

**A COMPARATIVE STUDY OF THE
MORPHOLOGY OF THE BRAINCASE
AND ASSOCIATED STRUCTURES
OF EARLY THEROCEPHALIA
(AMNIOTA:THERAPSIDA)**

by

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DECLARATION

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in part been submitted to any university for a degree.

20/02/95

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Date

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ABSTRACT

The early Therocephalia lies at the base of the line of mammal-like reptiles which eventually gave rise to mammals. The phylogenetic position of this taxon is therefore of great value in establishing mammalian ancestry and the description of the braincase forms a vital part of this research. However, a valid description of the early therocephalian braincase is still lacking. The aim of this study is to describe the braincase of the early Therocephalia in an effort to fill this hiatus and provide additional morphological information which may be utilized in future phylogenetical analysis.

The primary study is based on serial sections of *Glanosuchus macrops*. This study was aided by reconstructions produced firstly, by means of two computer programs, secondly Pusey's reconstruction techniques and thirdly, building a wax model. These techniques, except for the grinding of the fossil, constitute the practical part of this study.

The constituent bones of the braincase are individually described, with emphasis on the internal structure and foramina. The internal structure of the braincase is then discussed completely, especially the structure of the inner ear, and compared to other relevant therapsid groups. A postulate concerning the shape of the early therocephalian brain, based on a cranial cast derived from the serial sections is presented. Possible activity rates and metabolic tempo are deduced from the proposed structure of the brain.

Keywords: Early therocephalian, braincase, inner ear, brain reconstruction.

OPSOMMING

Die vroeë Therocephalia lê aan die basis van die lyn van soogdieragtige-reptiele wat oorsprong gegee het aan die soogdiere. Die filogenetiese posisie van hierdie takson is dus van groot belang in die bepaling van die voorouers van soogdiere. Die beskrywing van die breinkas vorm 'n noodsaaklike onderafdeling van hierdie navorsing. Desondanks die belang van hierdie taxon is 'n beskrywing van die breinkas van die vroeë Therocephalia nog steeds afwesig. Die doel van hierdie studie is dus om die breinkas van die vroeë Therocephalia te beskryf in 'n poging om hierdie gaping te vul en addisionele morfologiese data te voorsien wat in toekomstige filogenetiese analises gebruik kan word.

Die primêre gedeelte van hierdie studie is gebaseer op serie snitte van *Glanosuchus macrops*. Aan die hand van hierdie snitte, is die breinkas met behulp van verskeie rekonstruksietegnieke, naamlik rekenaarpakette, Pusey se grafiese rekonstruksietegniek en 'n wasmodel gerekonstrueer. Al hierdie tegnieke, behalwe die slyp van die snitte, behels die praktiese gedeelte van hierdie studie. Met behulp van hierdie rekonstruksies is 'n gedetailleerde studie van die breinkas gemaak.

Die bene van die breinkas word individueel bespreek met die klem op interne struktuur en foramina. Die interne struktuur van die breinkas word volledig bespreek met spesiale verwysing na die strukture van die binne oor en vergelyk met ander groepe binne die Therapsida. Die vorm van die brein van die vroeë Therocephalia word gepostuleer op grond van 'n afgietsel van die breinholte gebaseer op die snitte van die breinkas. Verdere postulate behels afleidings rakende die aktiwiteitstempo en metabolisme.

Slutelwoorde: Vroeë therocephalieër, breinkas, binneoor, breinrekonstruksie.

CHAPTER 1

INTRODUCTION

Within the therapsids, the Therocephalia are of great phylogenetical importance because they are situated at the base of the evolutionary line that gave rise to mammals. The origin of mammals via the therocephalians and cynodonts is now well established and generally accepted (Hopson and Crompton 1969, Hopson 1969, Kemp 1982, Hopson and Barghusen 1986). See Fig. 28.

As early therocephalians lie at the base of the Therocephalia, the skull anatomy of this taxon can form the basis for comparative cranial studies of mammal-like reptiles approaching the mammalian threshold, a fact already recognized by Olson (1944). He (Olson 1944) described and discussed the morphology of various serially sectioned therapsid skulls. His description of the internal aspect in the early Therocephalia was largely based on a specimen designated as "Therocephalian B". Owing to the lack of well-preserved, serially sectioned skulls this description became the standard for the early Therocephalia. Subsequently it was discovered by Van den Heever and Hopson (1982) that "Therocephalian B" was misidentified and that the specimen was in actual fact a badly weathered gorgonopsian. This means that a detailed description of the internal structure of the braincase in the early Therocephalia is still lacking.

As serial sectioning is extremely time consuming, and effectively destroys the specimen, only a small number of therapsid skulls have been prepared in this manner. Consequently, comparisons between the inner braincase of early therocephalians and other therapsids are hampered by the lack of sufficient comparative material. In addition, published information on sectioned therapsid skulls available for comparative purposes often lacks the detailed description necessary for a study of this kind.

A number of dicynodont skulls have been serially sectioned and this group is reasonably well-documented, more so than any other therapsid taxon. The first therapsid sectioned serially was a dicynodont (Sollas and Sollas 1914). A possible

reason for the larger number of sectioned dicynodonts is that these fossils are relatively abundant and are more readily sacrificed for sectioning.

Studies based on sectioned dicynodont taxa include *Dicynodon* (Sollas and Sollas 1914, Agnew 1958), unidentified dicynodonts (Olson 1944), *Lystrosaurus* (Cluver 1971) and *Emydops* (Fourie 1991). Studies based on other therapsid groups include various therocephalians (Broom 1936), *Cynariops* (Olson 1938a), an unidentified therocephalian (Olson 1938b), various therapsids (Olson 1944), *Ictidosuchops* (Crompton 1955), *Scalopocynodon* (Brink 1960), *Thrinaxodon* (Fourie 1974), *Gorgonops* (Sigogneau 1974), cynodonts *Massetognathus*, *Probelesodon* (Quiroga 1979) and *Moschorhinus* (Durand 1991)

In these studies, the inner ear is particularly well-described from the sectioned therapsids, and some of these descriptions have been compared to the inner ear of the early Therocephalia.

The main objective of this project therefore is to describe the braincase of a correctly identified early therocephalian using a serially sectioned skull. The intention is to concentrate on the internal anatomy of the braincase, as the external anatomy has been described (Van den Heever 1987). In addition, this study also includes a description of the internal braincase structures, which are compared with those known in therapsid taxa.

A further objective is to deduce the shape of the brain in the early Therocephalia, by studying the cranial cavity of the sectioned specimen together with the complete acid-prepared braincase of *Ptomalestes avidus* SAM 11942. This information is then compared with mammalian and reptilian brains in an attempt to determine whether the brain structure holds relevant information concerning the lifestyle and activity levels of the early Therocephalia.

In reptiles, the brain is much smaller than the cranial cavity, and not a great deal of detail of the brain is present on the medial walls of the braincase. However, in mammals, the brain occupies most of the cranial cavity, and detail from the brain is evident on the medial walls. It appears that the brain of the early therocephalians occupied much of the posterior part of the braincase cavity. The reconstructions of the cranial cavity can reveal a great deal of detail.

CHAPTER 2

MATERIALS AND METHODS

The description of the braincase is based on a serially sectioned skull and lower jaw as well as several mechanically prepared specimens.

2.1 The Sectioned Specimen

The sectioned skull, SAM K238a, is small, approximately one hundred and twelve millimeters long (Figs 1A, B, C, D, E, F) and was identified as an early therocephalian prior to sectioning. Reconstruction of the skull sections confirmed this identification. It displays a sloping mentum, separate lower jaw rami, a sharp angle in the dentary below the coronoid process, suborbital fenestrae and a narrow intertemporal region, all characteristic features of the early Therocephalia.

The specific name of the specimen was later confirmed by reconstructing the teeth in the premaxillary and maxillary using the Pusey graphic method. Six upper incisors indicate that the specimen is *Glanosuchus macrops* (Van den Heever 1987).

The skull is badly weathered on the right side (Fig. 2B), but the left side is well-preserved (Fig. 2A). The lateral walls of the braincase suffered reasonable damage, with complete loss of the epipterygoids, the processes of the prootics, the squamosal flanges and the quadrate processes of the opisthotic. However, the internal braincase anatomy is complete, suffering only a little distortion (Fig. 5).

