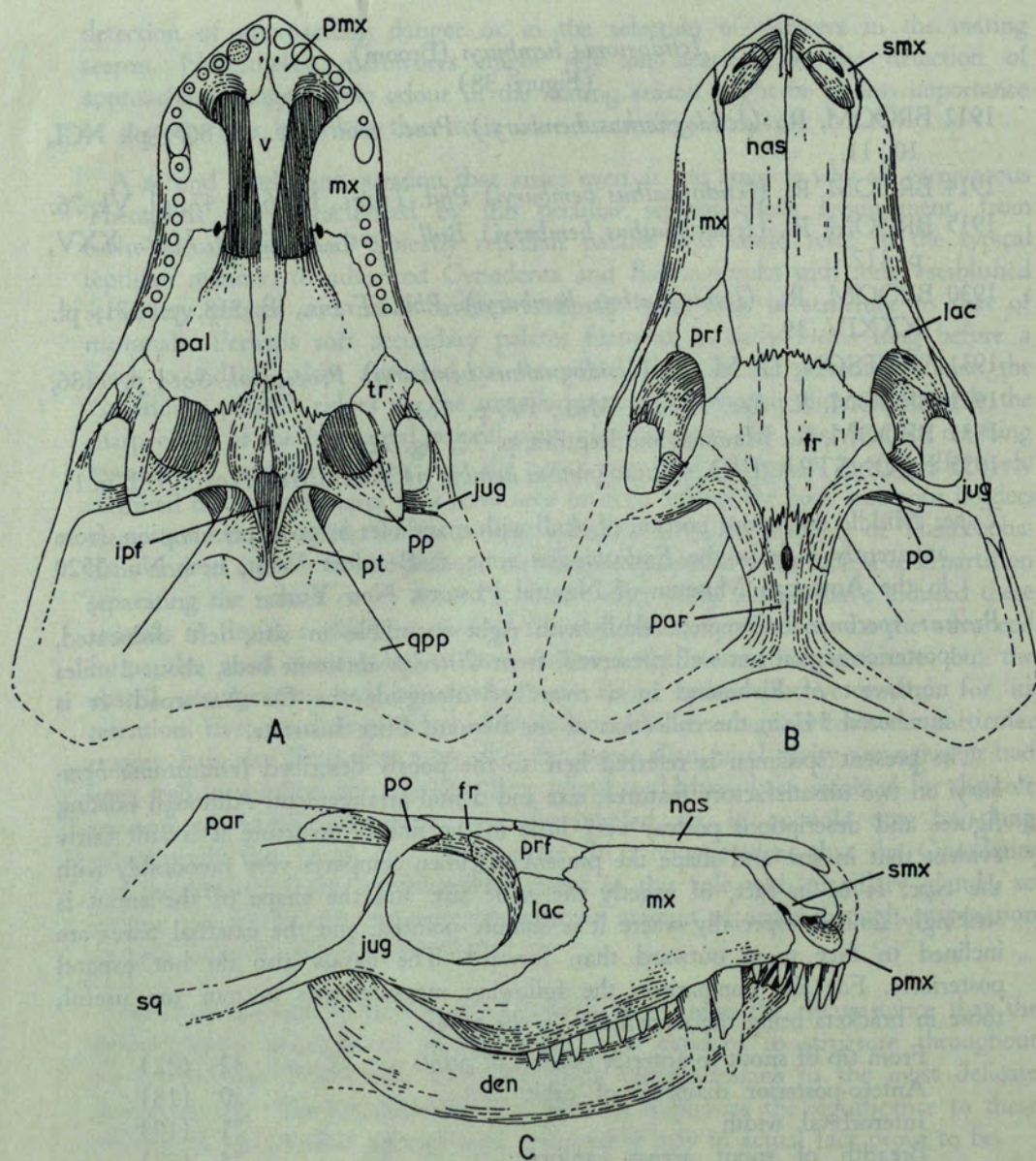


Figure 38

A, Palatal; B, Dorsal and C, Side views of the skull of *Ictidostoma bemburyi*. Natural Size.
For abbreviations see end of article.

As far as dental arrangement is concerned, not only does the present specimen agree in having six incisors, two canines and eight post-canines, but also in the more conspicuous features where the subequal incisors agree in general size range with the postcanine teeth. In both series the anterior teeth are appreciably larger than the posterior teeth.

