# *A Revision of the Scaloposauridae with Special Reference to Kinetism in this Family*

by

A. W. CROMPTON

*With 10 text-figures*

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## I INTRODUCTION

Recent investigation of the skulls of Ictidosaur A and B (Broom 1929) has indicated that the nature of the articulation of the lower jaw with the skull in these forms is such that they could possibly form a morphological stage between the therapsids on the one hand and the mammals on the other. This study has also shown that these forms are related to the scaloposaurid — bauriamorph line of evolution. Consequently a revision of the Scaloposauridae and a detailed description of a scaloposaurid skull was considered necessary.

It is mainly due to the work of Watson (1931) that the structure and taxonomy of the Scaloposauridae is understood as well as it is, and Watson's conclusion that this family represents an intermediate stage between the typical therocephalians and the bauriamorphs has been generally accepted. Subsequent to Watson's paper, however, many additional scaloposaurids have been collected mainly as a result of the exceptional enthusiasm of Mr. S. H. Rubidge, and the keen eye of Mr. J. W. Kitching. In this paper an effort has been made to place all the known salopo-saurids in four evolutionary stages.

The scaloposaurid skull chosen for detailed description is *Ictidosuchoides intermedius* Broom. This form was described by Broom (1938, 40b, 41) who considered it to be one of the "prebauriamorphs" and close to the mammalian ancestor. For reasons which are discussed in detail in section III, this form has been removed from the genus *Ictidosuchoides* and placed in the scaloposaurid genus, *Ictidosuchops*.

A well-known feature of reptiles is movement or "kinetism" within the skull. The term kinetism was first employed by Versluys (1912) and he treated the problem as well as material available at that time allowed. Further intensive investigation of this problem since Versluys' paper has resulted in a comprehensive understanding of this phenomenon in "diapsid" reptiles and their derivatives and the evidence has recently been reviewed by Kuhn-Schnyder (1954). Practically nothing, however, is known of kinetism in the advanced mammal-like reptiles. Versluys (1912) pointed out that the pelycosaur skull has the build of a typical metakinetic skull (in this type the movement line is situated in the posterior region of the skull) with the exception of two pecularities: the supra-occipitals are extremely broad and there is an ossification of the interorbital septum which firmly connects the frontal to the basisphenoid to restore the rigidity of the two segments (maxillary and occipital) so as to eliminate any metakinetic movement. Although the pelycosaur skull studied by Versluys was considered akinetic he concluded that the pelycosaur ancestor must have possessed a metakinetic skull. The therocephalians, anomodonts and cynodonts are according to Versluys akinetic as a result of the fusion of the occipital segment to the bones of the skull roof, ossification of the interorbital septum and fusion of the pterygoids to the skull base. Apparently the only other reference to kinetism in mammal-like reptiles is that by Goodridge (1930) who considers all the "theromorpha" to be akinetic. In this paper the problem of kinetism in advanced mammal-like reptiles has been studied.

## II MATERIAL AND TECHNIQUE

By the courtesy of the Bernard Price Institute for Palaeontological Research two beautiful skulls of *Ictidosuchops* (*Ictidosuchoides*) *intermedius* were loaned to the National Museum in order that the present work could be undertaken. The one (B.P.I. 267) is almost perfectly preserved and was collected, identified and partially prepared by Mr. J. W. Kitching. It was found on the farm "Ringsfontein", Murraysburg district, C.P., and according to Mr. J. W. Kitching comes from the lower or middle *Cistecephalus* zone. This specimen was further prepared with the aid of a small automatic mallet. The second specimen (B.P.I. 268), although fairly well preserved is slightly crushed dorso-ventrally; with the kind permission of Dr. A. S. Brink the posterior portion of this skull was serially ground away and a wax model built up from enlarged drawings of the successive polished surfaces. The actual technique employed has been described in an earlier paper (Crompton 1955a). A third skull of *Ictidosuchoides intermedius* was loaned to the National Museum by Mr. S. H. Rubidge and although imperfect, served to confirm doubtful features observed in the other two skulls.

Other material studied consisted of a small scaloposaurid skull in the National Museum and a skull of *Bauria cynops* already described by Brink (1953).

## III ICTIDOSUCHOPS INTERMEDIUS (BROOM)

## (B.P.I. 267)

Text-figures 1—4

**Ictidosuchops intermedius** (Broom)

1. *Ictidosuchoides intermedius* Broom, 1938, Ann. Transv. Mus., 19: 257, figs. 1—3. Type locality: New Bethesda, Graaff-Reinet. Cistecephalus zone. Permian.
2. *Ictidosuchoides intermedius* Broom, 1940, Ann. Transv. Mus. 20: 161, figs. 1—5.
3. *Ictidosuchoides intermedius* Broom, 1941, Ann. Transv. Mus. 20: 194, fig. 3.

### 1 Description of skull

Skull roof (Fig. 1A)

With the exception of the internarial bar, the skull is complete. The relationships of individual ossifications can best be understood from the figure. The septomaxillary (SEP. MAX.) is well exposed in dorsal view and projects sightly inwards into the external nostril. The nasals (N.) are long and broad, expanding slightly before making contact with the prefrontals (PF.). An outstanding characteristic of this specimen is the large and bulbous prefrontals; they project slightly dorsal of the general level of the skull roof so that a shallow depression is formed between them. A slender process of the prefrontal projects backwards alongside the lateral edge of the frontal (F.) to all but meet the postorbital (PO.). As a result only a small portion of the frontal enters into the formation of the orbit. The parietal (P.) is broad and flat. The pineal foramen is small.

From that part of the squamosal (SQ.) which forms the posterior-lateral corner of the temporal fossa, three processes of this bone project inwards. All are thin vertical sheets of bone; the dorsal process (SQ. PROC. 1) overlaps the lateral edge of the parietal and its dorsal edge abutts against the dorsal edge of the tabular (TAB.). A sutural connexion does not appear to exist between the squamosal and the tabular since they are separated by a thin strip of matrix. The second process of the squamosal is not visible in dorsal view. The third process (SQ. PROC. 3) passes inwards and slightly forwards, with its ventral edge lying upon the dorsal edge of the quadrate ramus of the pterygoid (PTER.) and terminates anteriorly against the posterior-ventral edge of the epipterygoid (EPI.). Boonstra (1938) has illustrated a similar process in *Bauria cynops*. A slender jugal (J.) forming part of the infratemporal bar, has a well pronounced process projecting dorsally towards the laterally and downwardly projecting spur of the postorbital in the middle of its length. Anteriorly the jugal passes below the lacrimal (LAC.) to meet the maxilla.

The ventral portion of the lacrimal which is visible in dorsal view is a broad plate extending inwards from its lateral attachment to the jugal and forms an

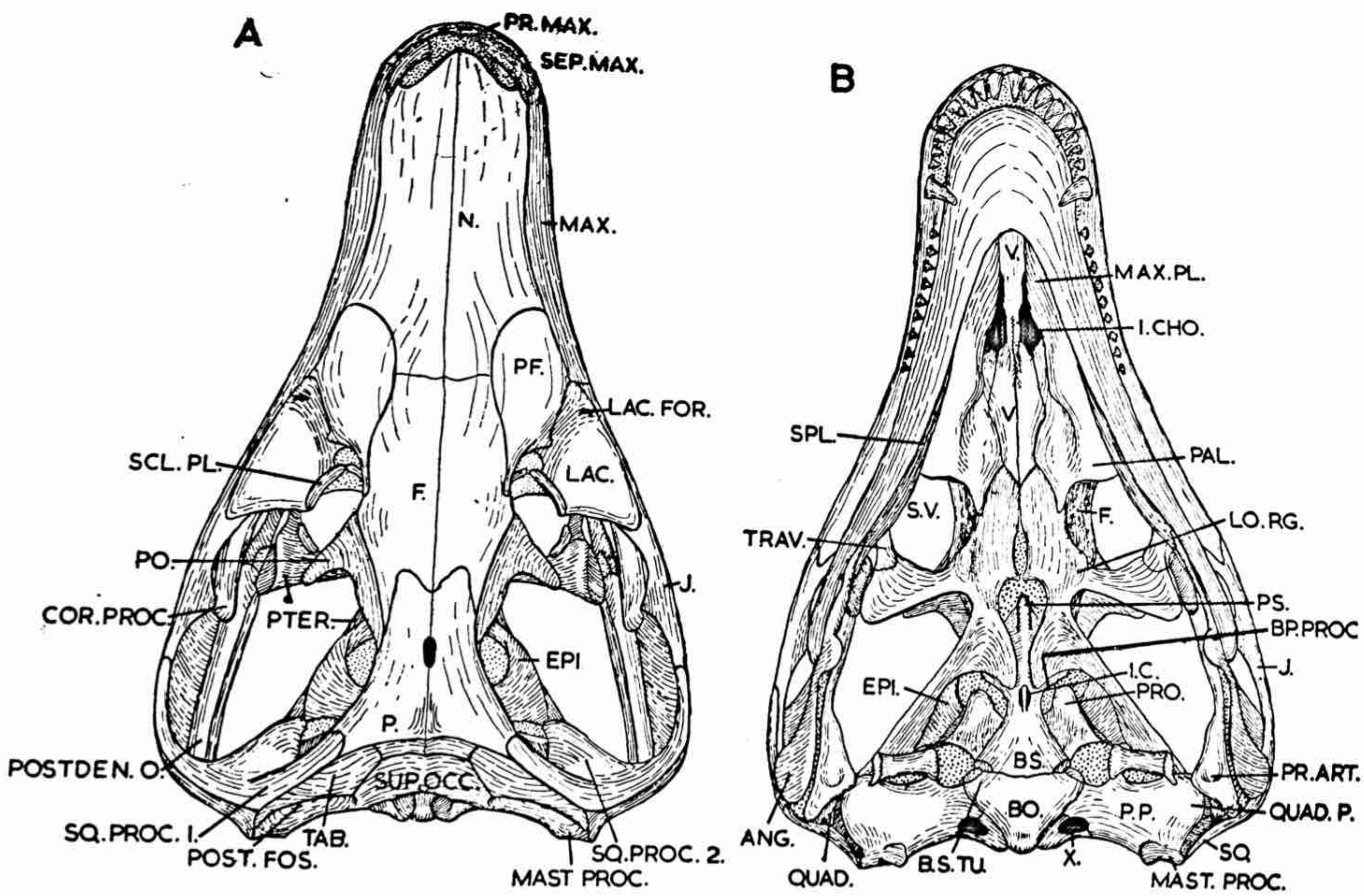


Fig. 1.—*Ictidosuchops intermedius.* A, dorsal view and B, ventral view of the skull, both natural size. (Key to lettering on p. 180).

incomplete floor to the orbit. The postero-medial corner of the lacrimal is suturally connected to the dorsal edge of the transversum (TRAV.) A small lacrimal foramen (LAC. FOR.) is visible in dorsal view.

Palate (Figs. 1B & 3)

The basioccipital (BO.) is a triangular shaped bone which terminates posteriorly in a small but distinctive condyl. The antero-lateral corners of this bone form two outstanding tubera which abutt against two corresponding tubera on the postero-lateral corners of the basisphenoid (BS.). A shallow median concavity separates these tubera. Passing forward from the tubera the basisphenoid narrows considerably and immediately behind the pterygoids it flares out laterally to form the basipterygoid processes (BP. PROC.). A small median keel arises from the narrow portion of the basisphenoid and is projected forwards into the interpterygoid vacuity (INT. VAC.) as a distinct parashenoid (PS.). Its dorsal edge is fused to the basisphenoid. On either side of the median keel two small foramina (I.C.) for the internal carotid arteries are present.

The pterygoids have the form typical to the therocephalians. Of particular importance is the nature of the junction of the pterygoid to the basipterygoid process; this will be described in greater detail in the following section where a series of sections through a skull of the same species have been described. The quadrate rami of the pterygoids are extremely slender vertically orientated sheets of bone which pass backwards to the quadrates and are widely separated from the otic bones. The inter-pterygoid vacuity is large and pear shaped. Anterior to this vacuity there is a small and narrow vacuity which separates the two pterygoids for a short distance. Outstanding longitudinally orientated ridges (LO. RG.) upon the ventral surfaces of the pterygoids divide the main body of the pterygoid from the sturdy transverse rami. The suborbital vacuties (S.V.) are extremely large with a slender transversum (TRAV.) forming the entire lateral border to this vacuity. The anterior border is formed by the palatine and the median and posterior borders by the pterygoid.

The posterior ends of the vomers (V.) are broad and clearly divided by a median suture. They overlap the anterior ends of the pterygoid and their lateral edges appear to lie below the median edges of the palatines (PAL.). As they pass forwards the vomers narrow to a keel shaped undivided structure which separates the internal nostrils (I. CHO.). The posterior border of the internal choanae are formed by the palatines which in this region pass sharply dorsally. Anterior to the choanae the vomers expand into a broad plate the edges of which are either in contact with or very nearly in contact with the palatal plates of the maxilla (MAX. PL.) so that a primitive secondary palate is formed. A similar arrangement was found by Broom (1941) to exist in his specimen of *Ictidosuchops* (*Ictidosuchoides*) *intermedius* and this fact has also been confirmed in a section through the snout a specimen of *Ictidosuchops intermedius* in the collection of Mr. S. H. Rubidge. The median edges of the maxillo-palatine ossification (no dividing suture could be indentified) underlies the lateral edges of the internal choanae, and posteriorly this median edge is continued backwards to form an outstanding ridge on the palatine which terminates immediately anterior to the suborbital fossae. This ridge most probably supported a fleshy secondary palate.

In ventral view the exoccipitals (EX. OCC.) are plainly visible and form the posterior and medial borders to the jugualar foramina. One of the most important features of this skull is the form of the paroccipital process (P.P.). Medially it is firmly attached to the lateral edge of the basioccipital immediately behind the basisphenoid tubera. The medio-anterior edge of this structure is thickened, lacks perichondral ossification and forms the posterior border to an extremely large foramen ovalis (F.O.). Passing distally from this point the bone flares out anteriorly and posteriorly to terminate in two blunt but nevertheless distinct processes in which perichondral ossification is absent. The anterior or quadrate process (QUAD. PROC.) extends further laterally than the posterior process and for all but an extremely short distance abuts against the medial face of the quadrate (QUAD.). The posterior or mastoid process (MAST. PROC.) extends postero-laterally and but for a millimeter articulates with the ventral edge of the squamosal.