The skull was serially sectioned from snout to occiput by grinding away the fossil at 200 micron (0.05mm) intervals. Nitrocellulose peels were made of each section, in much the same manner used by Olson (1944), Sigogneau (1974) and Fourie (1974). The number of peels totalled five-hundred-and-eighty for the entire skull, and only one-hundred for the braincase.

The peels were then redrawn to a 1:5 scale using an epidiascope. The drawings of the sections were used to recreate three-dimensional reconstructions of the complete skull. Three methods of reconstruction were used, namely that of Pusey (1939), computer reconstruction and wax model reconstruction.

2.2 Reconstruction Methods

2.2.1 Pusey Reconstruction Method

The Pusey Graphic and Contour reconstruction method was applied to make contour drawings of the anterior and posterior views, and graphic drawings of the dorsal, ventral, sagittal and lateral views. A description of this method is given by Pusey (1939). It is important to note that restoration was done to the drawings where it was felt necessary.

The distance plotted between points was calculated using Pusey's equation, listed in Appendix A.

2.2.2 Computer Reconstruction

Two different computer packages were used to reconstruct the skull from the sections. The first, PC3D, is especially designed to recreate three-dimensional images from sectioned material. The reproduction of six images was attempted, namely anterior, posterior, dorsal, ventral, left and right lateral views. The programme proved extremely inadequate, and only the anterior view was successfully produced (Fig. 26A). The other reconstructions were ambiguous and did not provide any useful information. Further information regarding the package is supplied in Appendix B.

Additional reconstructions were produced using IDL, another reconstruction computer package used at the National Accelerator Centre at Faure in the Western Cape. The information of the sections drawn into PC3D with the tablet and stilette was adapted for this programme. However, it was found that the information was not accurate enough for the package to produce perfect reconstructions of the interior of the braincase. The information would have to be redrawn in, or scanned into the programme to obtain

better results. The reconstructions of the exterior of the skull were successful and of high quality (Fig. 26B). This package should be further investigated, since it has a definite function designed specifically for reconstructing sectioned material.

One disadvantage of the IDL package is that the commands are complicated to learn. But the means of rotating the image on the screen is quicker and more effective than PC3D.

2.2.3 Wax Model Reconstruction

The drawings produced from the sections were used to make wax plates each having a thickness of one millimeter, calculated from Pusey's equation (see Appendix A). The sections of the braincase used were numbers 428 through 528, a total of one hundred sections. The wax plates were then cut out with a scalpel, stacked and moulded together.

The braincase was reconstructed into four parts, each consisting of approximately twenty-five sections. This was to prevent the loss of any detail in the interior of the braincase, since the stacking of great numbers of plates tended to cover underlying detail. Secondly, the separate wax parts were easier to handle for studying and drawing, and could be instantly stacked to obtain the whole reconstructed braincase.

The second wax model produced, is a cast of the braincase cavity. The posterior part of this cast provides valuable detail of the postero-ventral portion of the brain. This points to the fact that this part of the brain filled the cranial cavity in therocephalians, resembling the condition in reptiles. The antero-dorsal portion of the endocast does not indicate detail and the anterior portion of the brain probably did not fill the cranial cavity.

These wax portions were then photographed and drawn, and used for description of detailed portions of the braincase. Of all the methods used for the reconstruction, this method proved to be the most effective in revealing fine detail.

2.3 List of Prepared Specimens

The prepared therocephalian specimens studied were obtained from the South African Museum in Cape Town, the Geological Survey in Pretoria and from the collection at the Department of Zoology at the University of Stellenbosch. They consist of the following:

Early Therocephalians:

Glanosuchus macrops GS M796

Lycosuchus keyseri GS C60

Lycosuchus vanderrieti GS M793

Lycosuchus vanderrieti US D173

Ptomalestes avidus SAM 11942

Later Therocephalians:

Unidentified whaitsiid specimen SAM K5512

CHAPTER 3

DESCRIPTION OF THE BRAINCASE BONES

This chapter forms the basis for the description of the braincase, as each braincase bone is individually described. The lateral surfaces of the bones are described but with lesser detail than the medial view. This is because the lateral view of the early therapsid braincase has been described in detail (Van den Heever 1987). The lateral and medial sides of the bones include detail of the presence of foramina, processes and ridges or fossae.

However, due to the lack of internal braincase descriptions of other therapsids, it is in most groups not possible to compare the medial surfaces of the bones with confidence.

3.1 Epipterygoid

3.1.1 Description

Since both epipterygoids are largely missing in the sectioned specimen leaving only the anterior basal part intact, it is necessary to describe the rest of the epipterygoid from prepared specimens.

In a few early therapsids in the Tapinocephalus zone, for instance *Scylacosaurus* and *Scymnosaurus*, the epipterygoid possesses a dorsal process that is still relatively narrow. In *Glanosuchus macrops* the epipterygoid is dumbbell-shaped, although not much widened (Fig. 20B). In the lycosuchid *Trochosaurus major* occurring in the same zone, the epipterygoid has developed into a large, broad plate that has constricted the trigeminal foramen. The epipterygoid has begun to resemble that of a cynodont, and the dorsal lamina has greatly expanded (Barry 1965 p413). This is in contrast to the epipterygoid of *Lycosuchus vanderrieti* US D173 which possesses a narrow dorsal process.

The epipterygoid of early therocephalians is not closely associated with the prootic as it is in later therocephalians, and is much broader than the epipterygoid found in gorgonopsians. In comparison with the more advanced therocephalians, this bone is the least antero-posteriorly widened, and consequently represents the most primitive condition of this structure amongst non-gorgonopsian theriodonts of South Africa (Van den Heever 1987 p172, Van den Heever and Hopson 1982 p425).

In lateral view, the epipterygoid is a convex bone, resembling an upside down T-shape. Its base stands on the quadrate process of the pterygoid and is parallel to the prootic. It consists of one dorsal process, and two basal processes, the antero-ventral process which faces anteriorly and the postero-ventral process posteriorly (Figs 12, 13, 14, 18).

These processes are referred to in a number of ways by various authors. Agnew (1958 p98) refers to the antero-ventral process in dicynodonts as the quadrate process, as does Barry (1965 p412) and Kemp (1979 p19). Cluver (1971) refers to the antero-ventral process as the pterygoid process in *Lystrosaurus*. Crompton (1955 p167) calls the antero-ventral process the pterygoid process and the postero-ventral process the quadrate process in *Ictidosuchops intermedius*.

The early therocephalian epipterygoid has sutural contacts with four bones. Firstly, it has a short suture with the anterior process of the supraoccipital, visible in *Glanosuchus macrops* GS M796. Anterior to this, the ventral process of the parietal contacts the dorsal lamina of the epipterygoid. Thirdly, a portion of the antero-ventral process is embedded in the anterior portion of the parabasisphenoid, where it also contacts the pterygoid. The Fourth suture is the contact of the ventral margin of the epipterygoid with the quadrate process of the pterygoid.

In *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942, the dorsal lamina appears only to rest against the parietal and the basal region appears to merely stand upon the quadrate process of the pterygoid. The sections of *Glanosuchus macrops* SAM K238a shows that the anterior end of the antero-ventral process of the epipterygoid is embedded into the parabasisphenoid.

The lateral side of the antero-ventral process extends upwards from the cavity in the quadrate process to eventually rest on top of the quadrate process. This occurs in an anterior-posterior direction. The medial side remains embedded in the quadrate process

up to the point where the dorsal process arises. The postero-ventral process is not present in the sections.

The dorsal process rises vertically upwards and slightly inwards. The dorsal tip expands antero-posteriorly to form the dorsal lamina which contacts the ventral margin of the parietal and the postero-dorsal margin of the supraoccipital. According to Mendrez (1972 p200, fig.10 p205) in the more advanced therocephalian *Regisaurus*, a minute apophysis is present at medium height on the posterior edge of the dorsal process. This structure possibly separated the second and third rami of the trigeminal nerve and is not present in the early Therocephalia. This apophysis developed in later therocephalians, and contact with the prootic lead to the formation of the trigeminal foramen seen in cynodonts.

In medial view, the anterior processes of the prootic are situated parallel to the medial surface of the epipterygoid, but do not contact it. The large cavity between these two bones is called the cavum epiptericum (Figs 13, 18).