The only difference between the new specimen and the type lies in the geological age. The type comes from *Endothiodon*-zone beds and, although this might be at a fairly high level, the Richmond site is well in the middle *Cistecephalus*-zone. This rather appreciable difference in age could justify the recognition of the new specimen as a form specifically distinct from *Ictidostoma hemburyi*, but it is inadvisable to do so while the separation of *I. hemburyi*, even specifically, let alone generically, from its nearest ally *Ictidognathus parvidens*, is anything but substantial.

Ictidostoma hemburyi does, however, appear to be different from *Ictidognathus parvidens*. In the latter the snout has a different shape, is much longer and more slender, features which could provisionally be regarded as more substantial than the number of post-canine teeth on which the generic distinction has thus far been based.

The present specimen is quite satisfactory. It lacks the left temporal and postorbital arches and although the outline of the posterior region of the skull is clear, substantial pre-fossilization damage has rendered it impossible to analyze it in detail. The left mandible is dislocated and associated with some other skeletal bones, principally of a front limb and some ribs, which have arranged themselves around the back and dorsal sides of the skull, the latter having become embedded on its side. The right angular is also dislocated.

The specimen seems to support views held earlier that this form is not a very close ally of the Scaloposaurids. It lacks the more delicate, slender build of the Scaloposaurids. The skull is deeper and the snout shorter and more robust. In having lost an anterior small canine it is an unlikely direct ancestral form. The postorbital bar is still complete. The dentary is more distinctly curved.

The palate is nevertheless rather Scaloposaurid-like, even though the secondary palate ridges are less distinct and still widely separated.

The nasals are Scaloposaurid-like in that they do not expand posteriorly.

There are definitely no postfrontals, unlike Broom's interpretation in his figure of 1932.

Ictidosuchops intermedius (Broom)

(Figures 39 & 40)

- 1938 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 19 p. 257, figs. 1—3.
1940 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 20 p. 161, figs. 1—5.
1941 BROOM, R., (*Ictidosuchoides intermedius*) *Ann. Transv. Mus.*, 20 p. 194, fig. 3.
1955 CROMPTON, A. W., *Res. Nas. Mus.*, 1, p. 149, figs. 1—7.