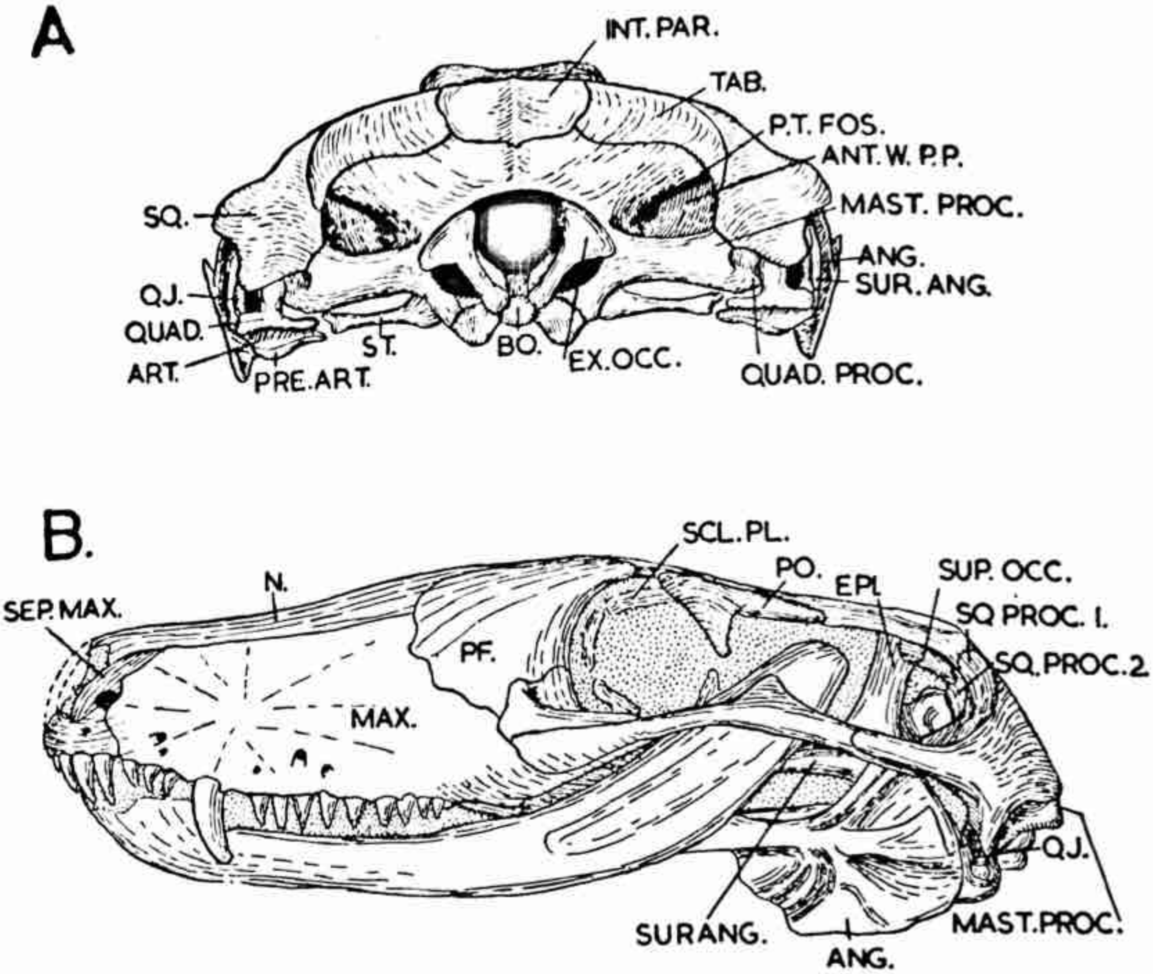


Fig. 2.—*Ictidosuchops intermedius*. A, occipital view and B, lateral view of the skull, both natural size. (Key to lettering on p. 180).

The term mastoid process was first introduced by Watson (1931) who observed it in *Scaloposaurus*. He considered it for muscular attachment, but since his material was poorly preserved and the posterior part of the squamosal badly damaged, the approximation of this process to the squamosal could not be observed. In view of the lack of perichondral ossification on these two processes, it is more than likely that they were both extended laterally by cartilage so as to form definite articulations with the structures towards which they are directed.

A portion of the prootic (PRO.) is visible in ventral view. Immediately anteriorly to the fenestra ovalis (F.O.) the prootic appears to be firmly connected to the dorso-lateral edge of the basisphenoid. Anterior to this attachment the ventral surface of the prootic has the form of a broad horizontal shelf which as it passes forward draws away from the basisphenoid and forms the dorsal and lateral border to the pituitary fossa. The ventral border of the pituitary fossa is formed by the dorsal edge of the basisphenoid. Because of the lack of perichondral ossification it could not be ascertained whether the anterior edge of the prootic actually makes contact with the basisphenoid anterior to the pituitary fossa so as to completely surround the pituitary fossa. Identical relationships of the prootic to the basisphenoid were shown by Watson (1931) to exist in *Scaloposaurus.* In *Bauroides* Watson (1931) showed the anterior edge of the prootic suturally joined to the basisphenoid.

Superficially it appears that this form has a particularly large fenestra ovalis. The anterior, dorso-lateral and posterior borders of this fenestra are formed by the periotic bones. The ventral border is formed by the basioccipital and basisphenoid bones. The dorsal portion of this foramen opens directly laterally and the medial portion directly ventrally. On both sides the stapes (ST.) are in position. These structures are dorso-ventrally flattened and there is no indication of a stapedial foramen. The foot plate of the stapes lacks perichondral ossification and its dorsal edge nestles firmly into the dorsal and lateral portion of the fenestra ovalis. Consequently an extremely large portion of the fenestra ovalis is unoccupied by the foot plate of the stapes. It is improbable that the stapes would have had a cartilaginous extention large enough to cover the entire fenestra and it is reasonable to assume that the medial portion of the large fenestra ovalis represents an unossified portion of the ventro-lateral wall of the cranium. If this is the case then the fenestra ovalis is completely surrounded by the otic capsule. The sectioned skull (section IV) supports this interpretation. The main distal part of the stapes is separated from the main body of the quadrate by a wide space, but a slender and poorly ossified process of the stapes is directed towards the quadrate. This is most probably the extra-stapedial process which in life was continued by cartilage to obtain an attachment with the tympanic membrane. In view of the great distance which already separates the stapes from the quadrate it is unlikely that the stapes had been forced laterally and thereby exposed the extremely large fenestra ovalis.

Side wall (Figs. 2B & 4A)

In side view the skull is depressed in the temporal region. This is most probably due to dorso-ventral pressure subsequent to death, but since no marked dislocation of the individual bones in this region could be discerned, no attempt has been made to reconstruct this region.

A feature of the maxillae (MAX.) are the small foramina in the ventral region of the bone for the transmission of the branches of the fifth cranial nerve and blood vessels. Two large anterior foramina open forwards and two posterior open downwards. Watson (1931) described similar foramina in the maxilla of *Ericiolacerta* and *Scaloposaurus* and claimed that these foramina could be explained by " . . . existence of a series of important tactile sense organs grouped around the end of the muzzel, that is what in a mammal would be called a rhinarium". Clearly visible in this view is the bulbous nature of the prefrontal and the small size of the lacrimal. The jugal is slender. That portion of the squamosal supporting the quadrate and quadratojugal is extended downwards to a horizontal plane almost coincident with the ventral border of the lower jaw. A small quadratojugal (Q.J.) is visible in lateral view. From the suspensorial region of the squamosal, the posterior edge of this bone passes latero-posteriorly and slightly ventrally to form a distinct process which articulates with the mastoid process. This is best seen in the view of the occiput (fig. 2A).

In figure 4A an illustration of the posterior region of the side wall of the skull is given with the temporal arcade removed in order to expose the side wall of the brain case. Clearly illustrated here is the relationship of the transversum to the other palatal bones. Posteriorly the transversum has a long sutural connection with the transverse ramus of the pterygoid, dorsally with the jugal and lacrimal and anteriorly with the palatine and maxilla. The quadrate ramus of the pterygoid (Q.R.P.) has the form of a thin vertical plate of bone. The posterior termination of this structure articulates with the lateral end of the paroccipital process and pterygoid process of the quadrate (PT. PROC.). The relations of the pterygoid to the basipterygoid process and the lateral opening to the pituitary fossa is well shown in side view. The epipterygoid (EPI.) is a broad flat plate firmly connected to the dorsal surface of the pterygoid. The antero-ventral portion of the epipterygoid extends well forward on the quardrate ramus of the pterygoid to terminate as a fairly broad plate which all but meets the lateral edge of the basipterygoid process.

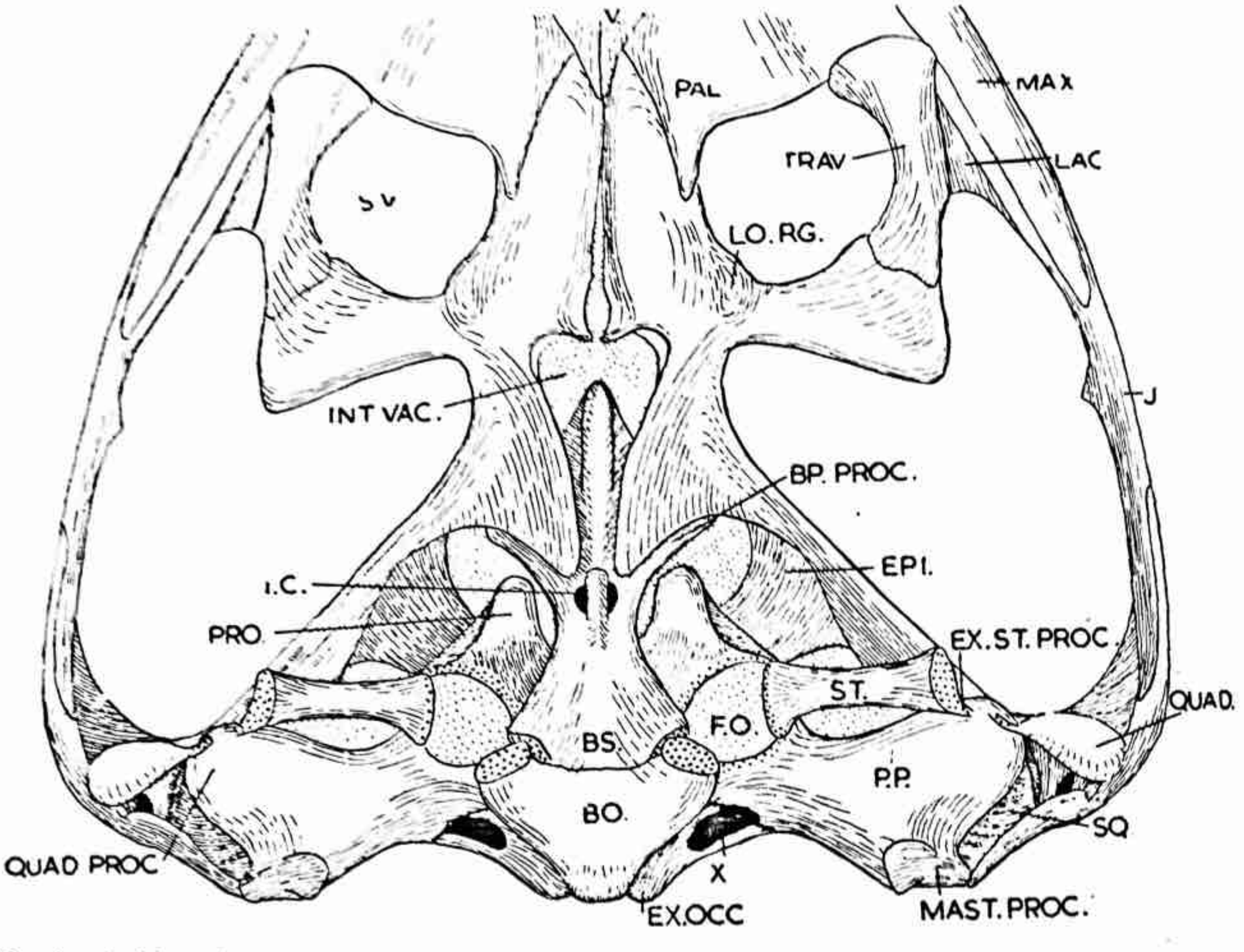


Fig. 3.—*Ictidosuchops intermedius.* View of the palate, x2. (Key to lettering on p. 180).

Also well shown in this view are the medially directed processes of the squamosal. The second process of the squamosal (SQ. PROC. 2) which could not be seen in dorsal view passes directly inwards below the dorsal process (SQ. PROC. 1) and has the form of a flat vertical sheet of bone, the medial termination of which abuts against, but is not suturally connected to, the prootic. A foramen opening forwards is enclosed between the prootic medially and ventrally, the second process of the squamosal dorsally and the third process of the squamosal laterally. This is the anterior opening of the post-temporal fossa. The prootic forming a lateral wall to the brain is visible between the epiterygoid and the squamosal.

The paroccipital process in lateral view is roughly U-shaped. The posterior wall of the "U" is formed by the mastoid process; the anterior wall (ANT. W. P. P.) is high and extends dorsally to meet the lateral extention of the supraoccipital. This relationship is best seen in the view of the occiput. The lateral portion of the third process of the squamosal (SQ. PROC. 3) lies against the anterior face of the anterior wall of the paroccipital process. The ventral portion of the paroccipital process which forms the base of the "U" is fairly thin.