Medially, the basal processes are concave. In *Glanosuchus macrops* GS M796, the postero-ventral process differs slightly from the antero-ventral process in that the medial surface is less concave. The antero-ventral process widens medially and forms a suture with the parabasisphenoid. The width of the antero-ventral process is gradually reduced, towards the narrow, concave postero-ventral process. The height of the dorsal edge of the postero-ventral process is more or less constant, unlike the antero-ventral process which originates anteriorly as a small point (section 380), gradually increasing in height in a posterior direction to finally expand upwards into the dorsal process. There is no indication of bosses or ledges on the medial side of the epipterygoid of *Ptomalestes avidus* SAM 11942 and *Glanosuchus macrops* GS M796.

Posteriorly, the antero-ventral process broadens (section 398). The lateral portion becoming rounded and overlying the quadrate process (section 400). The medial side of the antero-ventral process is a pointed wedge, embedded into the anterior portion of the parabasisphenoid, which forms a suture with the pterygoid. The pterygoid becomes reduced in size as it forms a suture with the parabasisphenoid. The sections indicate that the medial edge of the antero-ventral process of the epipterygoid fits into a v-shaped groove formed by two laterally-directed prongs of the parabasisphenoid (section 408-414).

The contact between the antero-ventral process of the epipterygoid and the parabasisphenoid remains constant for approximately ten sections (sections 400-410), until the quadrate process moves into a more lateral position away from the parabasisphenoid. At the position where the paired vidian canals are centered in the parabasisphenoid (section 415), the quadrate process of the pterygoid appears to consist of solid bone, not porous bone. The quadrate process resembles an inverted gutter, and shows on the sections as a semilunate or sickle-shaped sliver of bone. The lateral edge of the quadrate process is extended into a long, ventrally projecting spine. The width of the base of the quadrate process gradually decreases until the ventral side of the epipterygoid is wider than the process (section 415). The epipterygoid base protrudes beyond the quadrate process on the medial side. The dorsal process of the epipterygoid is developing at this point. A dorsally-facing lip is present on the dorso-lateral edge of the epipterygoid (section 415-421), a structure not present on the epipterygoid of *Glanosuchus macrops* GS M796. Only in whaitsiid therocephalians are ridges present on the lateral surface of the epipterygoid (Kemp 1972 p21), seen also in the whaitsiid SAM K5512 (Fig.17C).

The antero-ventral process of the epipterygoid has lost all contact with the parabasisphenoid in section 415, and an opening has developed between the parabasisphenoid and the quadrate process. The lateral side of the epipterygoid is no longer embedded in the quadrate process in this region and has begun to develop a concave shape. At the level of section 413, the medial edge of the antero-ventral process is still embedded in the quadrate process.

The dorsal and the dorso-lateral margin of the antero-ventral process has a very thickened outer bone layer, and the ventral margin of the epipterygoid base has also begun to develop a thickening of the outer bone layer. This layer serves to strengthen the bone. The ventral margin would possibly be reinforced by its contact with the quadrate process. At section 417, the dorsal margin of the antero-ventral process forms an overhanging medially-facing lip. This lip consists of a thickened outer bone layer, and for a series of seven sections (sections 417-423) the lip persists, then disappears. It is possible that this is similar to the ridges persistent in the whaitsiid epipterygoid, but *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 show no such features. The lateral edge of the antero-ventral process of the epipterygoid (section 421) develops into an almost S-shape, convex dorsally and concave ventrally. The medial

side has a widened concave shape, which posteriorly gradually reduces until almost vertical (section 433). The shape of the lateral edge remains more or less constant, the concave curve becoming larger and the convex curve becoming smaller.

At section 439, the antero-ventral process of the epipterygoid disappears, signifying the position at which the epipterygoid has broken off.

3.1.2 Comparative View

In dicynodonts, the epipterygoid is a long, narrow rod. Agnew (1958) and Cluver (1971) describe the distinguishable parts of the dicynodont epipterygoid as resembling the early therocephalian epipterygoid. The main differences being the absence of a postero-ventral process and the narrowness of the dorsal process.

Dorsally, the slightly broadened tip of the dorsal process contacts the inside margin of the ventro-lateral parietal flange in an interdigitating suture. The footplate or base is positioned parallel to the median plane of the braincase.

The base of the dicynodont epipterygoid is also situated on the lateral edge of the quadrate ramus of the pterygoid. The base is laterally compressed at the origin of the dorsal process, and makes medial contact with the parabasisphenoid complex.

The length of the antero-ventral process of the epipterygoid varies from very short to very long, depending on the genus. Posterior to the dorsal process the base is sharply truncated. In *Lystrosaurus*, the posterior edge has a groove running posteriorly along the quadrate ramus of the pterygoid towards the quadrate (Cluver 1971 p181).

According to Kemp (1972 p19), the epipterygoid of whaitsiid therocephalians is very similar to that of cynodonts. The whaitsiid epipterygoid is dorsally widened, more so than in early therocephalians, to form a broad, thin sheet lying between the pterygoid and the parietal. It is similarly positioned in the early Therocephalia. In lateral view, the anterior part of the epipterygoid is concave, smooth and featureless. The postero-ventral process of the epipterygoid runs towards the quadrate, but terminates well before reaching the quadrate. The posterior edge is sharp and irregular. Behind the anterior edge of the epipterygoid, the bone is curved in a complicated manner. The

upper part stands almost in a parasagittal plane except for a slight lateral flaring immediately below its contact with the parietal. The ventral part of the bone turns to run postero-laterally alongside the quadrate ramus of the pterygoid. At the same time, the medial surface curves slightly in a dorso-ventral direction (Kemp 1972 p19). This is visible in the whaitsiid SAM K5512 (Fig. 17C).

The most prominent feature of the epipterygoid is the large foramen which conducted the two branches of the trigeminal nerve. It is formed dorsally by a narrow posteriorly directed process from the posterior edge of the dorsal process below the epipterygoid-parietal suture, which meets a second dorsally directed process formed from the dorsal edge of the postero-ventral process of the epipterygoid. Although these two processes meet one another, they do not fuse. Together they meet the antero-dorsal process of the prootic. These two epipterygoid processes are absent in the early therocephalians, the dicynodonts and the gorgonopsians (Kemp 1972 fig.9 p20).

The dorsal posterior process has a sharp, slightly turned-out upper edge. This process lies well below the dorsal lamina and parietal suture. Above the posterior process is a second foramen bounded by the parietal and supraoccipital above, and the epipterygoid anteriorly and posteriorly (Kemp 1972 fig.9. p20). This is the venous foramen that has been discussed in several later therocephalians, i.e. *Moschorhinus* (Mendrez 1974a), *Ictidosuchops* (Crompton 1955) and cynodonts i.e. *Thrinaxodon* (Fourie 1974). See Sub-section 3.7.2.

The dorsal notch in early therocephalians is positioned similarly to the dorsal venous notch (Fig. 5). This notch, present between the prootic and the supraoccipital, is not formed by the epipterygoid as it is in later therocephalians. The dorsal notch functioned in the same way as the dorsal venous foramen in conducting blood vessels through the braincase wall. It appears that the dorsal venous notch found in early therocephalians and the dorsal venous foramen found in later therocephalians appear to be synonymous.

In whaitsiid therocephalians, the contact between the epipterygoid and the parietal extends from the postero-dorsal corner of the dorsal lamina forwards along a horizontal line, but the anterior part of the dorsal lamina appears not to have contacted the skull roof. Where the two bones do make contact, the resulting suture interdigitates.

Ventrally, the base of the whaitsiid epipterygoid is positioned next to the quadrate ramus of the pterygoid. The postero-ventral process of the epipterygoid overlaps the dorsal surface of the quadrate ramus of the pterygoid. Kemp (1972 p21) reasons that the connection between these two was ligamentous only, because they are separated in one of the specimens he used for his description. The whaitsiid SAM K5512 does not display this separation (Fig. 17C). In *Glanosuchus macrops* SAM K238a, the two bones are closely associated, and a separation is not evident. Furthermore, in *Glanosuchus macrops* SAM K238a, the postero-ventral process of the epipterygoid is absent, and therefore the connection cannot be closely studied.

More anteriorly, the quadrate ramus in whaitsiids becomes plate-like and horizontal. It retains a low vertical ridge along its lateral margin which is continuous with the ventral spine of the quadrate ramus. Anterior to the quadrate ramus, the epipterygoid remains in contact with the lateral margin of the pterygoid. It also sends a horizontal process medially over the dorsal surface of the pterygoid, adjacent to the basiptyergoid articulation (Kemp 1972 fig.10B p24). The anterior part of the horizontal process runs medially over the pterygoid towards the parasphenoid. A dorsal flange of the pterygoid arises alongside the processus cultriformis of the parasphenoid and veers laterally to enclose the epipterygoid in a slit (Kemp 1972 p21).