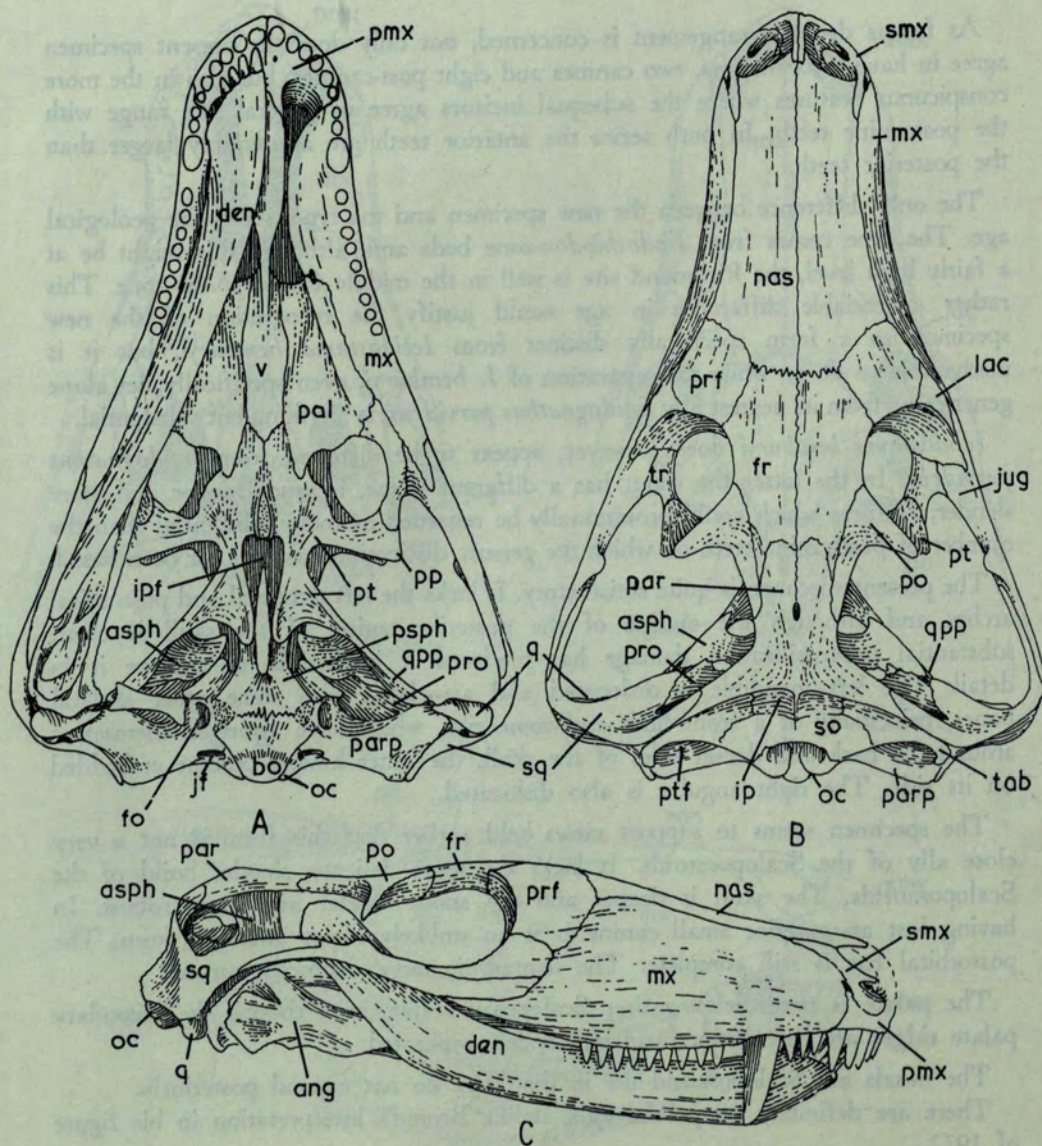


Figure 39

A, Palatal; B, Dorsal and C, Side views of the skull (No. 267) of *Ictidosuchops intermedius*. Natural size. For abbreviations see end of article.