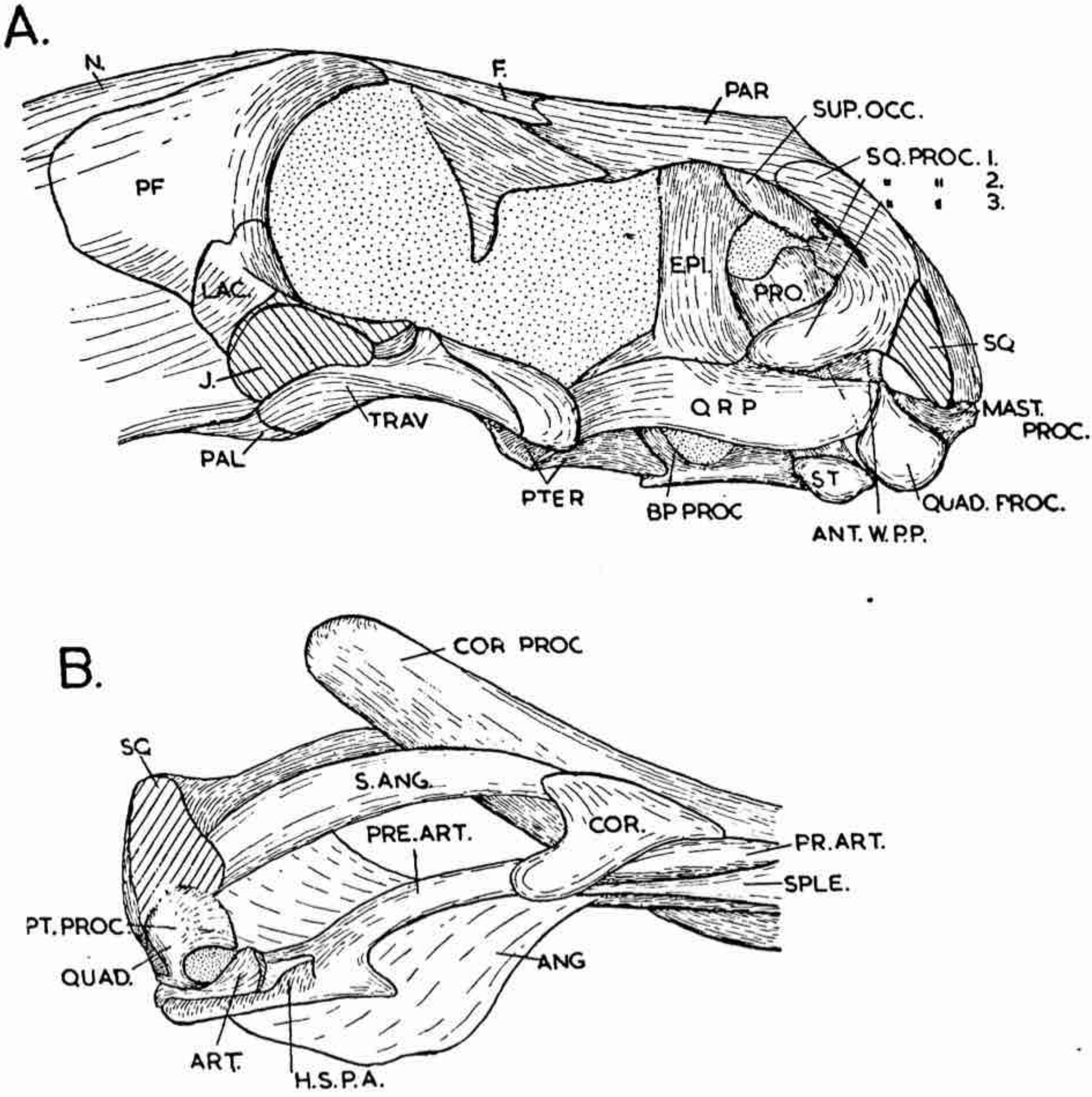


Fig. 4.—*Ictidosuchops intermedius.* A, lateral view of the skull with the infratemporal bar removed to expose the brain case and B, inner view of the posterior portion of the lower jaw, both x2. (Key to lettering on p. 180).

Projecting forwards below the parietal and clearly visible in side view, is the anterior termination of the dorsal region of the supraoccipital (SUP. OCC.).

Within the orbit a series of four sclerotic plates (SCL. PL.) arranged in a circle are visible. Each one is separated by a short distance from the other. Unfortunately these plates are not well preserved and it is impossible to say from this specimen alone whether each of these plates is made up of small closely articulated ossifications or not. Broom (1941) has illustrated a series of small closely articulated sclerotic plates in his description of *Ictidosuchops* (*Ictidosuchoides*) *intermedius*.

Dentition (Fig. 2B)

The dental formula for this form is $I \frac{5}{4} C \frac{4}{1} PC \frac{9}{?}$

The incisors are simple conical and slightly recurved teeth. Anterior to the main canine there are three small canines in the maxilla. The incisors are slightly larger than the three small canines anterior to the canine. The main canine is a sturdy sabre-shaped structure with its apex directed slightly posteriorly. The nine postcanines, which are separated from the main canine by a diastema of 3 mm., are all simple conical sharply pointed teeth. There is no evidence of dental succession.

Occiput (Fig. 2A)

Well illustrated in this view is the articulation of the mastoid process and the squamosal. The probable reason that this observation has not been made before is that the slightest crushing of the material would dislocate the two structures. The articulation of the quadrate process of the paroccipital with the quadrate is also well shown in this view. Although this form probably had a single functional occipital condyl, it is quite clear that the withdrawing of the basioccipital from the formation of the condyl has already begun since the posterior edges of the exoccipitals form distinct articular facets. The supra-occipitals and periotic bones are fused. There appears to be no sutural connection between the supraoccipital and the interparietal, but the supraoccipital does appear to be fused to the tabulars. The main body of the squamosal which forms the postero-lateral corner of the skull is slightly concave. This is probably indicative of the course of the external auditory meatus. The squamosal is drawn downwards as a support for the quadrate. An identical arrangement was shown by Watson (1931) to exist in *Scaloposaurus*.

The ventral portion of the tabular abuts against the medial border of the squamosal. The post-temporal fossa is bordered by the paroccipital ventrally, the supra-occipital and periotic medially and dorsally and the tabular and squamosal laterally. Because of the large anterior posterior extent of the paroccipital process and the vertical anterior wall (ANT. W.P.P.) of this structure a large cavity or sinus is formed within the occiput.

In posterior view the quadrate is "T" shaped with the horizontal component of the "T" forming the articular facet for the articular. A slender process from the quadrate extends towards the stapes. The vertical component consists of a high longitudinally orientated plate, the dorsal edge of which fits into a shallow pocket in the squamosal. The relations of the quadrate to the squamosal are illustrated in fig. 4B. It will be seen in this figure that the dorsal part of the quadrate is supported by the squamosal both laterally and dorsally while the median face of the quadrate is exposed and is supported by the quadrate process of the paroccipital. Extending forwards and slightly medially from the main body of the quadrate is a thin vertical sheet of bone against the medial face of which lies the quadrate ramus of the pterygoid. There appears to be no sutural connection between the two. A small quadrato-jugal is present, but unfortunately it is not well preserved.

Lower jaw (Figs. 2B & 4B)

The dentary is long and slender and terminates posteriorly in a well pronounced coronoid process (COR. PROC.). It has a total length of 80 mm. One of the most marked features of this form is the gigantic size of the angular (ANG.) and the series of ridges and folds upon its outer surface. The pattern formed is best understood from the illustration of this structure. Visible below the jugal in lateral view is the surangular (SUR. ANG.). This structure is separated by a large foramen from the angular. The edge of the surangular which passes ventrally to fuse with the articular is visible in lateral view behind the posterior edge of the angular.

The posterior portion of the lower jaw was separated from the rest of the skull so that its internal aspect could be studied (fig. 4B). The articular (ART.) is slightly broader (latero-medially) than the quadrate so that the entire ventral border of the quadrate is in contact with the articular. The articular does not have a great antero-posterior extent. The greater part of the prearticular (PRE. ART.) consists of a thin vertically standing sheet of bone which terminates anteriorly between the splenial (SPLE.) and the dentary. A ventral extention of the coronoid (COR.) overlies a part of the prearticular. Towards the articular region the prearticular is considerably deepened dorso-ventrally and from the ventro-anterior corner of this deepened portion a short process is directed forwards. A horizontal shelf (H.S.P.A.) (triangular in ventral view, fig. 1B) arises from the dorsal region of the deep portion of the prearticular and supports the articular. A shallow pit (fig. 1B) upon the ventral surface of this shelf is probably for muscular attachment. A horizontal shelf to the prearticular was shown to exist by Watson (1931) in *Scaloposaurus* and *Ericiolacerta* and by Boonstra (1938) in *Bauria*. The relations of the other bones constituting the lower jaw can be understood from the figure.

Several features of the skull described above suggest the presence of kinetism. The paroccipital process is not suturally connected to either the squamosal or quadrate: a strip of matrix separates the tubular and the squamosal: no sutural connection is apparent between the supraoccipital and the interparietal: the supraoccipital is extended forwards below the skull roof and not fused to it. However, to confirm this point it was necessary to section a skull of the same or closely allied species in order that more detailed information upon the nature of the basipterygoid process, the degree of ossification of the interorbital septum, and the relationship of the epipterygoid to the skull roofing could be obtained.

The chief skull measurements of this form are:

| | |
|---|---|
| Total length of skull | 100 mm. |
| Maximum width | 65 mm. |
| Minimum intertemporal width | 12 mm. |
| Minimum interorbital width | 18 mm. |
| Premaxilla to the anterior orbital border | 54 mm. |
| Total length of the dentition | 40 mm. |
| Incisors | 7 mm. |
| Canines | 10 mm. |
| Diastema | 3 mm. |
| Postcanines | 20 mm. |

## 2 Taxonomic position of *Ictidosuchops intermedius*

Comparison of the above skull with material described in the literature

The external features of the skull described above and those of *Ictidosuchoides intermedius* described by Broom (1940 b) are practically identical. Broom's specimen is slightly narrower, but it is not considered that this slight difference is sufficient to warrant the creation of a new species.

Broom (1940 b) gives the dental formula of *I. intermedius* as I. *6*, C. *3*, PC. *8* claiming that there are only two small teeth anterior to the main canine. However, Broom does not illustrate a premaxillary-maxillary suture. Broom illustrates five large incisors and, between the posterior large incisor and the main canine, three small teeth are drawn. Broom gives no indication as to why the first of these three small intervening teeth should be considered an incisor. In the new specimen that has been described in this paper conditions exactly similar to those described by Broom were found to exist. However, it is perfectly clear that all the three small teeth are situated in the maxilla. If we are to consider all the premaxillary teeth as incisors, and in the case of this specimen it seems to be the only reasonable assumption to make, then the dental formula of *I. intermedius* should be I. 5, C. 4, PC. 8 or 9. Since it is more than probable that these animals increased the length of the postcanine row by adding teeth posteriorly, the difference of one tooth in the postcanine row in the new specimen and in the specimen described by Broom is of little taxonomic importance. In the late therocephalians much confusion exists at present as a result of giving the dental formula without any reference being made to the premaxillary-maxillary suture.

Comparison of *I. intermedius* with the other species of the genus *Ictidosuchoides*

Three species have been included in the genus *Ictidosuchoides*: *longiceps*, *intermedius* and *rubidgei*. *I. intermedius* obtained its name from the fact that the length of its postcanine row lies between that of *longiceps* and *rubidgei*. *I. longiceps* is a fairly well known species (Boonstra, 1934), but *I. rubidgei* consists only of a snout. Haughton and Brink (1954) have given as a diagnostic feature for the genus *Ictidosuchoides* the presence of two small canines anterior to the main one.

For the reasons tabulated below it appears that *intermedius* should be removed from the genus *Ictidosuchoides*.

| *I. longiceps* | *I. intermedius* |
|---|---|
| 1. Two small canines anterior to the main canine. | Three small canines anterior to the main canine. |
| 2. No primitive secondary palate [Boonstra (1934)]. | Primitive secondary palate well developed. |
| 3. Narrow intertemporal region. | Fairly broad intertemporal region. |
| 4. High parietal crest. | Parietal crest absent. |
| 5. Complete postorbital arcade. | Incomplete postorbital arcade. |

Although any one of these characteristics may not have warrented the removal of *intermedius* from the genus *Ictidosuchoides* it does appear to be reasonable that the sum of them is sufficient to warrant its removal.

For *I. rubidgei,* Broom (1937) claims six incisors in the premaxilla; three canines and eight postcanines in the maxilla, but in his illustration shows four incisors and five canines. This form is probably best left in the genus *Ictidosuchoides* until more reliable material is found.

Relationship of *I. intermedius* to the family Ictidosuchidae

Not only does it appear that *intermedius* should be removed from the genus *Ictidosuchoides* but that it should also be removed from the family Ictidosuchidae and transferred to the family Scaloposauridae. Haughton and Brink (1954) give as a diagnosis for the Ictidosuchidae the following: "Inferior temporal and postorbital bars slender, but complete. Large suborbital vacuities. Long and large temporal fossae. Large pineal foramen". The only requirements which *intermedius* fulfills to warrant its inclusion in the Ictidosuchidae are the slender infratemporal bars and the large suborbital vacuities, but these characteristics are also found amongst the members of the Scaloposauridae. In *Choerosaurus dejgeri* (Haughton 1929), *Ictidosuchops watermeyri* (Broom, 1941), *Scaloporhinus angulorgatus* (Boonstra 1953) and *Tetracynodon tenius* (Broom and Robinson, 1948), all members of the Scaloposauridae, the infratemporal bar is slender. In *Scaloposaurus* (Watson 1931) itself the suborbital vacuites are extremely large.

The marked features which distinguish *intermedius* from the members of the Ictidosuchidae are: (1) the presence of long and large temporal fossae in the Ictidosuchidae, while those of *intermedius* are short: (2) the presence of a primitive secondary palate in *intermedius* which is absent in the Ictidosuchidae.

Taxonomic position of *intermedius* within the Scaloposauridae

Having established the fact that *intermedius* should be removed from the Ictidosuchidae and placed within the Scaloposauridae, the taxonomic position of this form within the Scaloposauridae must be discussed, but before doing this a few remarks on this interesting and important family are relevant.

The Scaloposauridae according to Haughton and Brink (1954) are characterised by the following: "Skull small. Snout usually long. Intertemporal bar fairly broad. Postorbital bar either complete or incomplete, but always feeble. Secondary palate in the process of development. Teeth numerous and pointed, with one or two small canines in front of the main canine. Pineal foramen present or absent". The characteristic " . . . with one or two small canines in front of the main canine" is not a reliable feature since both *Scaloposuchus rubidgei* (Broom, 1940) and *Tetracynodon tenuis* (Broom and Robinson, 1948) have three small canine anterior to the main canine. Consequently there is nothing in the definition of the family Scaloposauridae to exclude the inclusion of *intermedius*.

Unfortunately as a result of the overall poor state of preservation of the Scaloposauridae and the lack of information as to the exact horizon in which they occur, the classification of this family is extremely difficult. Watson (1931) has pointed out that it is a family stretching from the Endothiodon to the Lystrosaurus zones bridging the gap between the typical therocephalians and the bauriamorphs. The occurence of a great deal of diversity within the Bauriidae suggests very strongly that in the Scaloposauridae we are dealing not with a simple phylogenetic line, but rather with several lines of parallel evolution all developing in a "bauriamorph-like" direction. As a result of this added difficulty it is convenient to divide the family into four stages of advancement. A grouping of this type does not imply a close phylogenetic relationship between the forms included in a single group, but does illustrate the different stages of development. Forms which are poorly known such as *Ictidognathus parvidens, Ictidostoma hemburi, Nanictocephalus richardi* and *Polycynodon elegans* have not been included in this grouping.

Group A

*Icticephalus polycynodon* (Watson, 1931; Boonstra, 1934) and possibly *Silpholestes jackae* (Broom, 1948) can be placed together in the most primitive group. They are characterised by the following:

1. Postorbital arcade complete (?).
2. Pineal foramen present.
3. Outstanding canine.
4. All maxillary teeth simple sharp cones.
5. Apparently no development of the secondary palate.