Medially, immediately above the inner opening of the trigeminal foramen in the whaitsiid therocephalian epipterygoid, is a sharp ridge of bone which curves downwards around the antero-dorsal margin of the foramen. It then turns to run anteriorly from the front of the foramen for a short distance before terminating. A small fossa is formed under the ridge anterior to the inner opening of the trigeminal foramen. This fossa possibly housed the semilunar ganglion of the fifth nerve, similar to that indicated by Cluver (1971 p167) in *Lystrosaurus*.

A second less prominent ridge runs antero-dorsally from the termination region of the first ridge, almost to the antero-dorsal limit of the epipterygoid. The medial surface of the epipterygoid is marked by a distinct boss in the central dorsal part of the bone. The antero-ventral process of the prootic in no way contacts the epipterygoid and is not involved in the epipterygoid-braincase relationship (Kemp 1972 fig.9B p20, p21).

No such features are described in the other groups, but the ridge described on the medial surface of the epipterygoid of *Glanosuchus macrops* SAM K238a (section 417)

could signify such a structure. However, the lack of ridges, fossae or bosses on the medial surface of *Glanosuchus macrops* GS M796 or *Ptomalestes avidus* SAM 11942 do not support this suggestion.

Mendrez (1974a p84, fig.11 p102) describes the epipterygoid of *Moschorhinus kitchingi* as being a bowtie-shaped bone, similar to whaitsiids. The dorsal lamina is broadened, especially in the posterior direction. The posterior side of the dorsal process shows an apophysis, posteriorly directed towards the antero-dorsal process of the prootic. Mendrez (1974a p84) refers to this structure as the posterior apophysis of the epipterygoid. It appears that although the apophysis contacts the antero-dorsal process of the prootic they are not fused, which is similar to the condition in whaitsiids.

The contact between the dorsal lamina and the antero-dorsal margin of the prootic, and the contact between the apophysis with the prootic results in a round foramen. Mendrez (1974a, fig.11. p102) refers to this foramen as the "foramen venieux". This feature is absent in early therocephalians, but present in whaitsiids. Durand (1991 p386, fig.16. P397) refers to this foramen as the posterior foramen of the epipterygoid.

The apophysis, which in *Regisaurus* (Mendrez 1972 fig.10 p205) is present as a small protuberance on the posterior margin, has developed in *Moschorhinus* (Mendrez 1974a p84) into a posterior process of the epipterygoid. This apophysis contacts the antero-ventral process of the prootic. Mendrez (1974 p84) refers to this posterior process as a supplementary process.

In *Moschorrhinus*, ventral to the antero-dorsal process and antero-ventral processes of the prootic and the posterior apophysis, is the opening for the trigeminal nerve. This foramen differs from the foramen in whaitsiids, in that the dorsal process is absent from the postero-dorsal process of the epipterygoid. The posterior apophysis and antero-dorsal process of the prootic meet in a suture and do not fuse. The ventral edge of the foramen is formed by the antero-ventral process of the prootic that passes medial to the epipterygoid (Mendrez 1974a fig.12 p103).

The base of the epipterygoid is well developed in *Moschorhinus*, with the antero-ventral process smaller than the postero-ventral process. The epipterygoid appears to overlap the quadrate ramus more on the lateral side than the medial side (Mendrez 1974a fig.11 p102).

Promoschorhynchus platyrhinus differs from *Moschorhinus* in that the epipterygoid is broader, and the posterior apophysis more ventrally located. The cavum epiptericum is wide in *Promoschorhynchus* and the postero-ventral process flares broadly (Mendrez 1974b p70). The general shape of the epipterygoid is otherwise similar to *Moschorhinus*.

Ictidosuchops intermedius is a later therocephalian serially sectioned and described by Crompton (1955). The dorsal process of the epipterygoid is slightly expanded (Crompton 1955 p167). The posterior portion of the dorsal lamina fits into a shallow depression in the antero-dorsal wall of the periotic. Crompton (1955) states that the epipterygoid forms "part of the true wall of the braincase" in contrast to Sigogneau-Russel (1989) and Mendrez (1972, 1974a, 1974b), who do not include the epipterygoid into the braincase.

The central ventral edge of the footplate overlaps the quadrate process of the pterygoid laterally. The antero-ventral process of the epipterygoid (also called the pterygoid process) is fairly slender, but at the anterior end forms a wide plate that lies on the quadrate process of the pterygoid. It contacts and contributes to the basiptyergoid articulation (Crompton 1955 fig.6 p164). A posterior apophysis above the postero-ventral process on the posterior edge of the dorsal process supports the trigeminal nerve (Crompton 1955 p167). Unfortunately Crompton (1955 fig.4A p157) does not indicate this feature in his illustrations of *Ictidosuchops*.

In *Thrinaxodon*, the contact zone of the epipterygoid and the prootic is rather broad in cross-section. The epipterygoid sends a vertical tongue into a deep groove in the prootic. In addition, above the anterior border of the trigeminal foramen, the medial surface of the epipterygoid has a raised area providing support for the antero-dorsal process of the prootic (Gow 1986 p138).

There is a similarity between the epipterygoid of whatsiids and cynodonts. This region is well known in *Thrinaxodon* (Parrington 1946, Fourie 1974). The epipterygoid is antero-posteriorly widened, more than whatsiids or *Moschorhinus*. The development of the epipterygoid is posteriorly extended, resulting in an interconnection between the anterior braincase bones. The epipterygoid contacts all surrounding bones, and forms

definite nerve foramina with processes that were absent in the early therocephalians, dicynodonts and gorgonopsians.

The lateral aspect of the epipterygoid in cynodonts shows the deeply concave anterior margin and the complex curvature. The postero-ventral process of the epipterygoid is postero-laterally orientated while the main portion remains in a parasagittal plane. The trigeminal foramen of the cynodont epipterygoid is formed by a connection between a posterior horizontal process of the epipterygoid and the antero-dorsal process of the prootic. The large foramen positioned below the parietal and supraoccipital, described above in several therocephalians, also occurs in *Thrinaxodon*. The foramen is situated between the parietal, epipterygoid and prootic bones.

The only feature of the *Thrinaxodon* epipterygoid not already discussed in earlier publications, according to Fourie (1974 p367), is the relationship between the tip of the antero-ventral process of the epipterygoid and the quadrate ramus of the pterygoid. The contact between the epipterygoid and pterygoid in *Thrinaxodon* (Fourie 1974 fig.22B p366) is similar to the condition discussed in the sectioned *Glanosuchus macrops* SAM K238a. The quadrate ramus of the pterygoid widens laterally and dorsally a short distance posterior to the division of the pterygoid body and the quadrate ramus. The antero-ventral tip of the epipterygoid rests in a groove in the quadrate ramus (Fourie 1974 p367). This part of the epipterygoid appears to closely resemble the same region in *Oligokyphus* (Kühne 1974 p55). The slight overlap of the frontal and epipterygoid is a feature also found in cynognathid skulls, and is also described in *Diarthrognathus* by Crompton (1958 p185, fig.3A p187).

In *Thrinaxodon* (Fourie 1974 p367), the postero-ventral portion of the lateral flange of the frontal anterior to the pineal foramen has elongated. The lower end of the frontal makes contact with the antero-dorsal margin of the epipterygoid. The frontal flange protrudes well below the parietal in this region. In early therocephalians, the frontals and the epipterygoids do not make contact. The sutural contact between the epipterygoid and the antero-dorsal process of the prootic in *Thrinaxodon* is relatively long and complicated, instead of the simple overlap in whatsiids.

The postero-ventral process of the epipterygoid of *Thrinaxodon* (Fourie 1974 p367) overlaps the quadrate process of the pterygoid laterally. More anteriorly, the epipterygoid projects a medially directed horizontal process over the pterygoid. This

process is clasped in a slit in the pterygoid, similar to the situation found in whaitsiids. The horizontal process of the epipterygoid posteriorly contacts the basiptyergoid process of the basisphenoid.