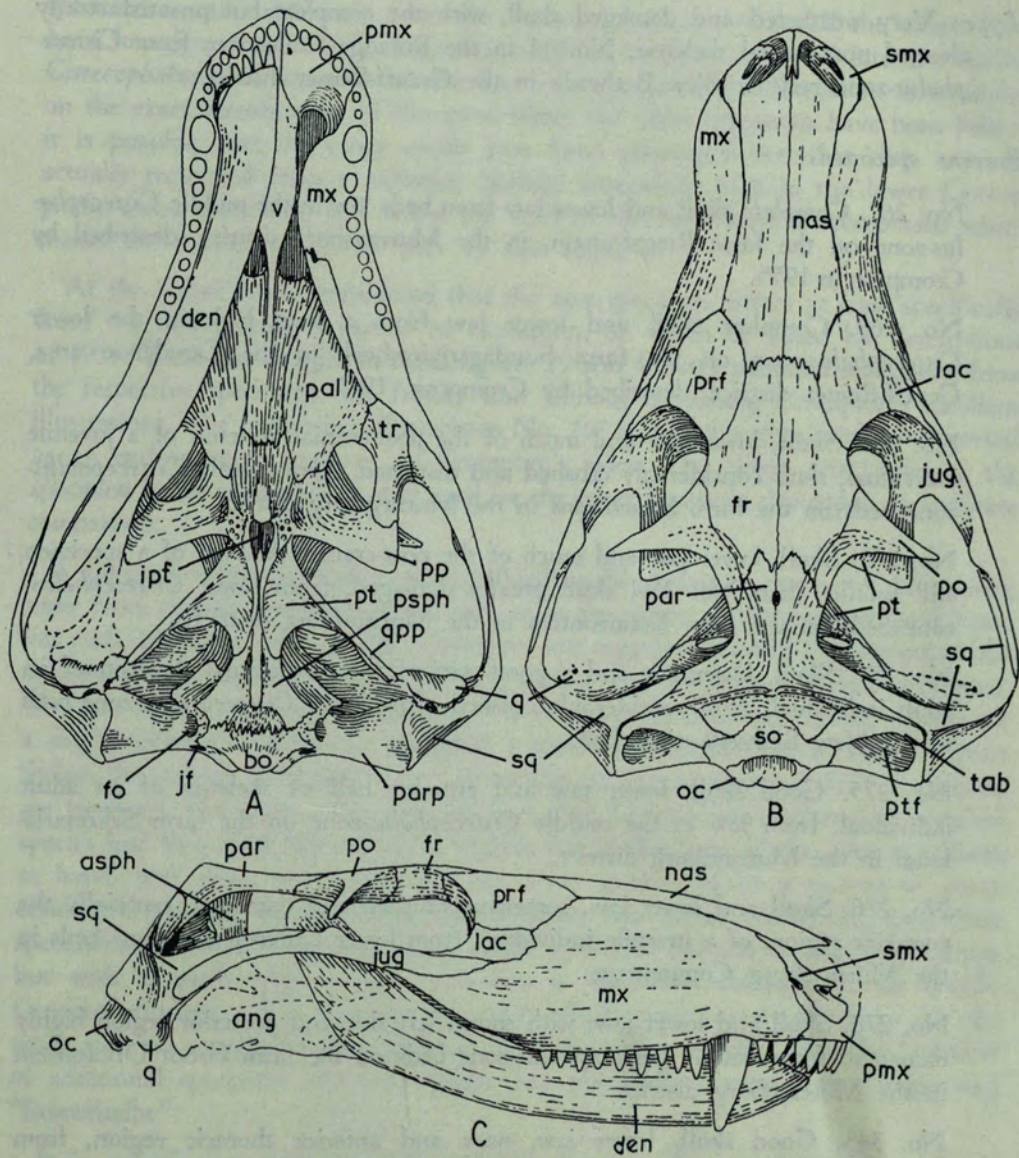


Figure 40

A, Palatal; B, Dorsal and C, Side views of the skull (No. 343) of *Ictidosuchops intermedius*. Natural size. For abbreviations see end of article.

Type: Very weathered and damaged skull, with the complete but unsatisfactorily cleaned post-cranial skeleton, No. 11 in the Rubidge Collection, from *Cistecephalus*-zone beds at New Bethesda in the Graaff-Reinet district.

Present specimens:

No. 267. Complete skull and lower jaw from beds low in the middle *Cistecephalus*-zone on the farm Ringsfontein, in the Murraysburg district, described by Crompton in 1955.

No. 268. Complete skull and lower jaw from a level high in the lower *Cistecephalus*-zone on the farm Sondagsriviershoek in the Camdeboo area, Graaff-Reinet district, described by Crompton, 1955.

No. 269. Skull, lower jaw and much of the post-cranial skeleton of a juvenile individual, skull considerably crushed and distorted, from middle *Cistecephalus*-zone beds on the farm Swaelkrans in the Murraysburg district.

No. 270. Skull, lower jaw and much of the post-cranial skeleton of a specimen still smaller than No. 269, skull greatly damaged, from lower *Cistecephalus*-zone beds on the farm Kraaifontein in the Murraysburg district.

No. 271. Skull, lower jaw and a good part of the post-cranial skeleton of an adult individual, skull considerably crushed, from lower *Cistecephalus*-zone beds in the New Bethesda river bed.

No. 275. Good skull, lower jaw and anterior half of skeleton of an adult individual, from low in the middle *Cistecephalus*-zone on the farm Sekretaris-kraal in the Murraysburg district.

No. 276. Skull and lower jaw, somewhat crushed and damaged, especially the posterior region, of a juvenile individual, from lower *Cistecephalus*-zone beds in the Murraysburg Commonage.

No. 278. Skull and lower jaw, with snout, left side and posterior region highly damaged, from middle *Cistecephalus*-zone beds on the farm Groot Driefontein in the Murraysburg district.

No. 343. Good skull, lower jaw, neck and anterior thoracic region, from *Endothiodon*-zone beds on the farm Driehoeksfontein in the Murraysburg district.

All the above specimens are in the collection of the Bernard Price Institute.

The discovery recently by Mr. J. W. Kitching of a specimen in the *Endothiodon*-zone (No. 343) which agrees very closely with *Ictidosuchops intermedius*, a typical *Cistecephalus*-zone form, has induced the author to investigate more closely several specimens in this collection, which had previously merely been identified. The new

specimen is quite definitely from the *Endothiodon*-zone, while all the others have been found in strata which range from high in the lower, to well into the middle *Cistecephalus*-zone. In view of the fact that no detailed information is available on the exact stratification of the areas where the other specimens have been found, it is possible that the range could have been misjudged and that they were all actually recovered from a narrower horizon somewhere high in the lower *Cistecephalus*-zone, apparently still below the level of the zone fossil *Cistecephalus* which marks the top of the lower part of this zone.

At the outset it was considered that the new specimen differs at least specifically from the two specimens loaned to Crompton, on which he based his descriptions of 1955. With this thought in mind figures 39 and 40 were prepared separately, from the respective specimens, the former also without consulting Crompton's excellent illustrations. The re-figuring of specimen No. 267 should therefore not be interpreted as an endeavour to improve on Crompton's work. The object was to figure the specimen in the same style as that used for the other figures in this paper, to facilitate comparison.