Group B

In this more advanced group the following forms may be included: *Choerosaurus dejageri* (Haughton, 1929), *Ictidosuchops bauroides* (Broom 1940b), *I. watermeyeri* (Broom 1941), *Nanictidops kitchingi* (Broom 1940a), *Pelictosuchus paucidens* (Broom 1940), *Scaloposuchus rubidgei* (Broom 1940a) and possibly also the very poorly known *Scalopcephalus watsonianus* (von Huene, 1938). This group is characterised by

1. Postorbital arcade incomplete.
2. Pineal foramen present.
3. Outstanding canine.
4. All maxillary teeth simple sharp cones.
5. Primitive secondary palate present. (This feature has not been confirmed in all the specimens included within this group).
6. A short spur on the jugal which is directed towards the postorbital.
7. All these forms come from the *Cistecephalus* zone.

Group C

In this advanced stage is included: *Scaloposaurus constrictus* (Watson, 1931); Broom, 1936). *S. hoffmanni* (description later in this paper), and also possibly *Cybrasiodon boycei* (Broom, 1932). This group is characterised by

1. Postorbital arch incomplete.
2. Pineal foramen absent.
3. No outstanding canine.
4. Some of the postcanine teeth are cusped. (This is the reason for the inclusion of *Cybrasiodon* within this group).
5. Primitive secondary palate present (Broom, 1936).
6. No dorsally directed spur on the jugal.
7. *Scaloposaurus* is found in the *Lystrosaurus* zone. This has recently been confirmed by Mr. J. W. Kitching who discovered a practically complete skull and skeleton of *Scaloposaurus* sp. in this zone.

Group D

Whether *Ericiolacerta parva* (Watson, 1931) should be placed within the Bauriidae (Watson) or Scaloposauridae (Haughton and Brink) is uncertain, but it can certainly be considered as the most advanced scaloposaurid that is known. It is characterised by

1. Incomplete postorbital arch.
2. No pineal.
3. No outstanding canine.
4. Molariform cusped postcanines in the maxilla; simple tricuspid teeth in the lower jaw.
5. Advanced secondary palate with the vomers, palatines and maxilla contributing to its formation.
6. No dorsally directed spur on the jugal.
7. This form comes from the *Lystrosaurus* zone.

*Scaloporhinus angulorugatus* (Boonstra, 1953) and *Tetracynodon tenuis* (Broom and Robinson, 1948) both appear to be closely allied to *Scaloposaurus,* but are distinct from this genus and every other genus of the Scaloposauridae in that the lacrimal meets the nasal.

Quite clearly *intermedius* falls into the second group of development within the Scaloposauridae and the genus to which it appears to be most closely related is *Ictidosuchops.* The three species, *rubidgei, baurioides* and *watermeyeri* which are included in the genus Ictidosuchops are not well known, but the external features agree very closely with those of *intermedius.* In *I. baurioides* the skull is slightly broader between the infratemporal bars and the interorbital width is slightly less than in *intermedius.* In *I. bauroides* the dental formula is given as I. 6, C. 3, PC. 10, but the premaxillary and anterior maxillary regions are poorly preserved with the result that this formula is best regarded as tentative. Rather than to create a new genus for *intermedius* and in view of the apparent relationship between *intermedius* and *Ictidosuchops baurioides,* it is proposed that *intermedius* be tentatively included within this genus.

# IV STUDY OF THE SKULL OF ICTIDOSUCHOPS INTERMEDIUS WITH THE AID OF SERIAL GRINDING

Olson (1944) has described in great detail several therapsid skulls which he studied with the aid of serial sectioning. Although Olson sectioned a therocephalian, it came from the *Tapinocephalus* zone and was not identified. Consequently the study of a scaloposaurid from the base or middle *Cistecephalus* zone with the aid of a similar technique is of interest especially since this technique can reveal many features which cannot be observed in a dissected specimen.

Unfortunately the skull (B.P.I. 268) of *I. intermedius* to be described in this section was slightly crushed dorso-ventrally but in no way seriously damaged. The skull was embedded in "calistone" and ground away at intervals of 285 u with the aid of the Croft Parallel Grinding instrument. Enlarged drawings (x 25) were made of the sections on wax plates. These were cut out and superimposed to make an enlarged model of the original skull. Only the posterior half of the skull was sectioned; the right half transversely and the left half longitudinally. In this way many of the inaccuracies introduced could be corrected. Unfortunately a fairly large margin of error is introduced with the use of wax plates and consequently the drawings that have been given of this model should not be used for taxonomic purposes, but the interrelationship of the different entities of the skull are well shown and their actual proportions can be obtained from the dissected specimen of the same species. No attempt has been made in the illustrations of this model to place slightly dislocated structures such as the quadrate back into their true position or to compensate for the crushing of the skull.

## 1 Description of the skull

### Skull base (Figs. 5A & 6A)

The posterior portion of the basioccipital is damaged and consequently no details of condyles could be given. No suture between the basioccipital and the exoccipital could be distinguished. A narrow space separates the basioccipital tubera from the basisphenoid-parasphenoid complex (BS-PS.) and more medially a faint suture between the two entities is visible. In longitudinal section the suture dividing these bones is only visible on the ventral surface. There is no indication of the unossified zone found by Olson (1944) in a therocephalian and in several other therapsids. A pronounced process directed dorso-laterally arises from the dorsal surface of the skull base (DOR. SEL., fig. 6A). Olson (1944) found a similar process in a therocephalian but in this specimen it was formed by the basicranial processes of the periotic. In the present specimen a clear suture separates the periotic from the skull base, and consequently the process in the present specimen can be regarded a true dorsum sellae. In the region of the internal carotids the basisphenoid is constricted. A clear parasphenoid is present as a thin vertical ridge of bone between the two carotid foramina; it continues forward below the basioccipital between the pterygoids and a short parasphenoidal rostrum projects into the interpterygoid vacuity. Anteriorly the basisphenoid flares out laterally to form two large basipterygoid processes (BP. PROC., fig. 5A & C). The junction of the basisphenoid and pterygoid is complex and will be described in detail. The ventral surface of the basipterygoid process is practically flat and triangular shaped with the apex of the triangle directed laterally. This view of the basipterygoid process is shown in fig. 5C where the pterygoids have been removed. Except for a narrow strip posteriorly the entire ventral surface of the basipterygoid process is covered by the pterygoid. This ventral surface has a free standing medial edge (F. EDG., fig. 5C, D, E & F) which posteriorly is separated from the dorsal portion of the basisphenoid by a distinct groove (GR.) opening ventro-medially. In

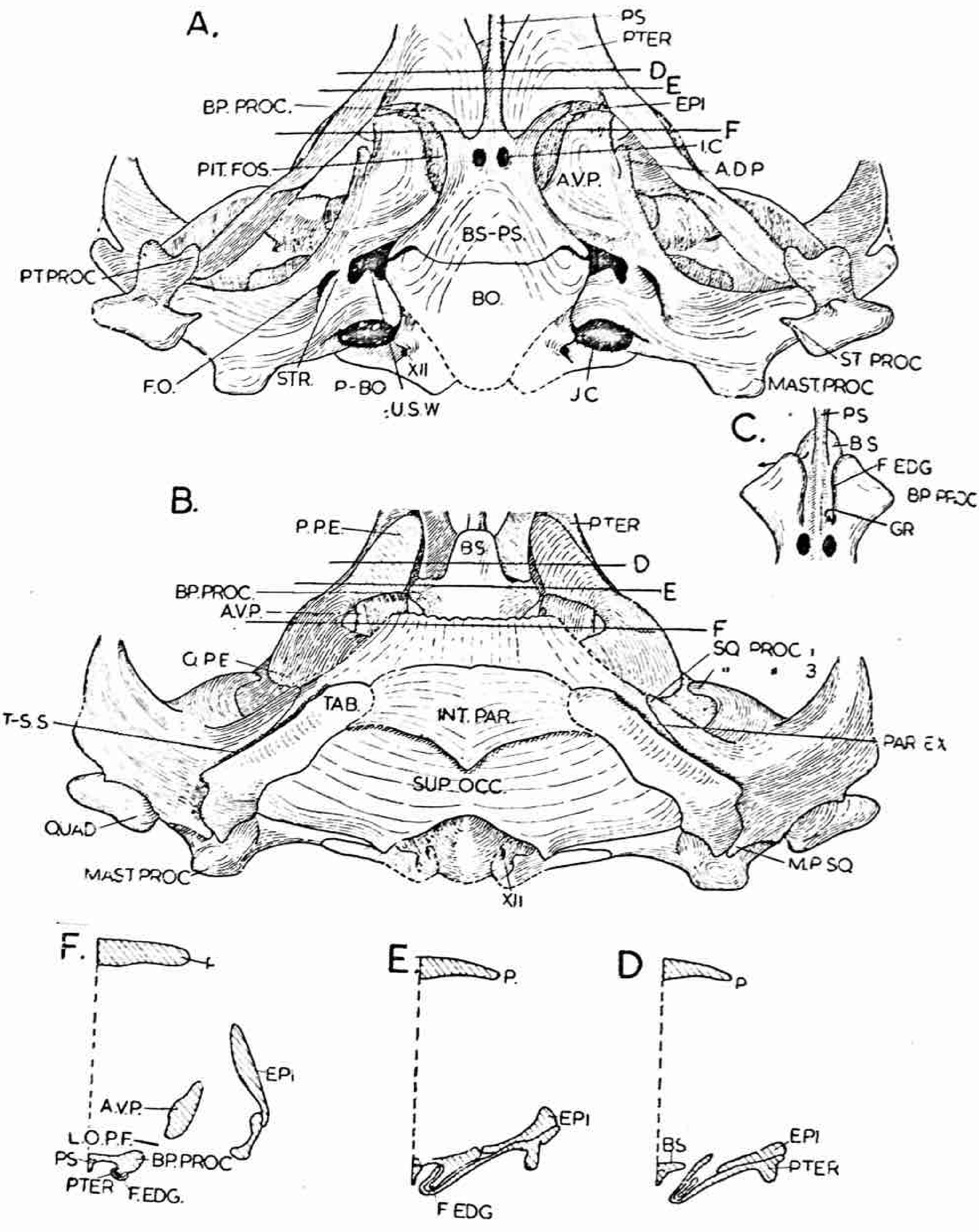


Fig. 5.—*Ictidosuchops intermedius.* A, ventral view and B, dorsal view of the skull reconstructed in wax plates. D, E and F, sections through the basipterygoid articulation. The levels of these sections are indicated by the parallel lines in figs. A and B. All x1½. (Key to lettering on p. 180).

an anterior direction this groove deepens considerably and anteriorly the basipterygoid process continues forward for a short distance as a separate process. This region is indicated by an arrow in fig. 5C.

Not only does the pterygoid lie upon the ventral surface of the basipterygoid process, but its medial edge curls around the free standing medial edge of the basipterygoid process. Since the relationship of the pterygoid to the basipterygoid process is rather difficult to understand three transverse sections through the basipterygoid articulation have been given (figs. 5D, E & F). The positions of these transverse sections are shown in figs. 5A & B by three parallel lines lettered D, E and F, (only the one half of the skull is shown in the sections). In fig. 5F the beginning of the free standing edge of the basipterygoid process (F. EDG.) is shown. In this region the posterior portion of the pterygoid is crescent shaped and fits around this free standing edge. In fig. 5E the groove between the free standing edge and the dorsal portion of the basisphenoid is well shown. The medial edge of the pterygoid extends well into this groove. In fig. D the basipterygoid process is separate from the rest of the basisphenoid and in this region the medial edge of the pterygoid extends dorso-medially beyond the horizontal level of the dorsal surface of the basisphenoid. This dorsal extention of the pterygoid is also shown in figs. 5B and 6A & B. Anterior to the basipterygoid process the basisphenoid takes the form of a thin horizontal plate. The parasphenoid is fused to the under surface of this plate. This region of the basisphenoid extends a short distance into the interpterygoid vacuity. The postero-lateral edge of the basipterygoid process almost establishes contact with the antero-ventral process of the periotic (A.V.P.) to enclose a lateral opening to the pituitary fossa (PIT. FOS., figs. 5A & B and 6A). An open contact is present between the medial edge of the pterygoid process of the epipterygoid (P.P.E., figs. 5B & E) and the basipterygoid process.

## The periotic

The periotic is a large single ossification; Olson (1944) also found no dividing sutures in this structure. A sutural connection exists medially between the periotic and the exoccipital and dorsally between the periotic and the supraoccipital (fig. 6C). Ventrally there is a sutural connection between the basioccipital and the periotic posterior to the foramen ovale. Anterior to the foramen ovale there is a sutural connection between the periotic and the parasphenoid-basisphenoid complex (BS-PS., fig. 5A). Anterior to this connection the periotic (Antero-ventral process of the periotic) draws away from the basisphenoid to form a dorsal boundary to the lateral opening (L.O.P.F., fig. 5F) of the pituitary fossa (PIT. FOS., fig. 5A & F and 6A). Anteriorly the antero-ventral process of the periotic all but establishes contact with the basipterygoid process.

In the description of the dissected specimen of *Ictidosuchops intermedius*, mention was made of the large fenestra ovalis which was far larger than the foot plate of the stapes. It was concluded that the medial portion of the large fenestra ovalis represents an unossified region of the ventro-lateral wall of the cranium and in life was probably closed by cartilage. The sectioning of a skull confirms this opinion. In the sectioned specimen the large fenestra is divided into two by a slender strip of bone (STR., fig. 5A). This structure could quite easily be destroyed during mechanical preparation. The lateral foramen undoubtedly is the foramen ovalis (F.O., fig. 5A) and the medial foramen (U.S.W.) an unossified portion of the side wall of the brain case. It follows, therefore, that the foramen ovalis in this form is completely surrounded by the periotic as in mammals and that the basioccipital and the parasphenoid-basisphenoid complex do not enter the formation of its ventral border. If these results are confirmed in other scaloposaurids it will be of particular interest since in all the therapsids sectioned by Olson (1944) the medial border of the fenestra ovalis was formed by the basioccipital; in cynodonts the periotic very nearly surrounds the fenestra.

The anterior wall of the periotic is best shown in fig. 6A. In this figure the inner view of the right half of the brain case is shown. Two processes, both directed forwards arise from the anterior region of the periotic; a stout ventral process, the antero-ventral process of the periotic (A.V.P.), and a slender dorsal process, the antero-dorsal process of the periotic (A.D.P.). The ventral edge of the antero-ventral process forms the dorsal border to the lateral opening to the pituitary fossa. The base of this process is penetrated by a small foramen, probably for the facial nerve (VII). The antero-dorsal corner of the antero-ventral process is drawn out into a distinct process (PIL. ANT.); this process is considered by Olson (1944) to be an ossification of the pila antotica (pleurosphenoid). Seen in ventral view the antero-ventral process is roughly triangular (fig. 5A) with the apex of the triangle directed forwards.