The antero-ventral process of the prootic does not contact the epipterygoid in *Thrinaxodon*, as it is situated medially to the epipterygoid as in whaitsiids (Kemp 1972 p21). A further similarity between cynodonts and whaitsiids is a small recess which is present between the epipterygoid and the prootic in the antero-dorsal region of the trigeminal foramen. This recess corresponds to the recess in whaitsiids that presumably housed the semilunar ganglion (Kemp 1972 p22). The ridges noted on the medial surface of the whaitsiid epipterygoid are not apparent in *Thrinaxodon*.

The cynodont *Procynosuchus* (Kemp 1979 p110) is less well known than *Thrinaxodon*. The epipterygoid possesses the characteristic cynodont form, with the broad dorsal process contacting the frontal and parietal in a fine interdigitating suture dorsally. A dorsal venous foramen between the parietal, epipterygoid and supraoccipital is absent, unlike the condition found in later theriocephalians and *Thrinaxodon*. A short ridge is positioned on the inner surface of the epipterygoid immediately in front of the antero-dorsal process. More posteriorly, the base of the epipterygoid in *Procynosuchus* is situated against the quadrate ramus of the pterygoid, and sends a short flange a short distance down the medial face of the pterygoid (Kemp 1979 p110). The posterior ramus of the epipterygoid ends abruptly at the level of the posterior edge of the trigeminal foramen. The quadrate ramus of the pterygoid continues posteriorly towards the quadrate.

Brink (1960 p145, p146) refers to the epipterygoid of *Scalopocynodon gracilis* (renamed as *Procynosuchus* by Hopson and Kitching, 1972) as the alisphenoid. He states that it is cynodont-like in that it is broadly expanded, but theriocephalian-like "in their feeble overlap of the prootics". The antero-ventral processes are long and broad. Brink (1960 fig.34B p131) furthermore notes that the antero-ventral processes of the epipterygoids swing inward underneath the rostrum. They barely touch the basisphenoid, and their terminal margins reach towards the interpterygoid fossa. In fact, the ventral margins of the antero-ventral processes conform to the dorsal margins of the quadrate process of the pterygoid, but nowhere is there contact between the two epipterygoids (Brink 1960 p145).

The epipterygoid of *Procynosuchus* forms the anterior margin of the trigeminal foramen. Immediately in front of this foramen is a second much smaller foramen which conducted the maxillary branch of the trigeminal nerve (Kemp 1979 p110). This maxillary foramen is entirely surrounded by the epipterygoid.

In well-known gorgonopsians, for example *Tangagorgon (Lycaenops?) tenuirostris* and *Arctognathus breviceps*, the dorsal process of the epipterygoid is narrow, more so than in early theropcephalians (Boonstra 1938 p180). The footplate of the gorgonopsian epipterygoid is well-developed and wide (Van den Heever and Hopson 1982 p425). The dorsal lamina is slightly widened and sits against the parietal.

The base of the gorgonopsian epipterygoid has an antero-ventral and a postero-ventral process. The antero-ventral process of the epipterygoid is long and tapered, and positioned on the quadrate ramus of the pterygoid. The postero-ventral process of the epipterygoid is reduced, and ends a distance anterior to the quadrate (Barry 1965 p413, Kemp 1969 p30). Kemp (1969 p37) suggested that the footplate of the epipterygoid was connected to the quadrate ramus of the pterygoid by ligaments, based on the manner of separation in some specimens. He (Kemp 1972 p21) explained the separation of the epipterygoid and the quadrate process in whatsiids in a similar way to the whatsiid specimens.

Olson (1938a, 1944) provided information on the relationship between the quadrate process and the epipterygoid in gorgonopsians. In Olson's (1938a) sections of the Gorgonopsia, the epipterygoid appears antero-dorsally to the quadrate as a thin sliver of bone. More posteriorly, a medial process from this splint contacts the basiptyergoid process of the basisphenoid. The pterygoid does not contribute to the basicranial articulation in gorgonopsians (Olson 1938a p171). The palate bone and the basisphenoid articulate anterior to the basiptyergoid process, and it is here that the epipterygoid has a large, rounded medial boss which fits into a cavity in the basisphenoid. Anterior to this pocket, the quadrate process of the pterygoid and epipterygoid swing away from the basisphenoid. Anterior to the insertion of the epipterygoid into the pocket in the basisphenoid, the pterygoid sends a process dorsally and medially, both which eventually engulf the epipterygoid completely (Olson 1938a p171).

3.2 Prootic

3.2.1 Description

The prootic makes the most important contribution towards the medial braincase wall. Reconstruction of *Glanosuchus macrops* SAM K238a indicates that the most delicate and complicated braincase structures are situated on the medial walls of the prootic and opisthotic. These two bones form the main part of the bony inner ear structures (see Section 4.3).

Olson (1944 p11, 1938a p145, 1938b p76) refers to the prootic and opisthotic as the periotic in various therapsids, because no "evidence of a suture" was found between them. This implies that the two bones have fused. Romer (1956 p181, p182), like Olson, claims that "in therapsids, the prootic and opisthotic tend to fuse into a single structure comparable to the mammalian periotic". Other authors referring to the periotic, are Crompton (1955 p165) for *Ictidosuchus intermedius* and Agnew (1958 p100) for *Dicynodon gracilis*. However, the following authors refer to a prootic and opisthotic, namely Mendrez (1972) for *Regisaurus*, (1974a) for *Moschorhinus* and (1974b) for *Promoschorhynchus*, Van den Heever (1987) for early therocephalians and Kemp (1972) for whatsiid therocephalians.

According to Olson (1944 p13), the fusion of the "periotic" with the surrounding bones is less common in therocephalians than in the other groups. He also claims that the supraoccipital is fused to the "periotic" posteriorly. This was not found in any of the early therocephalian specimens studied, and definite sutures separate the bones from each other. Furthermore, therapsids other than dicynodonts also show a tendency towards separate prootic and surrounding bones, for example *Regisaurus* (Mendrez 1972) and gorgonopsians (Kemp 1969).

A fact that the study of therocephalian specimens was able to clear, is the presence of cartilage in the prootic. It appears that the medial wall of the prootic consisted of a large amount of cartilage. The lateral wall is mainly bone. Kemp (1969 p65) indicated that cartilage makes up a portion of the prootic in gorgonopsians as well. A portion of the periotic of "Therocephalian B" (a gorgonopsian) may have been cartilaginous (Olson 1944 p14).

The prootic contacts the supraoccipital dorsally, the opisthotic postero-ventrally, the squamosal posteriorly, the parabasisphenoid antero-ventrally and the basioccipital ventrally. It forms the antero-dorsal rim of the fenestra ovalis. The prootic forms a quarter of the fenestra ovalis lip in *Glanosuchus macrops*. The prootic of the sectioned *Glanosuchops macrops* SAM K238a appears to make a greater contribution to the rim of the fenestra ovalis than in *Glanosuchus macrops* GS M796. This could be attributed to distortion of the skull (Fig. 5). The bones forming the fenestra ovalis are the prootic (antero-dorsally), the opisthotic (dorso-posteriorly), the basioccipital (postero-ventrally) and the parabasisphenoid (antero-ventrally).

In lateral view, the prootic of early therocephalians is very similar to that of the prootic of *Regisaurus* (Mendrez 1972 p204, fig.11 p207) (Fig. 20). It is a complex bone and consists of two anterior, one central and one posterior process, and two anteriorly directed notches. The postero-ventral process present in *Regisaurus* is not clear in *Glanosuchus macrops* SAM K238a and *Glanosuchus macrops* GS M796.

The anterior processes are broken off *Glanosuchus macrops* SAM K238a, and distortion is extensive. The antero-ventral process is most often damaged because of its narrow character, and therefore the exact length is difficult to establish. *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 show these processes well (Figs 18A,B). In *Glanosuchus macrops* GS M796, the antero-ventral process is equal in length to the vertical height of the epipterygoid (Fig. 18B). Crompton (1955 p180) assumed the antero-ventral process to be the ossified pila antotica, and the antero-dorsal process the ossified taenia marginalis.

The antero-dorsal process is much shorter and more slender than the antero-ventral process. In the undistorted braincase of *Ptomalestes avidus* SAM 11942, the antero-dorsal process is partially wedged between the epipterygoid and the supraoccipital (Van den Heever 1987 p124). The antero-ventral and antero-dorsal processes lie in an almost parasagittal plane. Posterior to the antero-dorsal process, the dorsal lamina is a broad plate which forms a suture with the dorsally positioned supraoccipital.