A comparison between figures 39 and 40 will readily indicate a number of differences, some more conspicuous than others, such as in the region of the interpterygoid fossa, but each difference, after careful evaluation, was regarded as possibly being either due to distortion, or incorrect interpretation in areas not well enough preserved or cleaned. The fact is that on structural grounds it is extremely difficult and unsafe to indicate a single substantial difference on which a specific distinction can be based. Nevertheless the striking difference in age is enough to suggest that two different species are involved. No doubt these two specimens would have been referred to separate species had they been the only ones known, but in the light of the other specimens at hand, and those described previously, there appears to be a variety of minor conditions ranging between and around these two forms. Evidently, too, these specimens do come from levels, not inside a narrow horizon as suggested above, but with a much wider range, from low in the lower to high in the middle *Cistecephalus*-zone, thus linking the upper *Endothiodon*-zone specimens to the series with no appreciable time interval. With the discovery of a substantial number of additional specimens this form might then eventually present a very interesting "formenreihe".

It is actually not specimens 343 and 267 that suggest a confusion here of two different species. Among the specimens listed above there are three (Nos. 269, 270, 271) that appear to differ more substantially but they are so highly distorted and crushed that it is here even more unsafe to rely on any particular feature in the different impressions they tend to create. Specimens 269 and 270, for example are smaller but their orbits are in proportions appreciably smaller than in the other specimens, while their skulls (including No. 271) appear to be narrower. The general impression is that No. 270 is not an *Ictidosuchops intermedius*, but a *Scaloposaurus constrictus*.

Table 1

	Type	Broom 1940	Broom 1941	No. 267	No. 268	No. 269	No. 270	No. 271	No. 275	No. 276	No. 278	No. 343
Total length of skull	92?	98	106	106	110	90	83	95	101	80	98?	100
Minimum breadth of skull	—	55	56	66	70	±45	±45	±50	61	±45	±60	64
Minimum breadth of snout	—	22	22	22	22	—	15?	—	20?	20?	25	22
Interorbital breadth	—	19	—	19	20	15?	14	14	20	18	18	18
From snout to pineal	—	72	—	78	83	66	±66	70?	77	64	75?	74
Length of snout to anterior borders of orbits	50	49	—	52	55	45?	43	43	50	40	±50	50
Minimum intertemporal width	—	12	—	12	14	11	—	10?	10	10?	10	10
Tip of snout to interpterygoid fossa	—	—	66	67	71	—	—	—	68	—	70?	67
Antero-posterior diameter of orbit	17?	21	—	23	21	14	15	20	21	17	±20	20
Length of row of post-canine teeth	15.5	18	19	20	24	16	±17	21	19	—	20	23
(Number of teeth in post-canine row)	(8)	(8)	(8)	(9)	(9)	(9)	(9?)	(9)	(9)	—	(9)	(9)

The idea was entertained at one stage in the initial investigation, that these three specimens are comparable with the types of *Ictidosuchops intermedius* and that the four specimens differ at least specifically from the rest of the specimens at hand and those described by Broom in 1940 and 1941. Should they actually prove to be generically different, the specimen described by Broom in 1940 will have to be taken as the type of *Ictidosuchops intermedius*, while the specimen described by Broom in 1938, with at least No. 271 in this collection, will have to remain as *Ictidosuchooides intermedius*, or be given a new generic name on account of the substantial difference between this form and *Ictidosuchooides longiceps*. The "*Ictidosuchooides intermedius*" specimens seem to be more closely related to *Ictidodraco longiceps* than to either *Ictidosuchooides longiceps* or *Ictidosuchops intermedius*. However, when difficulty is encountered in finding a substantial feature in which *Ictidodraco* differs from *Ictidosuchops*, it is realised that final conclusions about the intimate relationship of these forms had better wait until more undistorted specimens come to hand. Provisionally all specimens are here referred to *Ictidosuchops intermedius*.

Even in the light of the wider range of specimens at hand, it is not possible to elaborate, as far as structure is concerned, on Crompton's descriptions of 1955. It should, however, be mentioned here that the dental formula of this form is i6, c3, pc9. The maxillary-premaxillary suture suggests very obviously that it passes between the 5th and 6th teeth, but in depth, there is no doubt whatever that the 6th tooth is situated inside the premaxillary.

Table 1 gives a list of measurements in mm. for all the specimens provisionally recognised as *Ictidosuchops intermedius*.

Ictidosuchops baurioides Broom.
(Figure 41)

1940 BROOM, R., *Ann. Transv. Mus.*, XX, p. 162 fig. 6.

1941 BROOM, R., *Ann. Transv. Mus.*, XX, p. 212.

Type: Nearly complete, crushed skull, No. 30, in the Rubidge Collection from *Cistecephalus*-zone beds on the farm Zuurplaas in the Graaff-Reinet district.