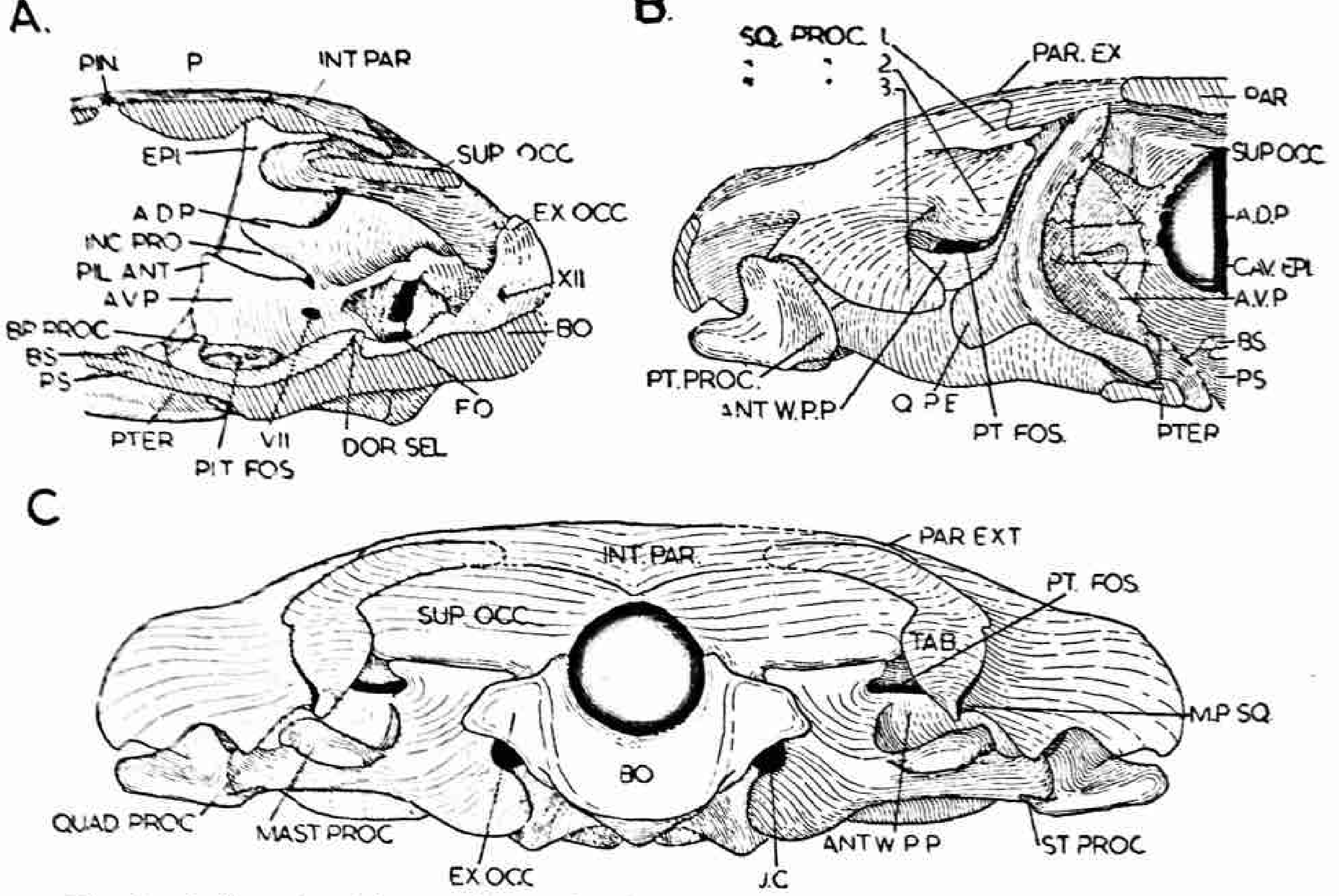


Fig. 6.—*Ictidosuchops intermedius*. A, view of the brain case from the middle line, B, anterior view of the posterior portion and C, occipital view of the skull reconstructed in wax plates. All x1½. (Key to lettering on p. 180).

A wide and deep incisura prootica (INC. PRO.) separates the antero-dorsal and antero-ventral processes. This incisura is not visible in lateral view as it is entirely covered by the epipterygoid. However, a wide space, the cavum epiptericum (CAV. EPI., fig. 6B), is enclosed between the two lateral processes of the periotic and the epipterygoid. The ganglion for fifth cranial nerve was probably situated in this space. Dorsal to the antero-dorsal process a shallow depression is formed in the antero-dorsal wall of the periotic. The expanded dorsal portion of the epipterygoid fits into this depression so that in this region the epipterygoid forms part of the side wall of the brain case itself (see fig. 6A). A similar condition is found to exist in cynodonts. Olson (1944) describes a deep notch above the incisura prootica which is bordered dorsally by a projection of the prootic forward below the interparietal. No such process was found in the sectioned specimen. In fact the anterior border of the periotic in the sectioned specimen agrees far more closely with that of a cynodont than with any other specimen sectioned by Olson.

The termination of the paroccipital process of the periotic by both a quadrate and mastoid process is confirmed in the sectioned animal. In fig. 7C a transverse section through the quadrate process of the paroccipital is given. The lateral surface of the quadrate process is in contact with the medial surface of the quadrate and no contact between this process and the squamosal was observed. The mastoid process (fig. 5A and C) is prominent, but contact between it and the mastoid process of the squamosal (M.P. SQ., fig. 6C) has been lost as a result of dorsal pressure. Although Olson (1944) described contact between the paroccipital process and both the quadrate and the squamosal he makes no mention of two separate processes in the forms he studied.

The supraoccipital has a long forward extention below the interparietal in the form of an open joint (fig. 6A). Medially this process of the supraoccipital has the form of a thin horizontal plate (SUP. OCC., fig. 6B) while its lateral edges are considerably thickened. These thickened lateral edges are indented by a fairly wide groove which in life probably received the dorsal end of the epipterygoid. Unfortunately since the skull is slightly crushed this point could not be confirmed. A wide fissure separates the dorsal border of the periotic and the ventral border of the anterior process of the supraoccipital.

Quadrate and Epipterygoid

Little additional information could be obtained about the quadrate from the sectioned specimen and this structure is unfortunately slightly dislocated from its pocket in the squamosal. Well shown, however, is the pterygoid process of the quadrate (PT. PROC., fig. 5A). The quadrate ramus of the pterygoid lies against the medial surface of this process. Unfortunately the quadratojugal is missing in the sectioned form.

Viewed laterally the epipterygoid consists of an expanded ventral portion, a broad ascending ramus and a slightly expanded dorsal portion (fig. 7B). The posterior edge of the expanded dorsal portion (EP. S.W.) fits into the shallow depression in the antero-dorsal wall of the periotic and consequently forms part of the true lateral wall of the brain case. The ascending ramus (A.R.) forms the side wall to the cavum epiptericum. The ventral edge of the central portion of the epipterygoid overlaps the pterygoid laterally (fig. 5F). A stout pterygoid process of the epipterygoid (P.P.E.) passes forward on the dorsal surface of the pterygoid. Near its junction with the ascending ramus this process is fairly slender, but more anteriorly it flares out to form a wide plate lying upon the expanded portion of the pterygoid in the region of the basipterygoid articulation (see fig 5B). This expanded portion of the epipterygoid is in contact with but is not suturally connected or fused to, the lateral edge of the basipterygoid process (fig. 5E). The pterygoid process of the epipterygoid terminates a short distance in front of the basipterygoid articulation, a short but deep quadrate process of the epipterygoid (Q.P.E.) extends backwards upon the lateral surface of the pterygoid. Above the quadrate ramus there is a shallow notch (V, II & III., fig. 7B) in the base of ascending process. This most probably lodged the maxillary or both the maxillary and mandibular branches of the trigeminal nerve during life. This feature was not observed in the dissected specimen, but could quite easily be destroyed by mechanical preparation.

Dermal bones of the skull

A thin splint of the parietal (PAR. EXT., fig. 5B) extends backwards to obtain a sutural connection with the squamosal (SQ. PROC. 1). Both the squamosal and the parietal are separated by a narrow split (T-S. S.) from the tabular. There appear to be a sutural connection between the tabular and the supraoccipital and an open joint appears to exist between the tabular and the interparietal although this region is not well preserved. A thin and narrow projection of the tabular extends downwards alongside the mastoid process of the squamosal (M. P. SQ.) and forms the lateral wall to the post-temporal fossa. The three medially directed processes of the squamosal (SQ. PROC. 1, 2 & 3) are well shown in fig. 6B. It has already been mentioned that an open joint exists between the supraoccipital and the dermal bones of the skull.

The sphenethmoid complex

An ossified sphenethmoid complex was dislocated from its true position. It consists of a ventral median plate and two dorsal crescent shaped wings. Although the ventral edge of the medial plate probably rested upon the dorsal edge of the parasphenoid-basisphenoid complex, this association could not be ascertained because the ventral edge of this medial plate is poorly ossified and in life was probably continued ventrally by cartilage. It is possible that the sphenethmoid complex was continued forward, but the anterior region of the skull was not sectioned. Olson (1944) has studied the sphenethmoid complex very thoroughly in several therapsid orders and the author is in agreement with Olson that the crescent shaped wings are homologous with the orbitosphenoids, and the median plate with the presphenoid of mammals.

## 2 Kinetism in the skull of *Ictidosuchops intermedius*

The sectioning of the skull of *Ictidosuchops* has revealed that it consists of two segments; a maxillary segment and an occipital segment. The occipital segment consists of the occipital ossifications, the tabular, the periotic, the basisphenoid and parasphenoid. The rest of the skull forms the maxillary segment.

Articulation between the two segments is found at the following places:

1. Between the quadrate process of the paroccipital and the quadrate.
2. Between the mastoid process of the paroccipital and the squamosal.
3. Between the tabular and the squamosal and the lateral extention of the parietal.
4. Between the tabular and the interparietal.
5. Between the dorsal edge of the epipterygoid and the lateral edge of the supraoccipital.
6. Between the pterygoid process of the epipterygoid and the basisphenoid.
7. Between the pterygoid and the basipterygoid process.
8. Between the supraoccipital and the interparietal.

Since the ventral edge of the presphenoid is probably cartilaginous and the orbitosphenoids do not appear to be fused to the frontal dorsally, the sphenethmoid would not rigidly connect the two skull segments. In view of the fact that the skull consists of two segments which are in no place fused to one another it is reasonable to conclude that kinetism was present in this form.

Versluys (1912) considered that kinetism was a means by which the jaws could be opened wider than by simply dropping the lower jaw and although this is most probably the correct interpretation for most of the diapsid reptiles and their derivitives it does not appear to be the case in the scaloposaurid specimen described above. Here the amount of possible movement that could take place between the two segments is small and the most probable interpretation is that a slightly kinetic skull would absorb the shock when an exceptionally hard bite was taken.

With all the open joints in the skull it is difficult to imagine that no movement within the skull took place, but it is difficult, however, to be quite certain as to how the maxillary segment moved relative to the occipital. In fig. 7A an attempt has been made to illustrate kinetism in *Ictidosuchops*. A simple pivoting of the maxillary segment around the paroccipital processes could not take place because the nature of articulation between the pterygoid and the basipterygoid

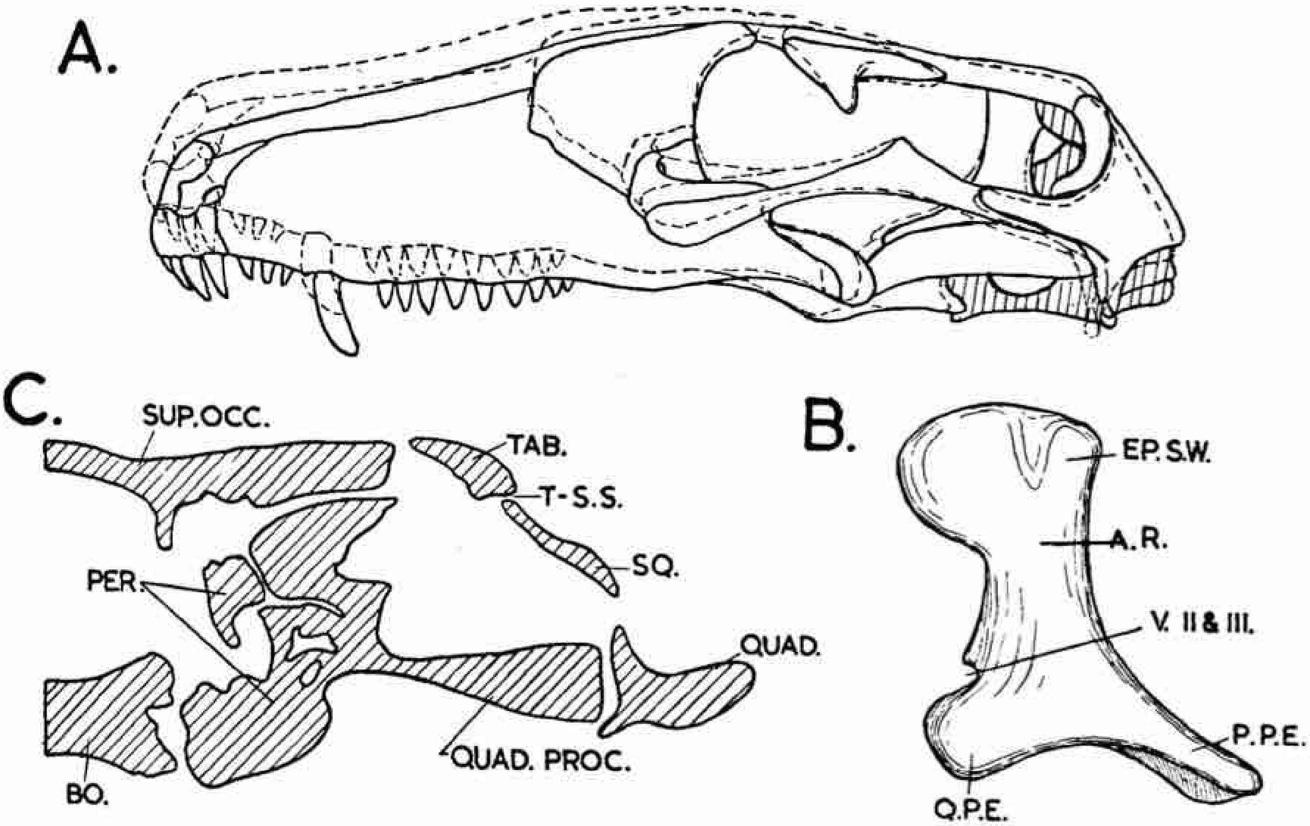


Fig. 7.—*Ictidosuchops intermedius*. A, diagram to illustrate kinetism in this form, B, epipterygoid of the skull reconstructed in wax plates and C, transverse section through the right half of the skull. A, not to scale, B and C, x2. (Key to lettering on p. 180).

processes would prevent direct vertical movement in this region. However, a slight forward movement of the maxillary segment would free the pterygoid from the basipterygoid joint sufficiently to allow dorsal movement to take place. Further, a very slight movement in this region would allow fairly considerable dorsal movement of the snout.