The anterior region of the prootic lies in close proximity to the epipterygoid and the anterior processes pass behind the epipterygoid. These two bones do not actually contact one another in early therocephalians, i.e. in *Glanosuchus macrops* GS M796. The cavum epiptericum is well-developed in the early Therocephalia.

The sturdy basal part of the prootic consists of a vertical plate, which extends from the parabasisphenoid anteriorly to the external foramina for the internal carotids posteriorly. The antero-ventral portion of the prootic immediately below the antero-ventral process has a medial projection which forms the dorso-lateral face of the dorsum sellae. The sellae turcica is situated immediately in front of the dorsum sellae and is formed by the parabasisphenoid. These two structures enclose the pituitary fossa (Figs 5, 13). The bases of the two medial projections are closely situated on the midline but do not contact one another, as is seen in *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 (Van den Heever 1987 p123) (Figs 12, 13). According to Olson (1938a p82), the prootics in therocephalians meet in the midline and form part of the dorsum sellae. Boonstra (1971 p34) claims that this is also the case in titanosuchids and tapinocephalids.

Near the base of the anterior processes is a foramen. This foramen is situated in the basal region of the prootic and was presumably for the exit of the facial nerve VII. Surrounding this foramen is a cup-shaped depression, presumed to be the position of the gasserian ganglion, as described by Mendrez (1972 fig.11 p207) for *Regisaurus*.

The antero-ventral process is separated from the antero-dorsal process by the incisura prootica which served as a pathway for a branch of the trigeminus nerve and the vena capitis lateralis (Olson 1944 P15). Positioned between the antero-dorsal process and the dorsal lamina is a dorsal notch. According to Watson (1913 p219) this notch was associated with the venous system of the cranium in *Diademodon*.

The posterior portion of the prootic bears the postero-dorsal process. The postero-ventral process of the prootic in *Regisaurus* (Mendrez 1972) is absent in *Glanosuchus macrops* SAM K238a. The postero-dorsal process contacts the intermediate process of the squamosal and the opisthotic. This process forms the antero-medial portion of the posttemporal fossa (fig.6). In *Glanosuchus macrops* SAM K238a, the postero-dorsal process is damaged and lacks the suture with the intermediate process of the squamosal. The suture between the supraoccipital and the postero-dorsal process is not damaged.

The prootic has an additional process, the central process, which meets the antero-ventral process of the squamosal. This resulting bar lies anterior to the posttemporal fenestra. This structure is damaged in *Glanosuchus macrops* SAM K238a, but is

evident in *Glanosuchus macrops* GS M796 (although compressed), and *Ptomalestes avidus* SAM 11942 (Figs 12. 13). In *Glanosuchus macrops* GS M796, the base of the central process is strengthened by two crests; one runs upwards along the centre of the antero-dorsal process, and the second runs up towards the middle of the dorsal notch in an S-shape (Fig. 20B).

An interesting feature found only in *Ptomalestes avidus* SAM 11942, is a minute anteriorly directed process positioned ventro-medially to the lower opening of the pterygo-paroccipital foramen. The dorsal surface of this structure appears concave and it may have supported neurovascular elements passing along the outer surface of the braincase (Van den Heever 1987 p167) (Fig. 14).

The medial side of the left prootic of *Glanosuchus macrops* SAM K238a is fairly undistorted and is used for the description of the medial view. A reconstruction of the undamaged left prootic shows a series of ledges and fossae on the medial surface. There are four fossae and four ledges. The ledges are positioned in a horizontal plane and protrude into the braincase cavity. According to Olson (1944 p27), the main function of these ledges is to support the inner ear canals and associated hearing structures. The fossae housed inner ear structures.

The first fossa (*pf1*) is positioned at the anterior end of the prootic, at the base of the antero-ventral process. It is formed by a smaller dorsal ledge and a larger antero-ventral ledge. The fossa is enclosed by walls on the dorsal and ventral sides and is quite deep. The antero-ventral ledge below the first fossa is the largest ledge and develops into the posterior ridge immediately behind the second fossa. It continues across the length of the prootic and terminates near the postero-dorsal process.

At the base of the antero-dorsal process of the prootic, postero-dorsally to the first fossa, is the foramen of nerve VII. On the posterior rim of this foramen is a second fossa. This fossa has a distinct margin except on the side adjoining the nerve opening.

The dorsal margin of the second fossa is formed by a ledge that is directed diagonally downward towards the posterior rim of the foramen. The ventral rim of the foramen is formed by a ledge which is directed diagonally upwards. The ventral and dorsal ledges meet and fuse at the posterior rim of the second fossa and form the posterior ledge.

The third fossa (*pf3*) originates below the ventral ledge as a shallow indentation and is situated below the posterior ledge. It deepens considerably as the ledge develops medially. It is the largest and longest fossa on the medial side of the prootic. The posterior ledge runs diagonally in an upward direction while increasing in width. It makes a diagonal turn downwards, then curves upwards. Above the dorsal rim of the this U-shaped turn in the ledge, lies the fourth fossa. This fossa is situated at the posterior extremity of the prootic in the postero-dorsal process. Its dorsal border is shorter than the ventral edge.

The development of the various ledges and fossae can be identified in the sections of *Glanosuchus macrops* SAM K238a. Section 455 indicates the anterior edge of the fenestra ovalis. The prootic forms the antero-dorsal margin (section 470). The first fossa is well-developed at the level of section 456, and the wall of the fossa becomes almost vertical with a horizontal antero-ventral ledge (*avlp*) perpendicular to it. In the sections the fossa it is almost L-shaped (section 458). This fossa is not very wide, and persists for a short distance over five sections (section 458-462).

At section 461, the foramen for the facial nerve VII lies at the base of the antero-ventral process of the prootic. At section 466, the basal region of the prootic broadens latero-medially, and one section further (section 467), the nerve foramen closes and the ventral ledge (*vlp*) is positioned centrally. The second fossa is positioned dorsally and the third fossa ventral to the ventral ledge.

The ventral ledge develops in a downward direction, until it forms a vertically elongated portion attached to the body of the prootic by a short horizontal suture (section 472). The second fossa becomes compressed until it forms an elongated slit. As the ventral ledge develops medially, the fossa terminates. This ventral ledge develops in a medial direction into the braincase cavity, with the fourth fossa (*pf4*) positioned dorsally and the third fossa (*pf3*) ventrally to it (sections 475-486).

At section 486, the ventral margin of the third fossa begins to elongate in a medial direction. The fossa remains small, and develops into a narrow slit (sections 487-490). Posteriorly it terminates as a small round sac-shaped fossa (section 491).

The fourth fossa increases in depth as the posterior ledge (*plp*) increases in length (sections 487-492). This fossa then proceeds to reduce in depth until it forms a shallow

cup-shaped hollow in the prootic (section 499). The fourth fossa forms the floccular fossa described by Olson (1944 fig.10 p27) and other authors in therapsids.

At section 493, there is a canal within the prootic formed from the fourth fossa. This canal appears to be an inner ear canal. However, this canal persists for four sections (sections 493-496), then opens onto the lateral surface of the prootic (section 497-500). Study of the wax model indicates that the lateral surface of the prootic has a shallow cup-shaped hollow (section 499), which implies that this bone has been damaged. This exposes the inner ear canal onto the lateral surface. In the undamaged condition, the canal would persist inside the prootic for a short distance before opening again onto the medial side of the prootic. Below this canal, a smaller cup-shaped indentation appears (section 494). It develops into a small, circular canal (section 495), which opens onto the medial surface again (section 496). This canal is also a semicircular canal.

At section 500, the prootic has reduced to a small bone that forms the roof of the large recess in the mastoid process of the opisthotic. This is the cochlear recess of the inner ear. At section 501, the prootic has reduced even further, and is situated between the supraoccipital medially and the squamosal laterally. The squamosal and prootic meet in an overlapping, diagonal suture. The posttemporal fenestra develops in the region of this suture. The fenestra is formed by three bones, namely the squamosal, the opisthotic and the prootic (section 503).

The posttemporal fenestra in the sectioned skull is U-shaped with a horizontal roof. Anteriorly, the posttemporal fenestra is formed medially by the prootic, dorsally by the internal process of the squamosal and laterally and ventrally by the mastoid process of the opisthotic. Posteriorly, the fenestra is formed by the squamosal dorsally, laterally and medially, and by the opisthotic posteriorly and medially. This portion of the foramen is missing from *Glanosuchus macrops* SAM K238a, as the skull is missing beyond section 528. The posttemporal fenestra of *Regisaurus* (Mendrez 1972 p206, fig.7 p201, fig.8 p203) is round, differing from *Glanosuchus macrops* SAM K238a. The anterior opening of the posttemporal fenestra in *Regisaurus* is formed by the internal process of the squamosal dorsally and laterally, the opisthotic ventrally, and the prootic medially.