Present specimen: Complete undistorted, slightly damaged skull, No. 342 in the collection of the Bernard Price Institute, from *Cistecephalus*-zone beds on the farm Bloupoort in the Murraysburg district.

The present specimen is quite definitely an *Ictidosuchops*, but it differs appreciably from *I. intermedius* as can clearly be seen when comparing figures 39 or 40 with 41. The other existing species are so poorly known that it is unsafe to introduce this specimen as a new species. There are some features about this new specimen which compares favourably with those of *I. baurioides*, hence its provisional reference to this species. The most conspicuous similarity is the rectangular (in cross section) blunt shape of the snout. The nasals reach far forward, with their anterior free margins so near to extending straight transversely that the external nares face

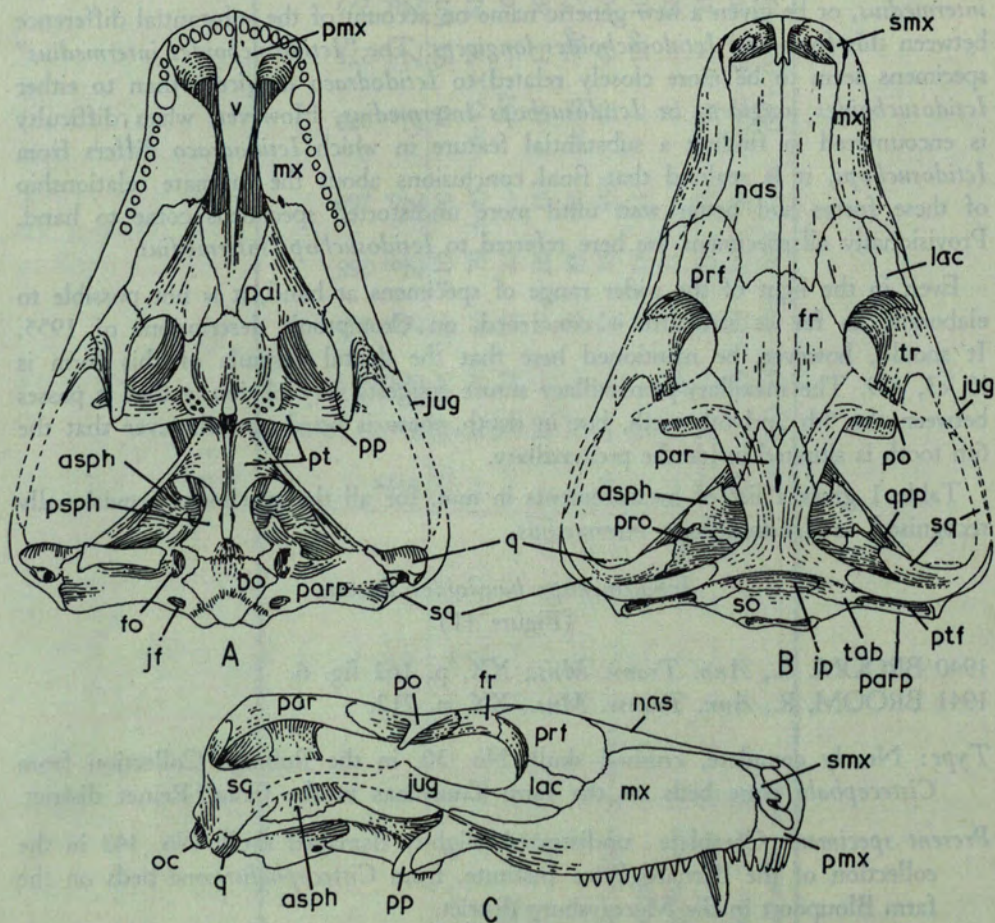


Figure 41

A, Palatal; B, Dorsal and C, side views of the skull of *Ictidosuchops baurioides*. Natural size.
 For abbreviations see end of article.

virtually straight forward. The septomaxillary wedges penetrating between the nasals and maxillaries are very feeble. This is apparently quite a characteristic *Ictidosuchops* feature and is distinctly different from the condition in *Ictidosuchoides*. Posteriorly the nasals are also similarly shaped in that they do not expand. The prefrontals are blunt anteriorly, also an *Ictidosuchops* feature differing from the *Ictidosuchoides* condition.

The major differences between the present specimen and the type are to be found in the posterior region of the skull, when comparing figures (fig. 41 with fig. 6A of Broom 1940). However, the type is a considerably crushed skull and it is obvious, not only in the light of the present specimen, but also of others described in this paper, that even in outline Broom's restoration is quite unreliable.