If the form of kinetism found in *Ictidosuchops* is to act as a shock-absorber system then there must be an effective system to stop movement within the skull once the initial shock has been absorbed. This could be effected by the basipterygoid articulation which would not allow much movement, the dorsal end of the epipterygoid being firmly pressed into the groove on the lateral surface of the anterior extention of the supraoccipital and the squamosal being forced against the tabular.

With the lifting of the snout there would be a slight depression of the posterior portion of the maxillary segment. The nature of the junction between the supraoccipital and the interparietal, the tabular and the squamosal and the squamosal and the mastoid process would allow a limited ventral movement of the maxillary segment to take place in this region.

Although Olson (1944) sectioned many specimens of therapsids and found many of the joints described in the above section, he makes no mention of kinetism. Versluys (1912) pointed out that the pelycosaurs have a skull construction almost identical to that found in the metakinetic diapsid reptiles. Two differences

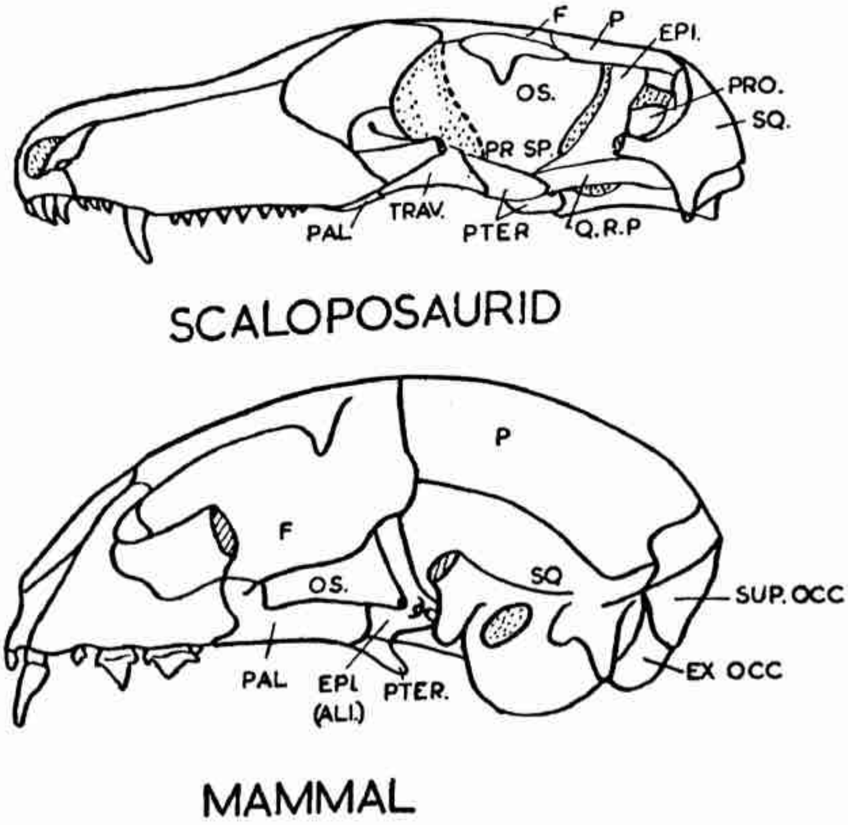


Fig. 8.—Comparison of the lateral views of the skull of a mammal and a scaloposaurid. No scale. (Key to lettering on p. 180).

he claimed did exist: the supraoccipitals are considerably expanded and the sphenethmoid complex is ossified and fused to the skull base and to the frontals. In the form Versluys studied he claimed that the ossified sphenethmoid complex united the two segments of the skull and ruled out any kinetism taking place but since the skull had the build of a metakinetic one, he concluded that the ancestors of the pelycosaurs must have had kinetic skulls. The findings of the present paper confirm to a large extent the findings of Versluys in that the skull has a metakinetic build, however, the scaloposaurid studied does appear to be kinetic because the sphenethmoid complex is not well ossified. The only real difference between a typical metakinetic skull and the one studied in this paper is that the tabular forms part of the occipital segment and not the maxillary segment.

It is of interest at this stage to compare the skulls of a scaloposaurid such as *Ictidosuchops* with that of a mammal (fig. 8). The most outstanding difference between the two skulls is the relatively large brain of the mammal and the comparatively small brain of the scaloposaurid. Associated with this feature, the skull of the mammal is designed to give greater protection to the brain. The frontals of mammals are extended downwards and sideways to form part of the lateral wall of the anterior part of the brain case and, intercalated between this ossification and the palatine, is a small orbitosphenoid. In the scaloposaurids the frontals are small bones forming only a dorsal covering to the brain case; the orbitosphenoids are relatively large. Intercalated between the palatine, pterygoid and orbitosphenoid anteriorly and the squamosal posteriorly in mammals is a small alisphenoid (epipterygoid). In the scaloposaurids the epipterygoid is fused to none of the surrounding bones except the pterygoid and therefore, the brain case is not completely closed laterally. In these forms the epipterygoid is widely separated from the squamosal. In the scaloposaurids a long quadrate ramus to the pterygoid is present while in mammals this ramus is absent. In mammals the pterygoid is fused to the skull base while in the scaloposaurids an open joint exists between these two entities. It is reasonable to assume that these above mentioned differences between the scaloposaurid and mammalian skulls are associated both with the increase in the size of the brain, and with the strengthening of the skull.

The following changes would have to take place in the scaloposaurid skull in order to firmly connect the two segments; a sutural connection between the skull base and the pterygoid, between the skull base and the presphenoid, between the frontals and the orbitosphenoids, between the orbitosphenoid and the epipterygoid, between the epipterygoid and the squamosal, and between the supraoccipital and the interparietal. It appears reasonable, therefore, to assume that a loss of kinetism could probably account for the above mentioned differences between the skulls of scaloposaurids and mammals.

In view of the fragmentary knowledge of the detailed structure of advanced mammal-like reptiles it is perhaps too early to speculate as to why the two sections of the skull fused in the development from therapsid to mammal, but the following theory is tentatively suggested. This theory is based upon the assumption that mammals could be derived from advanced scaloposaurids and not a form such as *Bauria cynops* which appears to be too specialized to be ancestral to mammals. The basis for this assumption has been fully discussed in a paper on the Ictidosaurs which will appear shortly. Kinetism is a useful adaptation in a carnivorous animal such as *Ictidosuchops intermedius* in which a large canine is present and which has a relatively flimsy skull in that it is a mechanism by which the shock placed upon the skull will be absorbed, when an exceptionally hard bite is taken. As long, therefore, as kinetism is of functional importance, it will probably be retained. For mechanical reasons it would be difficult if not impossible to retain both kinetism in the posterior region of the skull and at the same time increase the size of the brain, for although it is possible to bend a structure such as the spinal column in which the majority of the fibres run parallel, it would be more difficult to bend a complex structure such as the mammalian brain without causing damage. It was shown in the general section on the scaloposaurids that there is a tendency in the advanced forms such as *Scaloposaurus* and *Ericiolacerta* to decrease the size of the canines to such an extent that they cannot be distinguished in size from the postcanine teeth. A decrease in the size of the canines is accompanied by an overall decrease in the size of the skull. In these advanced scaloposaurids it is reasonable to assume that kinetism would not be as essential as it is in those forms with large canines. With the necessity of the kinetism removed it is possible that the two skull segments could unite, either at the advanced scaloposaurid stage or in the descendant of this stage, and allow the brain to enlarge. Unfortunately the advanced scaloposaurids have not been studied in sufficient detail (serial grinding) to ascertain whether an incipient fusion between the two segments has already taken place.

In this paper the discussion of kinetism has been limited to the scaloposaurids and no reference has been made to kinetism in early therocephalians and in other therapsid suborders. However, Parrington has been studying the problem of kinetism in mammal-like reptiles for several years and has a great deal of evidence (correspondence with Mr. Parrington) to support the contention that kinetism is present in at least some of the gorgons, anomodonts and cynodonts. In contrast to the results given in this paper, Parrington does not find an articulation between the basisphenoid and the pterygoid, but rather between the basisphenoid and basioccipital below the unossified zone. In the gorgons and anomodonts the sphenethmoid complex firmly unites the basisphenoid to the skull roofing. This would rule out the type of kinetism proposed in this paper. In the scaloposaurid sectioned here is quite clearly no articulation between the basiphenoid and the basioccipital and an unossified zone is not present. Parrington is of the view that the joint between the basisphenoid and the basioccipital is homologous to that found in the osteolepids (Watson 1954). In these forms there is also an articulation between the palatoquadrate and the skull base. It appears, therefore, that the basioccipital-basisphenoid articulation is lost in the diapsids and their derivatives, whereas the other articulation between the palatoquadrate and the skull base is retained. In the mammal-like reptiles on the other hand, both of these articulations appear to be present, although both have not as yet been found together in a single specimen. Despite the fact that the problem of kinetism in mammal-like reptiles is far from understood, the presence of two different kinetic lines in mammal-like reptiles presents the possibility that in the future this characteristic may possibly be employed as an additional feature for the classifying of this order.

## V SCALOPOSAURUS HOFFMANNI SP. NOV.

### 1 INTRODUCTION

Broom (1932) described and figured two scaloposaurid skulls from the *Lystrosaurus* zone. These were in the collection of the National Museum, Bloemfontein, but as van Hoepen was to have named them, Broom did not do so. Broom states that one of the specimens had a skull length of 55 mm. and the other 46 mm. Broom only illustrated one specimen and if his drawing is to scale (no scale is given with the drawing), it is the specimen with a skull length of 55 mm. He claimed that both belonged to the same species. Unfortunately the specimen with a skull length of 55 mm. has been lost and as neither of the two specimens were catalogued when they were found we have to rely on the evidence by Broom that they both came from the *Lystrosaurus* zone of Harrismith. This is perfectly reasonable since Mr. J. W. Kitching has recently found a skull and practically complete skeleton of *Scaloposaurus* at Brandkraal, Middelburg, C.P. which is clearly in the *Lystrosaurus* zone. Broom claimed (1932 & 1936) that these two specimens belonged to the same species as *Ericiolacerta parva* (Watson, 1931) which was also found at Harrismith. Although the dorsal view of the two skulls is similar, this is clearly not the case: the teeth, secondary palate and lower incisors are fundamentally different in the two types.

In this section that specimen with a skull length of 46 mm. has been described. It is quite clear that this specimen belongs to the genus *Scaloposaurus,* but for reasons to be discussed later it does not appear to be *constrictus.* It has, therefore, been made the type of new species, *S. hoffmanni,* and although confusion exists as to the exact horizon from which this specimen came, it is nevertheless of importance as it adds to what is already known of the genus *Scaloposaurus.*

The posterior region of the skull of *S. hoffmanni* is badly crushed and consequently no attempt has been made to reconstruct the occiput. Apparently it was the skull of a young animal as the occipital and periotic bones do not appear to have been firmly connected and have been dislocated by the dorso-ventral crushing. The infratemporal bars, the septomaxillae and the premaxillae are all missing. It is possible, however, to give the approximate length of the skull as 46 mm. because the anterior point of the dentary is preserved.

### 2 DESCRIPTION OF THE SKULL

Dorsal view of the skull (Fig. 9A)

This view of the skull is almost identical to that of *Scaloposaurus constrictus.* Minor differences are that the skull of *S. hoffmanni* is not as constricted in the nasal region and that the postorbitals do not extend as far laterally as in the type specimen. There is quite clearly no pineal. In the description *Ictidosuchops inter-*

*medius* the squamosal was described as having three medially directed processes. Both the dorsal and ventral processes (SQ. PROC. 1 & 2) are found in the skull of *S. hoffmanni*. The posterior surface of the ventral process abuts against the anterior surface of the paroccipital process. Similar conditions were described in *I. intermedius*. The dorsal surface of the posterior portion of the lacrimal forms a broad floor to the anterior region of the orbit and, a short distance below its

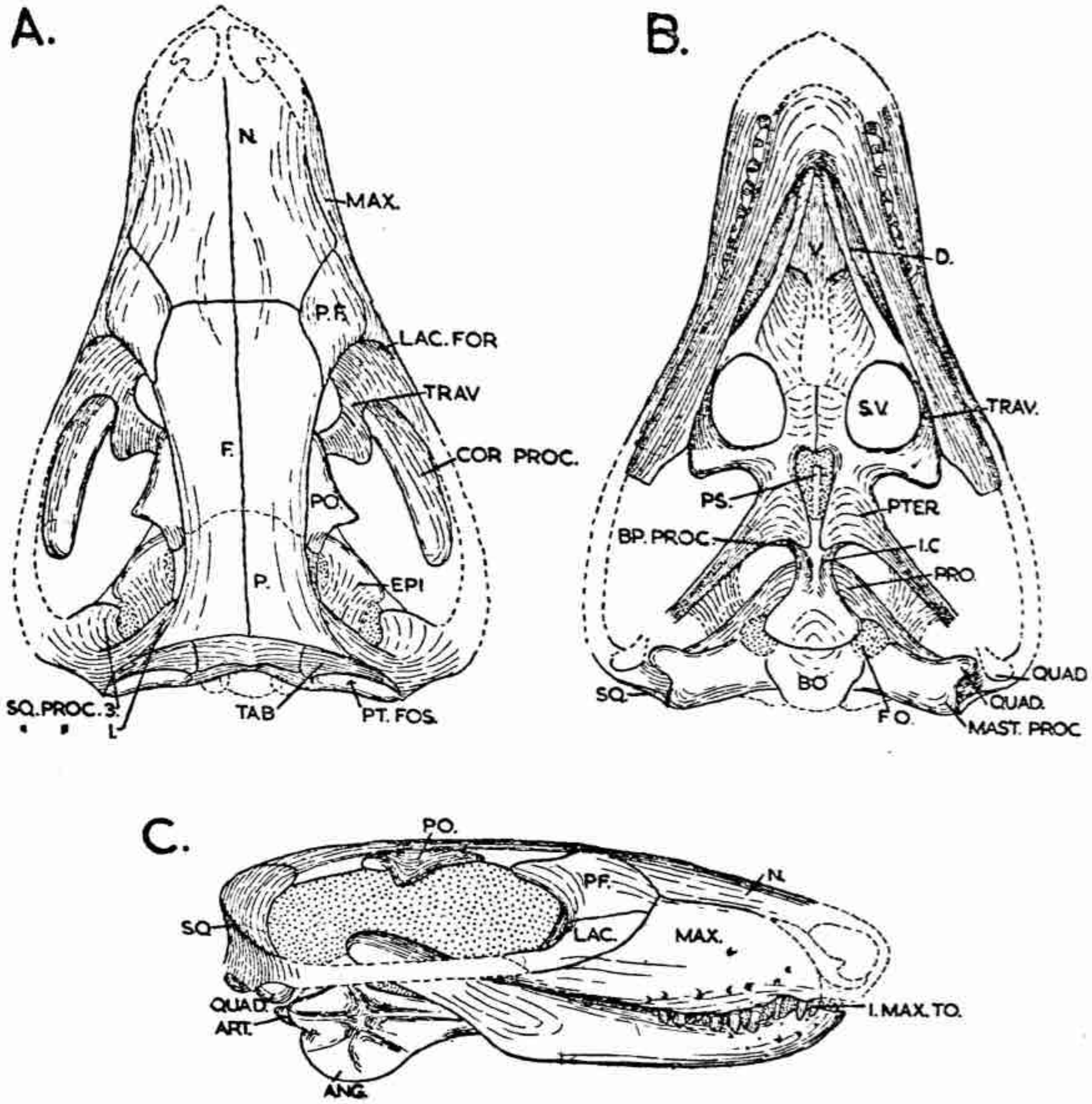


Fig. 9.—*Scaloposaurus hoffmanni* sp. nov. A, dorsal, B, ventral and C, lateral view of the skull, All x1½. (Key to lettering on p. 180).

junction with the postorbital, a small lacrimal foramen (LAC. FOR.) is visible near the lateral edge. The posterior border of the lacrimal is concave and the anterior border of the coronoid process fits into this concavity. The postero-medial corner of the lacrimal is joined to the transversum, but no dividing suture could be distinguished.