It is not certain whether the shape of the fenestra in *Glanosuchus macrops* SAM K238a is due to the distortion of the skull. This cannot be verified in *Glanosuchus macrops* GS

M796 either, because the skull is laterally compressed closing up the fenestrae, thus obliterating the sutures.

3.2.2 Comparative View

In dicynodonts (Olson 1944 p13), the prootic makes contact with the supraoccipital, the exoccipital, the squamosal, the basioccipital and the parabasisphenoid. This is similar to the sutures present in therocephalians. As previously stated, some authors claim that the prootic and opisthotic are fused to form a periotic. This is the case in dicynodonts according to Olson (1944 p13) and Agnew (1958 p100). Cluver (1971 p162) indicates that a definite suture is present between the prootic and opisthotic in *Lystrosaurus*. Olson (1944 p13) states that fusion of the periotic to other surrounding bones and complete ossification are characteristic in dicynodonts. However, in one of the specimens of *Dicynodon grimbeeki*, Agnew (1958 p100) found what he believed to be a suture between the prootic and opisthotic.

In all of the diagrams produced by Olson (1944, for example fig.5 p12) for the sectioned dicynodonts none of the specimens have a complete antero-ventral process. The antero-dorsal process is absent from all Olson's (1944) specimens. Although Cluver (1971) and Olson (1944) do not refer to an antero-dorsal process of the prootic in other dicynodonts, Agnew (1958 p101) does record its presence in *Dicynodon*. The prootic of *Lystrosaurus* also lacks the antero-dorsal process of the prootic. Cluver (1971 p168) states that the prootics of *Lystrosaurus* do not meet in the midline of the braincase, a condition also applicable to the early therocephalians.

The medial wall of the prootic in *Lystrosaurus* does not possess a definite floccular fossa, but only a shallow depression in some specimens. Olson (1944 fig.5 p12) indicates that all but one dicynodont specimen has a well-developed floccular fossa.

The anterior portion of the prootic in whaitsiids is similar to both dicynodonts and early therocephalians (Kemp 1972 fig.9B p20). The anterior processes of the whaitsiid prootic consist of the antero-dorsal process and antero-ventral process. In medial view, the antero-ventral process has become reduced in length, and protrudes towards the medial side of the postero-ventral process of the epipterygoid. The whaitsiid prootic

differs from the early Therocephalia in the contact between the epipterygoid and the prootic.

A dorsally directed process from the dorsal edge of the postero-ventral process of the epipterygoid connects the posterior process of the epipterygoid and the antero-dorsal process of the prootic (Kemp 1972 fig.9B p20). These processes do not fuse, but merely form a suture.

The ventro-lateral part of the prootic of whaitsiids has a process similar to the early therocephalians. This is the central process (lateral process) (Kemp 1972 fig.9a p20, p27). The central process is postero-laterally directed. It contacts the antero-ventral process of the squamosal at the point where the quadrate process of the pterygoid makes contact with the antero-ventral process of the squamosal. The central process also contacts the quadrate process of the pterygoid.

The incisura prootica in the whaitsiid prootic is still present, but appears smaller than the notch in *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942. It lies between the antero-ventral process of the prootic and the contact between the three processes described above. The dorsal notch has become enclosed to form a foramen. This foramen is surrounded by the supraoccipital dorsally, the antero-dorsal process of the prootic ventrally and posteriorly, and the postero-dorsal process of the epipterygoid anteriorly. This foramen which is formed from the dorsal notch is called the dorsal venous foramen and is similar to that described for *Moschorhinus* (Durand 1991 p407 and Mendrez 1974a), for *Promoschorhynchus* (Mendrez 1974b fig.6 p76 and fig.7 p77) and for *Thrinaxodon* (Fourie 1974). This foramen is absent from *Procynosuchus*, gorgonopsians and dicynodonts.

The prootic of *Regisaurus* (Mendrez 1972 p203) is very similar to that of early therocephalians. It appears that the antero-dorsal process of the prootic is not as elongated as it is in *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11492. This process is broad, protrudes anteriorly and is situated near the antero-ventral process. The dorsal lamina is also broad, elongated and anteriorly forms a point. This differs from the straight lamina in early therocephalians. It contacts the supraoccipital dorsally in a long suture (Mendrez 1972 fig.11 p207).

The postero-dorsal process and postero-ventral process is well-developed. The former contacts the intermediate process of the squamosal. In *Regisaurus*, the prootic contributes to the antero-dorsal margin of the fenestra ovalis, as in early therocephalians.

The prootic and opisthotic of *Promoschorhynchus* (Mendrez 1974b p76) show the general therocephalian pattern. The basal region of the prootic, similar to the early therocephalians, contacts the parabasisphenoid and the basioccipital. It also forms the antero-dorsal edge of the fenestra ovalis. The antero-dorsal process of the prootic is strongly developed. The ventral and lateral faces of this process is separated by a sharp crest. The foramen for nerve VII is situated at the base of the antero-ventral process. The antero-dorsal process lies slightly lateral to the antero-ventral process, and does not form a sutural contact with the epipterygoid, unlike the condition found in *Moschorhinus* (Mendrez 1974a), which is described below.

The central process in *Promoschorhynchus* is long and contacts the prootic process of the squamosal (Mendrez 1974b fig.5 p75). The central process is traversed dorsally and ventrally by grooves, and forms the medial portion of the bar anterior to the pterygo-paroccipital foramen. The postero-ventral process and the central process are of equal length. In dorsal view, the suture between the opisthotic and the prootic is laterally directed through the anterior portion of the posttemporal fenestra and emerges anterior to the paroccipital process. In lateral view, the suture runs medially towards and ventrally onto the dorsal border of the fenestra ovalis (Mendrez 1974b fig.7 p77).

As in *Promoschorhinus*, the prootic and opisthotic of *Moschorhinus* (Mendrez 1974a) are separate bones. The prootic is a complex bone, with similar processes to that described for *Regisaurus* (Mendrez 1972). The antero-dorsal process is broad, and the antero-ventral process curves upward in a crescent shape similar to that of *Regisaurus*.

A definite crest is present on the lateral surface of the prootic of *Moschorhinus*, similar to the crest found in *Glanosuchus macrops* GS M796 and *Regisaurus*, extending from the antero-dorsal process to the central process. Durand (1991 p389) refers to it as the "central ridge" in *Moschorhinus*. Mendrez (1972 p205) calls it a 'delicate rising crest' in *Regisaurus*.

A definite ridge runs from the fenestra ovalis to the base of the antero-ventral process of the prootic. Durand (1991 p389) refers to it as the "ventral ridge", and Mendrez the "sharp crest" for *Regisaurus* (1972 p203) and *Promoschorhynchus* (1974b p76). These crests are not distinguishable in *Glanosuchus macrops* SAM K238a, but are evident in *Glanosuchus macrops* GS M796 (Fig. 20B).

In *Moschorhinus*, a shallow, horizontal groove traverses the antero-ventral process of the prootic anteriorly. Above this groove, a low ridge runs from the posterior border of the incisura prootica, and flares out to form two small anteriorly directed projections. There is a small notch between the ventral border of the antero-ventral process of the prootic and the braincase floor. The posterior border is formed by the anterior edge of the prootic basal region. The ventral edge is formed by the parabasisphenoid (Durand 1991 p392). It is similar to the notch described by Crompton (1955 p166) for *Ictidosuchops*. No such condition was noted in the early Therocephalia.

Crompton (1955 p165) describes the prootic and opisthotic of *Ictidosuchops* as the periotic, as Olson (1944) does. The periotic has sutural contact with all the bones surrounding it. Crompton (1955 fig.5A p164) states further that the fenestra ovalis is completely surrounded by the periotic in *Ictidosuchops*, and the basioccipital and parabasisphenoid do not contribute to the ventral border. This is contrary to the condition found in early therocephalians (own observation). In cynodonts, the periotic forms most of the border of the fenestra ovalis. Crompton (1955 p155) also notes that the footplate of the stapes is much smaller than the fenestra ovalis, implying that the diameter of the fenestra was reduced by cartilage.