The present specimen is smaller and younger than the type. There are 6 incisors, 3 canines and 9 molars, the latter occupying 17 mm. With further growth in size the number of post-canines in this form could have increased.

Both temporal arches and both post-orbital bars are damaged. It is not possible, therefore, to establish whether the post-orbital bars were actually incomplete in the natural condition.

The parietals penetrate into the frontals each with its own wedge-like anterior end, in a manner comparable with that of *Ictidosuchops intermedius* and unlike the condition in *Ictidosuchoides* and *Ictidostoma*. There is a distinct, very small, preparietal, a feature which has proved in the past to have no diagnostic value whatsoever.

The interpterygoid fossa is well constricted but the tooth-bearing tuberosities either side are still well separated. These tuberosities are quite prolific in their tooth bearing, there being at least 6 long slender teeth on each.

The vomer expands broadly between the palatines. The maxillary secondary palate ridges approach the internarial bar quite closely, a distinct *Ictidosuchops* feature, and one on which a distinction from *Ictidosuchoides* can be based.

The following are some measurements in mm. with the corresponding measurements of the type in brackets.

Tip of snout to occipital condyle	79	(100?)
Tip of snout to occipital crest	71	(83?)
Tip of snout to pineal	60	(73)
Tip of snout to level of anterior borders of orbits	35	(43)
Breadth of snout across canines	22	(24)
Maximum breadth of skull	55	(63?)
Interorbital width	16	(3.5?)
Minimum intertemporal width	8	(11)

It is hoped that figure 41 successfully portrays the structural detail that can be gathered from the specimen and that any further detailed description will consequently be superfluous.

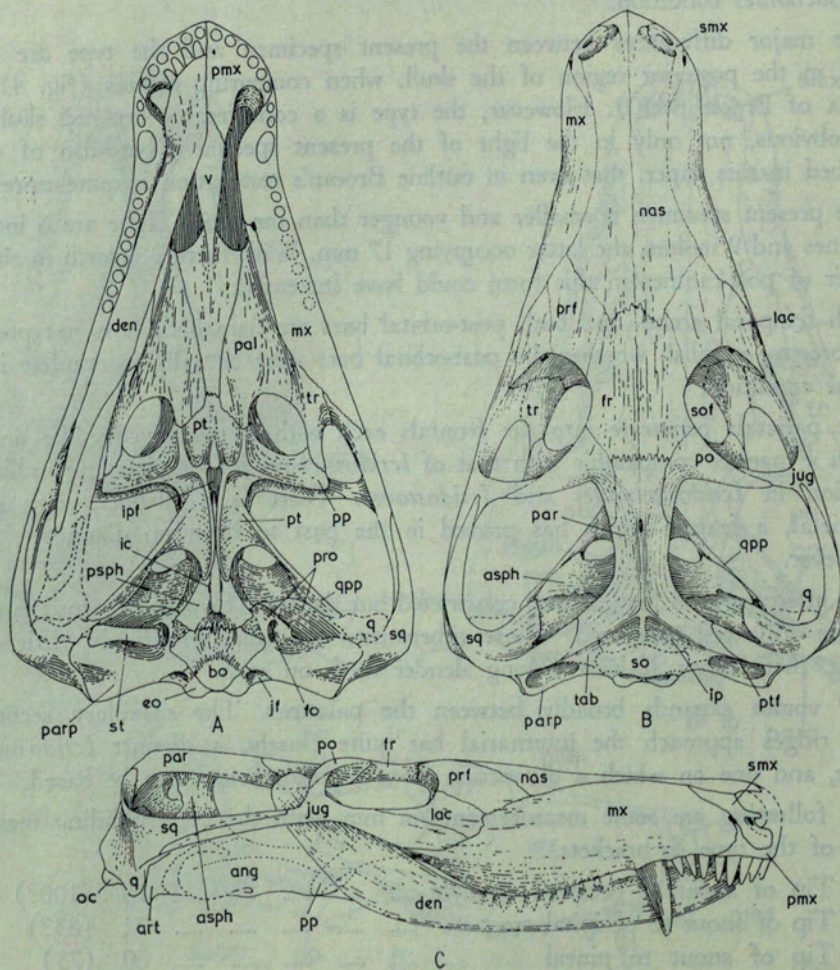


Figure 42

A, Palatal; B, Dorsal and C, Side views of the skull of *Ictidosuchoides longiceps*. Two-thirds natural size. For abbreviations see end of article.