On both sides of the skull the central portions of the epipterygoids are missing. The remaining dorsal and ventral portions indicate that the epipterygoid was a broad plate of bone. A well-developed pterygoid process of the epipterygoid extends well forward and makes contact with the lateral edges of the basisphenoid.

The palate (Fig. 9B)

The anterior portion of the palate in the type specimen is unknown, but Broom (1936) has shown that in a section through the snout of a poorly preserved specimen of *?Scaloposaurus constrictus*, the palatal plates of the maxillae abut against the lateral edges of the expanded vomers. In *S. hoffmanni* and in *I. intermedius* an identical relationship was found to exist close to the internal choanae. A section through the anterior ends of the maxillae in *S. hoffmanni*, however, exposed by the loss of the premaxillae, revealed that the palatal plates of the maxillae in this region actually meet one another below the vomer. It would be interesting to know whether this feature is found in many of the Scaloposauridae or whether it is confined to the advanced forms of this family.

The suborbital vacuities are extremely large and the stout transverse processes of the pterygoid form the posterior borders of these vacuities. The basisphenoid has two small tubera at its postero-lateral corners. Anteriorly the bone narraws and then flares out to form the basipterygoid articulations. A paraphenoid rostrum arises from the narrow portion of the basisphenoid between the two internal carotid foramina and extends forwards into the anterior regions of the interpteygoid vacuity. The pterygoid flanges which underlie the basipterygoid processes terminate posteriorly as two sharp backwardly directed processes. A clear demarcation line is visible between these processes and the overlying basipterygoid process but it is impossible in this small specimen to be certain as to whether this joint is open or closed. Watson's (1931) illustration of the pterygoid flanges in the type specimen show the posterior ends suturally joined to the anterior borders of the basisphenoid by a fairly broad suture. It appears possible that in the type specimen the posterior ends of the pterygoid flanges have been damaged in view of the conditions found to exist in the new specimen.

In the type specimen the basisphenoid has two large postero-lateral extentions so that the posterior border of this bone is almost twice as wide as the basioccipital. The posterior edges of the lateral portions of these lateral processes are suturally connected to the periotic in such a way that the basioccipital does not form any part in the ventral edge of the fenestra ovalis. *S. hoffmanni* does not have these lateral extentions to the basisphenoid and the basioccipital does appear to form part of the ventral border of the fenestra ovalis. Except for the paroccipital processes the periotic bones are not well preserved in *S. hoffmanni*. Each process is terminated by a distinct quadrate process which abuts against the quadrate and by a mastoid process; the squamosal appears to have a process which articulates with the lateral edges of the mastoid process in a manner similar to that described in *I. intermedius*. Watson (1931) described a mastoid process in the type of *S. constrictus*. Fracture of the left interparietal has revealed that the supraoccipital continues well forward below the interparietal.

Side view of the skull

In fig. 9C the skull is shown in lateral view. An outstanding feature is the large angular and the complicated pattern formed by the strengthening ribs of this bone. A large angular was not figured by either Watson (1931) or Broom (1932) for *S. constrictus*. There is no pronounced coronoid process to the dentary in *S. hoffmanni*. In both the type specimen and *S. hoffmanni* the dorsal surface of the skull is convex in side view. Watson figured several foramina in the snout of *Ericiolacerta parva*, but none in the type specimen of *S. constrictus*. In *S. hoffmanni* these foramina are numerous, not only in the maxilla, but in the anterior portion of the dentary as well.

The extent of the missing premaxilla could be approximated as the anterior edge of the right dentary was preserved. On the left side of the skull the entire ventral surface of the maxilla appears to be present, but on the left that portion of the maxilla containing the first maxillary tooth is missing.

Dentition

Nothing is known of the upper incisors in this form except for a small piece of tooth lying against the anterior border of the left dentary. As the premaxilla is missing it is impossible to say to which incisor it belonged. Judging from the anterior border of the left maxilla a small diastema must have separated the maxillary teeth from the incisors. There are ten teeth in the maxilla, but no outstanding canine is present. The first maxillary tooth is circular in cross-section and is sharply pointed. The remaining nine maxillary teeth are best preserved in the right maxilla. The second maxillary tooth is firmly held in the maxilla, and fairly sharply pointed. The third tooth appears to have been recently erupted or in the process of being shed as the alveolus is far larger than the root of the tooth. The crown of this tooth is slightly wider than the root. Unfortunately the apex has been destroyed. The fourth tooth is far larger than the third, is firmly held by the maxilla and its apex shows clear signs of wear. The fifth tooth appears to have recently erupted; it is sharply pointed and loosely held by the maxilla. The sixth tooth is firmly held in its alveolus and its apex shows clear signs of wear. The seventh tooth is sharply pointed and only partially erupted. The eighth tooth is firmly held in its alveolus and terminates in a blunt central cusp which is flanked by small cusps anteriorly and posteriorly. This tooth is not transversely widened. The ninth tooth is slightly dislocated from its socket and has a crown pattern identical to that of the eighth. The tenth tooth is only partially erupted and its crown, which is preserved in the left maxilla, consists of a main cusp with a small accessory cusp behind, but no anterior cuspule. In the maxillary teeth of this specimen we appear to have, therefore, alternate or "distichic" replacement. Teeth numbers 3, 5, 7 and possibly 9 have recently erupted. Teeth numbers 2, 4, 6 and 8 are all firmly held in their alveoli and show signs of wear. Presumably when the odd numbered teeth are firmly held by the maxilla, the even numbered teeth will be replaced. The tenth tooth is erupting but this may be the first appearance of this tooth and is associated with increasing the length of the tooth row.

There are four incisors in the lower jaw. The crowns of the first three are missing and that of the fourth is preserved; this tooth is circular in cross-section. The incisors are not procumbent as in *Ericiolacerta parva* (Watson, 1931). What appears to be a small canine follows immediately upon the incisors. It is covered laterally by the first and second maxillary teeth so that no information as to its exact length could be obtained. The grounds for calling this tooth a canine, are based on the fact that the exposed part of the tooth following it is slightly smaller. However, a possible explanation for this may be that the so-called canine has recently been replaced while the tooth following it has not. As both jaws were in position it was difficult to study the crowns of the mandibular teeth, but the medial aspect of the crowns of these teeth were exposed by removing the matrix on the medial surface of the dentary. As least the last five mandibular teeth i.e. possibly teeth numbers 6, 7, 8 9 and 10, all have crowns identical to that of the 8th and 9th maxillary teeth. Fracture of the lower jaw during preparation indicated that none of the mandibular teeth were transversely widened.

## 3 Discussion

Parrington (1936) has shown that in *Thrinaxodon, Parathrinaxodon* and *Tribolodon*, all cynodonts, and in the pelycosaurs, there is alternate or "distichic" replacement of the postcanine teeth. Crompton (1955b) has shown that this "distichic" replacement is also present in the incisor region of the gomphodont cynodont *Scaleodon angustifrons*. It is, therefore, of interest to note that this type of replacement is also found in the advanced scaloposaurids, an entirely different line of therapsid evolution than the cynodont line.

Broom (1932 and 1936) described tricuspid postcanines in a specimen of *S. constrictus* and the scaloposaurid with a head length of 55 mm. in the National Museum. Watson (1931) has also described tricuspid postcanines in the mandible of *Ericiolacerta:* this is to be expected since a very close relationship appears to exist between the two genera. Broom (1936) gave the dental formula for his specimen of *S. constrictus* from Bethesda Road as 4.1.11. The type specimen of *Scaloposaurus constrictus* according to Broom (1932) has twelve maxillary teeth. It is not considered that this difference in the number of maxillary teeth can be used as a diagnostic characteristic to distinguish between *hoffmanni* and *constrictus* since *hoffmanni* appears to be a young animal and it is very probable that these forms increased the length of the postcanine row by the addition of teeth at the back during growth. In fact the structure of *S. constrictus* and *S. hoffmanni* is so identical that they should perhaps both be placed in the same species. However, because of the fundamental difference in the shape of the basioccipital in the two specimens a new species has been created. It may well be that the difference is due to the difference in age between the two specimens, but until this has been proved it is perhaps better to leave the new specimen in the new species.

It can be seen from the description of *S. hoffmanni* that the skull construction in the majority of instances is identical to that of *Ictidosuchops intermedius*. Such points in the skull of *S. hoffmanni* as the relationship of the supraoccipital to the interparietal, the open joint between the quadrate process of the paroccipital and the quadrate, the mastoid process and the nature of the basipterygoid articulation indicate that even if the skull was not kinetic, it was derived from an ancestor with a kinetic skull. Only serial grinding of a scaloposaurid skull would establish beyond doubt whether it has a kinetic or an akinetic skull.

## VI SOME REMARKS ON BAURIA CYNOPS

### I General

Watson (1931) expressed the opinion that the scaloposaurids gave rise to the bauriamorphs and pointed out that close similarity in the structure of the skull bases of *Bauroides watsoni, Scaloposaurus constrictus* and *Ericiolacerta parva.* He also described a mastoid process of the paroccipital in *Microgomphodon* which was similar to that found in *Scalopsaurus.* This view of the origin of the bauriamorphs was questioned by Boonstra (1938) in his paper giving a more complete description of *Bauria cynops* than had previously been undertaken. Boonstra claimed that the bauriamorphs and the Scaloposaurids " . . . differ in a number of features of fundamental importance which definitely precludes the thesis that *Bauria* can be derived from the Scaloposaurids". Boonstra's main reasons are that the following features are found in *Bauria* and are not in the scaloposaurids: Narrow parietal crest, absence of mastoid process, no lateral extention of the basiphenoid and loss of a distinct quadratojugal. Brink and Kitching (1953) have given a revised description of *Bauria cynops,* but no mention is made of the relationships of this genus.

The specimen of *Bauria cynops* described by Brink and Kitching was loaned from the Bernard Price Institute and dissected further. Unfortunately the posterior region of the skull was badly crushed and as a result of this crushing the quadrate and squamosal have been widely separated from the skull base. The medial portion of the paroccipital process (fig. 10A) almost completely surrounds the jugular canal with only a small portion of the exoccipital forming part of the posterior border. Similar relationships were described in *I. intermedius.* Brink and Kitching illustrate the basioccipital forming part of the medial border. The lateral termination of the paroccipital process has been illustrated by Broom (1937a), Boonstra (1938) and Brink & Kitching (1953). All show it with a broad crescent shaped face. Broom shows its anterior border meeting the quadrate and its posterior border meeting the squamosal while Boonstra claims that it makes contact with the squamosal only and is separated from the quadrate by a broad strip of the squamosal.

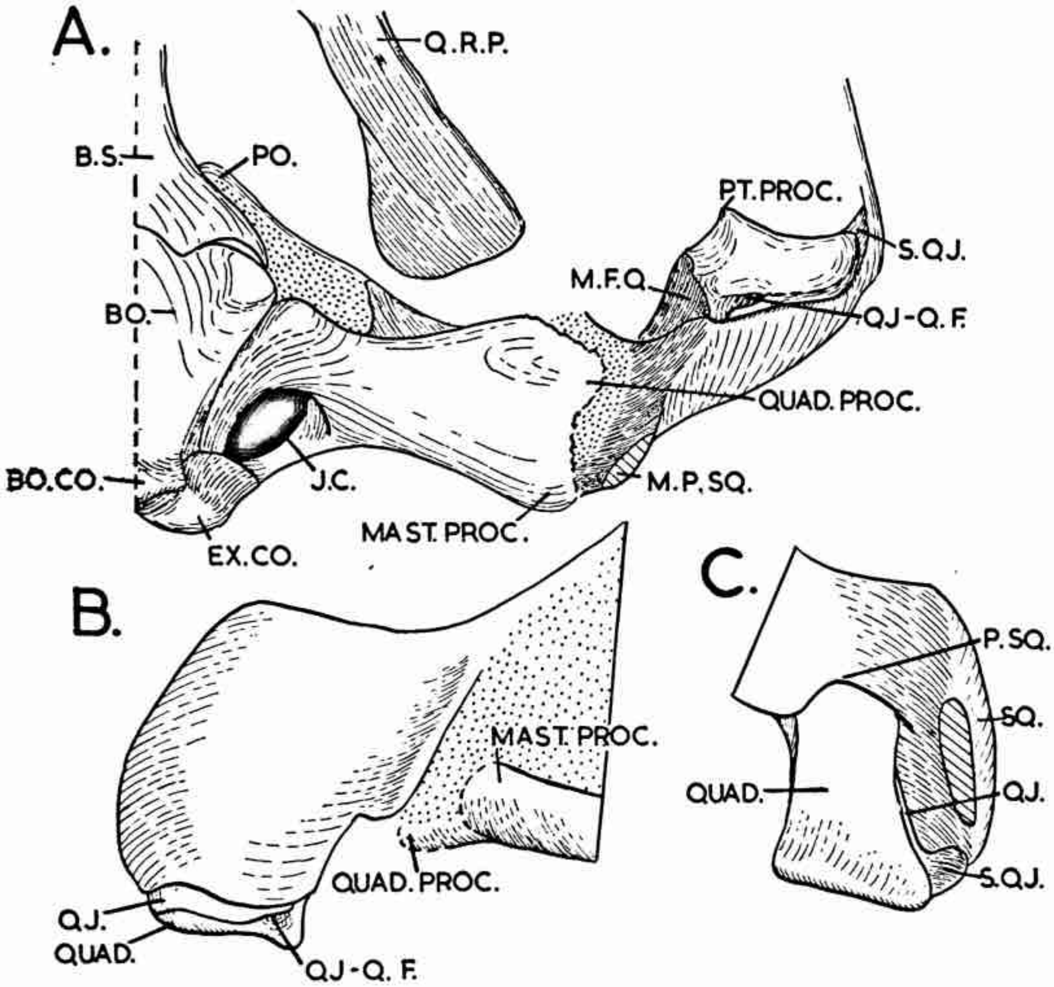


Fig. 10.—*Bauria cynops*. A, ventral view of the posterior portion of the left side of the skull, B, posterior view of the squamosal and quadrate and C, anterior view of the quadrate. All x2. (Key to lettering on p. 180).

In the specimen loaned from the Bernard Price Institute the lateral end of the paroccipital is not particularly well preserved, but there is a clear mastoid process (MAST. PROC.) directed towards a separate process of the squamosal (M.P. SQ.). Crushing of the specimen has separated these two processes. The quadrate process is damaged, but a fairly large triangular shaped face (M.F.Q.) of the quadrate is exposed medially and if the skull were restored the quadrate process would all but meet this face of the quadrate. These conditions are almost identical to those found in *I. intermedius* and *S. hoffmanni*. The quadrate has never been fully described in *B. cynops*, but fortunately it is well preserved in the Bernard Price specimen. This bone has a broad articulating face for the articular (fig. 10A). Boonstra illustrates a long pterygoid process meeting the quadrate ramus of the pterygoid, but in the Bernard Price specimen only a short process is visible (PT. PROC.), in fact so short, that it appears doubtful whether the quadrate ramus of the pterygoid actually did reach this process. A small foramen (QJ.-Q.F.) is present immediately behind the articular surface of the quadrate towards the medial side of the bone. This is the quadrato-quadratojugal foramen. The posterior border of this foramen is formed by a thin splint of bone, the medial termination of the quadratojugal. Laterally to this foramen the quadratojugal and the quadrate appeared to be fused, but a faint suture parallel to the posterior border of the quadrate is visible. A clear suture is visible between the lateral edge of the quadrate and the quadratojugal. A thin splint of the quadratojugal (S.QJ., figs. 10A & C), directed forward, is apposed to the medial surface of the squamosal. Dorsal to the articular surface the quadrate tapers away so that the medial surface has a triangular shape. In anterior view (fig. 10C) the quadrate is broad with its dorsal end fitting into a shallow pocket in the squamosal (P. SQ.). A narrow splint of the quadratojugal (QJ.) is visible alongside the lateral edge of the ascending portion of the quadrate.

In contrast to the scaloposaurids the squamosal extends further ventrally so that practically only the articular face of the quadrate is visible in posterior view (fig. 10B). In *I. intermedius* the entire medial surface of the quadrate is exposed, while in *B. cynops* the dorsal portion of the medial face is covered by an extremely thin plate of the squamosal directed forwards.

Boonstra (1938) claimed that the occipital condyle was broad, and that it consists almost entirely of the basioccipital with the exoccipitals forming a very minute portion of the dorso-lateral edges of this condyle. Brink and Kitching (1953) illustrate a narrow single rounded condyle, but are not explicit as to how it is formed. A careful dissection of the condyle of the Bernard Price specimen has revealed that there are two fairly large condyles formed by the exoccipitals (EX. CO.) and perhaps a very small condyle formed by the basioccipital (BO. CO.). A medial groove separates the two exoccipital condyles and the basioccipital condyle is situated anteriorly to the exoccipital condyles. In the description of *Ictidosuchops intermedius* it was shown that the basioccipital formed the major portion of the condyle, but that distinct articulation faces were visible on the exoccipitals. It appears therefore that the withdrawal of the basioccipital from the condyle which was initiated in the early scaloposaurids is practically completed in the bauriamorphs.

The lateral view of the brain case of *B. cynops* has been illustrated by Boonstra (1938). He shows a deep, interparietal continuing forward below the parietal. In the Bernard Price specimen it is quite clear that this structure is not an interparietal but a forward extention of the supraoccipital similar to that found in *I. intermedius* and *S. hoffmanni*.

## 2 Discussion

A distinct mastoid process and quadratojugal are thus found in *B. cynops*. There is no expanded basisphenoid in the two scaloposaurids studied in this paper. The parietal crest found in *B. cynops* could have developed in order to give greater insertion to jaw muscles associated with a grinding dentition. Other features mentioned by Boonstra; the preorbital bulging of the jugal and the maxilla, the approximation of the alveolar borders of the maxillaries and the secondary palate formed by the premaxillae and maxillae could have developed from a scaloposaurid condition. The features of *B. cynops* described in this section support the view of Watson (1931) that the scaloposaurids are intermediate between the therocephalians and the bauriamorphs. It is quite clear, however, as pointed out by Boonstra, that *B. cynops* could not have arisen from *Ericiolacerta* since in this form the palatines contribute to the formation of the secondary palate, but *B. cynops* could well have arisen from a more primitive scaloposaurid. The presence of a complete postorbital arcade in *Sesamodon* (Broom, 1911) and *Microgomphodon* (Watson, 1914) and the presence of a pineal foramen in *Microgomphodon* may indicate that the bauriamorphs arose from separate scaloposaurids.

The mastoid process and the forward extention of the supraoccipital in *B. cynops* may well indicate that the skull of this form was kinetic or arose from a form with a kinetic skull. Recently an almost perfect skull of *Bauria cynops* was discovered by Mr. J. W. Kitching. It is hoped that this specimen, when prepared will throw further light on the problem of kinetism in this form.

## VII SUMMARY AND CONCLUSIONS

1. A thorough study of the skull of *Ictidosuchoides intermedius* Broom has been undertaken with the aid of a specimen prepared with an automatic mallet and one serially sectioned by grinding at intervals of 285 u. The skull structure has been described in detail. It was concluded that the species *intermedius* should be removed from the genus *Ictidosuchoides* and placed in the genus *Ictidosuchops*. The skull of a new species of scaloposaurid, *Scaloposaurus hoffmanni* and a part of the skull of *Bauria cynops* have also been described.

2. It has been shown that in *I. intermedius* the fenestra ovalis is completely surrounded by the periotic and that the basisphenoid-parasphenoid complex and the basioccipital do not form part of the ventral border of this foramen as in most other therapsid suborders.

3. The skull which was serially ground and reconstructed in wax, shows that the skull of its form is made up of two segments, an occipital and maxillary. The points of articulation between the two segments have been described. Movement or "kinetism" can apparently take place between the two segments. The type of kinetism found in this form probably acts as a shock-absorber when an exceptionally hard bite is taken. Other than Versluys's findings that the pelycosaurs probably had ancestors with kinetic skulls, it has always been assumed in the literature that the Synapsida had akinetic skulls without exception. Except that the tabular forms part of the occipital segment and not the maxillary, the kinetism found in *I. intermedius* is identical to the metakinetic skulls of some of the "diapsid" reptiles and their derivatives. Evidence was given to show that both the skulls of *Scaloposaurus hoffmanni* and *Bauria cynops* are probably also kinetic. It was concluded that it it may be possible to correlate many of the differences in the skull structure of advanced therapsids and mammals with a loss of kinetism.

4. Watson's theory that the scaloposaurids represent a series of evolutionary stages between the therocephalians on the one hand and the bauriamorphs on the other has been expanded to include all the known scaloposaurids, most of which were unknown when Watson's paper appeared in 1931. The scaloposaurids have been grouped into four evolutionary stages. This grouping does not imply a close relationship between forms placed in the same group and although artificial, it has been attempted because practically nothing is known of the exact horizon from which the different scaloposaurids came and parallel evolution is probably present to a high degree in this family.

5. In all the forms studied in this paper the paroccipital process terminates in a clear mastoid process, articulating with the squamosal, and a quadrate process, articulating with the quadrate. A disinct quadratojugal was found to be present in *Bauria cynops*. A detailed description of the quadrate and quadratojugal and their relationship to the squamosal in this form has been given. It was concluded that there are no known facts to preclude the theory that the bauriamorphs may be derived from the scaloposaurids. The great diversity in skull structure within the bauriamorphs is probably accounted for by the fact that they were derived from more than one scaloposaurid. It has been shown that the occipital condyle of *B. cynops* does not consist of a single articulatory facet formed almost exclusively by the basioccipital, but rather that there are three separate condyles. The two exoccipital condyles are large and distinct. The basioccipital forms a small but distinct condyle an-

terior to the two exoccipital condyles. It was concluded that the withdrawal of the basioccipital from the occipital condyle was iniated in the early scaloposaurids and is practically completed in the later form, *B. cynops*.

6. It has been shown that in the maxilla of *Scaloposaurus hoffmanni* there is an alternate or "distichic" replacement of the teeth. The only other Synapsida that have been described as having distichic replacement of the maxillary teeth are the pelycosaurs and the cynodonts, but this feature may well prove to be universal in all synapsids without gomphodont dentitions.

## ACKNOWLEDGEMENTS

I am seriously indebted to the Bernard Price Institute for their wholehearted co-operation, to Mr. S. H. Rubidge for the loan of valuable material and to Mr. F. R. Parrington for his keen interest, extremely valuable criticism and free use of unpublished information.

## ADDENDUM

Since this paper went to the press the antero-ventral and antero-dorsal processes of the periotic described on page 166 have been reconsidered. In fig. 6A the pila antotica is shown as a small dorsally directed process on the antero-dorsal margin of the antero-ventral process. The high and long antero-ventral process forms a true wall to the brain case and is situated far in advance of the dorsum sellae and the facial foramen. The cavum epiptericum is situated between this process and the epipterygoid. In view of these relationships it would not be unreasonable to consider the entire antero-ventral process as an ossification of the pila antotica, viz. a pleurosphenoid. A prefacial commissure forms an anterior border to the facial foramen and stretches from the postero-dorsal corner of the pleurosphenoid to the otic capsule. The original connection between the pila antotica and the planum supraseptale (ossified as the orbitosphenoid) is not ossified.

The antero-dorsal process could reasonably be considered as an ossified part of the taenia marginalis. The incisura prootica is consequently delimited by the taenia marginalis dorsally, by the otic capsule and prefacial commissure posteriorly and the pila antotica ventrally. A similar arrangement is found in several modern reptiles.

## VIII LIST OF ABBREVIATIONS

A.D.P. Anterior dorsal process of the periotic.
ALI. Alisphenoid.
ANG. Angular.
ANT. W.P.P. Anterior wall of the paroccipital process.
A.R. Ascending ramus of the epipterygoid.
ART. Articular.
A.V.P. Anterior ventral process of the periotic.
BO. Basioccipital.
BO. CO. Basioccipital condyle.
BP. PROC. Basipterygoid process.
BS. Basisphenoid.
BS-PS. Basisphenoid-parasphenoid complex.
BS. TUB. Basisphenoid tubera.
CAV. EPI. Cavum epiptericum.
COR. Coronoid.
COR. PROC. Coronoid process.
DOR. SEL. Dorsum sellae.
EPI. Epipterygoid.
EP. SW. Portion of the epipterygoid forming a side wall to the brain case.

EX. CO. Exoccipital condyle.
EX. OCC. Exoccipital.
EX. ST. PROC. Extra stapedial process.
F. Frontal.
F. EDG. Free edge of the basipterygoid process.
F.O. Fenestra ovalis.
GR. Groove.
H.S. PA. Horizontal shelf of the prearticular.
I.C. Internal carotid foramina.
I. CHO. Internal choanae.
I. MAX. TO. First maxillary tooth.
INT. VAC. Interpterygoid vacuity.
INC. PRO. Incisura prootica.
INT. PAR. Interparietal.
J. Jugal.
JC. Jugular canal.
LAC. Lacrimal.
LAC. FOR. Lacrimal foramen.
L.O.P.F. Lateral opening to the pituitary fossa.
LO. RG. Longitudinal ridge.
MAST. PROC. Mastoid process of the paroccipital.
MAX. Maxilla.
MAX. PL. Maxillary plates.
M.F.Q. Medial face of the quadrate.
M.P. SQ. Mastoid process of the squamosal.
N. Nasal.
OS.: Orbitosphenoid.
P. Parietal.
PAL. Palatine.
PAR. EXT. Extension of the parietal.
PF. Prefrontal.
PIL. ANT. Pila antotica.
PIN. Pineal foramen.
PIT. FOS. Pituitary fossa.
PO. Postorbital.
POSTEN. O. Postdentary ossifications.
POST. FOSS. Post-temporal fossa.
P.P.E. Pterygoid process of the epipterygoid.
PR. SP. Presphenoid.
PRE. ART. Prearticular.
PRE. MAX. Premaxilla.
PRO. Prootic.
PS. Parasphenoid.
P. SQ. Pocket in the squamosal for the quadrate.
PTER. Pterygoid.
PT. PROC. Petrygoid process of the quadrate.
QJ. Quadratojugal.
QJ-Q. F. Quadratojugal-quadrate foramen.
Q.P.E. Quadrate process of the epipterygoid.
Q.R.P. Quadrate ramus of the pterygoid.
QUAD. Quadrate.
QUAD. PROC. Quadrate process of the paroccipital.
SCL. PL. Sclerotic plates.
SEP. MAX. Septomaxillary.
SPL. Spenial.

SQ. Squamosal.
SQ. PROC. 1, 2 and 3. First, second and third processes of the squamosal.
S. QJ. Splint of the quadratojugal.
ST. Stapes.
ST. PROC. Stapedial process.
STR. Narrow strip of bone forming the ventral border to the fenestra ovalis.
SUP. OCC. Supraoccipital.
SUR. ANG. Surangular.
S.V. Suborbital vacuity.
TAB. Tabular.
TRAV. Transversum.
T-S.S. Tabular-squamosal split.
V. Vomer.
V. 11 & 111. Notch in the epipterygoid for the maxillary and mandibular branches of V.
VII. Foramen for the seventh cranial nerve.
X. Jugular canal.
XII. Foramen for the hypoglossal nerve.

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