Ictidosuchoides longiceps (Broom)
(Figure 42)

- 1920 BROOM, R., (*Ictidosuchops longiceps*) *Proc. zool. Soc.*, p. 343, figs. 1—3,
1930, BROOM, R., *Rec. Albany Mus.*, iv, p. 162.
1932, BROOM, R., Mammal-like Reptiles, p. 78, figs. 26B, c.
1934, BOONSTRA, L. D., *Ann. S. Afr. Mus.*, xxxi, p. 232, figs. 12—14.

Type: Skull in the British Museum of Natural History (No. R.5744) from beds which appear to be in the *Endothiodon*-zone or low in the *Cistecephalus*-zone, at Bruintjieshoogte, west of Somerset East, in the eastern Cape Province.

Present specimens:

No. 344. Good skull, snout damaged, better part of left mandible missing, from low in the middle *Cistecephalus*-zone on the farm Aasvoëlkrans in the Murraysburg district.

No. 345. Skull, snout good but posterior half badly crushed, no lower jaw, from low in the middle *Cistecephalus*-zone on the farm Sekretariskraal in the Murraysburg district.

Both specimens are in the collection of the Bernard Price Institute. Figure 42 is based entirely on No. 344.

The following table of measurements, based on Boonstra's list (1934), illustrates how well the two new specimens agree with the type. All measurements are given in millimeters:

Table II

	Type	No. 344	No. 345
Length of skull to occipital condyle	150?	138	131?
Length to basisphenoidal tubera	140?	125	114?
Length to pineal foramen	110?	104	—
From pineal to edge of occipital plate	18	18	—
From premaxillaries to front of orbits	75?	68	67
Width across squamosals	80?	79	—
Interorbital width	24	20	16?
Intertemporal width	10	10	—
Width of snout	27	28	27
Width across pterygoid flanges	40	42	41
Height of snout	22	22	22
Height of occiput	28?	28	—
Length of molar series	25	27	26
Diastema	5	4.5	4
Length covered by three canines	11	11	12
Space occupied by six incisors	—	17	17

The two new specimens are of exactly the same size when measurements in the anterior half of the skull are compared. Crushing of the posterior region in specimen No. 345 has caused an apparent shortening of the skull as a whole. These specimens are slightly smaller than the type and it is interesting to note that this difference in size is not reflected in measurements related to the dentition.

The new specimens add substantially to our knowledge of this genus and species. Although it is a close ally of *Ictidosuchus* and a typical member of the family Ictidosuchidae, it differs in having three canines, a narrower and flatter skull, and a more straight lower jaw. The number of post-canine teeth is not taken as a reliable characteristic.

The dental formula $i6, c3, pc9$ seems to be characteristic for the families Ictidosuchidae and Scaloposauridae. Apparently various members of both families changed this formula by merely losing some of the small insignificant teeth in front of the large canine. These could be the last incisor and/or the first or both small canines, thus presenting combinations ranging from $i6, c3$, to $i5, c1$. The number of post-canine teeth apparently varied with age. The dental formula, therefore, presents nothing on which a family diagnosis can be based.

In the specimens of both these families at present at the author's disposal, the palates as a whole also do not exhibit any feature which appears to be of family diagnostic value. The two families are indeed very closely related. The only differences between these two families which can be seriously considered are the complete postorbital bars, the posteriorly expanded nasals, the longer prefrontals and the larger septomaxillary wedges between the maxillaries and nasals, these features being to some extent characteristic of the Ictidosuchidae. Although combined they present a picture reasonably different from that found in the Scaloposauridae, it is to be appreciated that individually each feature carries little weight as far as family diagnosis is concerned.

The new information derived from all the specimens investigated does not present substantial material on which views about the more intimate relationship of these two families can safely be expanded.

ABBREVIATIONS

ang, angular; art, articular; asph, alisphenoid; bo, basi-occipital; bsph, basisphenoid; cor, coronoid; den, dentary; eo, exoccipital; fo, fenestra ovalis; fr, frontal; ic, foramen for internal carotid artery; ip, interparietal; ipf, interpterygoid fossa; jug, jugal; jf, jugular foramen; lac, lachrymal; mx, maxillary; nas, nasal; oc, occipital condyle; pal, palatine; par, parietal; parp, paroccipital process; pmx, premaxillary; po, postorbital; pp, pterygoid process; prf, prefrontal; pro, pro-otic; psph, parasphenoid; pt, pterygoid; ptf, posttemporal fossa; q, quadrate; qpp, quadrate process of the pterygoid; sa, surangular; smx, septomaxillary; so, supraoccipital; sof, suborbital fossa; spl, splenial; sq, squamosal; st, stapes; tab, tabular; tr, transverse bone; v, vomer.