The posterior processes present in *Ictidosuchops* are very similar to those of *Regisaurus*. The anterior processes of the periotic resemble those of cynodonts. The antero-ventral process is very broad and does not extend upwards, but rather in a horizontal plane. It is slightly longer than the antero-dorsal process. The foramen for nerve VII is situated at the base of the antero-ventral process. In ventral view, the antero-ventral process is roughly triangular with the apex situated dorsally (Crompton 1955 fig.4A p157).

The incisura prootica is wide and deep, and the epipterygoid covers it completely. The cavum epiptericum is very wide and the ganglion for nerve V was supposedly situated

here. There is a dorsal venous foramen situated between the supraoccipital and the dorsal lamina of the prootic (Crompton 1955 fig.4A p157).

Olson (1944 p16) describes a projection in cynodonts above the incisura prootica which is bordered by a forward projection of the prootic below the interparietal. Crompton (1955 p167) claims this projection is absent from *Ictidosuchops*.

The general shape of the prootic of *Thrinaxodon liorhinus* (Fourie 1974 fig.24A p368) varies from that of *Glanosuchus macrops* SAM K238a, but similar antero-dorsal and antero-ventral processes are present. The postero-dorsal process of the epipterygoid meets the anterior tip of the antero-dorsal process of the prootic in a serrated suture. This is a typical condition in cynodonts (Fourie 1974 p368).

In *Thrinaxodon*, the dorsal lamina of the prootic has enlarged in an anterior direction to contact most of the dorsal border of the epipterygoid. The antero-ventral process is very slender and extends anteriorly for a short distance. The antero-dorsal process is very short and is slightly broader than the antero-ventral process. The posterior processes mentioned for *Regisaurus* (Mendrez 1972) are not as well defined for *Thrinaxodon* (Fourie 1974 fig.24A p368).

The postero-dorsal process of the prootic appears to be a large posterior process. The postero-ventral process of the prootic is not clearly defined. The prootic forms a well-developed fenestra ovalis. The ventral contact with the opisthotic appears to be complicated, consisting of several facets (Fourie 1974 fig.24a p368), unlike any therocephalian compared in this study.

The incisura prootica is very wide and is well-developed in *Thrinaxodon*. Due to the expansion of the dorsal lamina, the dorsal notch has become reduced. Fourie (1974 p368) claims that the dorsal notch has become constricted by the lower margin of the parietal, forming the foramen for the vena capitis dorsalis.

The position of the foramen of nerve VII appears to be more posterior than the position in the early therocephalians, and is positioned close to the antero-dorsal lip of the fenestra ovalis.

In *Thrinaxodon* (Fourie 1974 p382), the intermediate process of the squamosal is not very large, but is directed downwards toward the quadrate process of the pterygoid. The lateral process of the prootic contacts the squamosal at this point, just in front of the inner wall of the pocket for the quadrate.

The anterior and dorsal sides of the prootic in *Procynosuchus* are similar to *Thrinaxodon*, but differ from that of therocephalians (Kemp 1979 fig.13 p102). The prootic and opisthotic of *Procynosuchus* are separate, not fused. The antero-ventral process of the prootic is very small and lies medially to the epipterygoid. The antero-dorsal process is very broad and enlarged, and contacts the postero-dorsal process of the epipterygoid in an almost vertical suture. This is contrary to the condition referred to by Brink (1960 fig.34 p131) in his description of *Procynosuchus*. He (Brink 1960) claims that the antero-dorsal process of the prootic overlies the epipterygoid but does not contact it.

In *Procynosuchus*, the antero-ventral process of the prootic appears very short and broad, curving upwards in such a way that the tip faces vertically upwards. The antero-dorsal process lies very close to the antero-ventral process and appears to contact its dorsal edge, nearest to the origin point on the body of the prootic (Brink 1960 fig.34 p131). The incisura prootica is present as a foramen (Kemp 1979 fig.16 p112), whilst the dorsal lamina contacts the parietal and the supraoccipital in a diagonal antero-posterior suture.

The central process (lateral process) of *Procynosuchus* is a broad flange at the base of the lateral surface of the prootic. This process curves around the body of the prootic in an almost horizontal position. The body of the prootic contacts the quadrate process of the pterygoid. The distal edge of the central process runs postero-laterally and meets a facet on the quadrate immediately above the contact between the pterygoid and quadrate bones (Kemp 1979 p110-111). A central process or lateral flange is common in cynodonts (Hopson and Crompton 1969 p44, fig.9 p44).

The incisura prootica appears very reduced in *Procynosuchus*. The dorsal lamina is very enlarged and extends far anteriorly, to terminate at a point level with the posterior edge of the antero-dorsal process. The antero-dorsal process is very small, and is present as a tiny vertical process. The dorsal lamina does not contact the ventral edge of the supraoccipital, but an elongated notch separates the two bones. There appears to

be a long narrow dorsal venous foramen between the prootic and the supraoccipital, but Brink (1960 fig.34 p131) does not expand upon this feature.

The medial surface of the prootic has a complicated set of ridges, not unlike the prootic of *Glanosuchus macrops* K238a. The medial surface of the dorsal lamina has a wide deep trough stretching antero-posteriorly (Brink 1960 p133). The inner margin has a prominent ridge forming the roof of the deep floccular fossa. This fossa is separated from the vestibule by a more prominent ridge. Below this ridge, the prootic forms the roof of the vestibule (Brink 1960 p133).

The outer surface of the prootic of *Procynosuchus* according to Brink (1960 fig.34 p131) does not appear to possess ridges. Distally, the prootic contacts the postero-dorsal process of the epipterygoid. More posteriorly, the lateral surface is covered by the tapering quadrate process which is sharply turned inward. More posteriorly and lower down, the prootic forms a long slender process contacting the distal end of the paroccipital process of the opisthotic. The fenestra ovalis of *Procynosuchus* is formed by bones very similar to those of early therocephalians (Brink 1960 fig.34 p131).

The prootic and opisthotic of gorgonopsians are separate. The antero-dorsal process of the prootic is narrow and appears better developed than in any other therapsid (Kemp 1969 p64). The antero-ventral process is broad at its base and tapers towards its point.

As described in *Regisaurus*, *Moschorhinus* and *Glanosuchus macrops*, the lateral surface of the prootic possesses a number of ridges. The anterior edge of the prootic and antero-dorsal process is slightly laterally deflected to form a sharp ridge. The posterior edge of the antero-dorsal process also has a definite ridge which runs postero-ventrally over the base of the prootic. The rest of the lateral surface of the prootic is rugose (Kemp 1969 fig.22A p67).

In gorgonopsians, complete foramina are present in the position of the anterior prootic notches found in the early therocephalians (Kemp 1969 fig.22A p67). The dorsal foramen (dorsal notch) is closed off anteriorly by a process of the supraoccipital, and posteriorly by the body of the supraoccipital. This anterior process on the supraoccipital has not been recorded before for any other therapsid (Kemp 1969 p64). It forms a small part of the lateral wall of the braincase and it is attached anteriorly to the prootic above the anterior prootic processes.

According to Kemp (1960), the anterior edge of the antero-ventral process of the prootic has a sulcus into which the side of a crystalline structure fits. He (Kemp 1969 p65) believes this structure to have been cartilaginous. The foramen for nerve VII lies posterior to the base of the antero-ventral process of the prootic, as in *Glanosuchus macrops* GS M796 and *Glanosuchus macrops* SAM K238a. There is no indication in the early therocephalians of the presence of cartilage in the anterior processes of the prootic.

3.3 Opisthotic

3.3.1 Description

The opisthotic is not fused to the prootic to form a periotic as suggested by various authors because distinct sutures are present between these bones. The opisthotic forms the postero-dorsal border of the fenestra ovalis. It contacts the basioccipital ventro-medially and the prootic anteriorly in a long, upward diagonal suture (Fig. 5). In posterior view, the opisthotic extends upwards to meet the supraoccipital and the exoccipital medially.

The bone consists of three main processes, namely the postero-dorsal process, the internal process and the paroccipital process. The postero-dorsal process arises near the lateral process of the exoccipital, and curves up and around the edge of the posttemporal fenestra. This process forms the medial and dorsal edge of the posttemporal fenestra. The internal process forms the medial edge and floor of the jugular foramen.

The paroccipital process is the largest of the processes. It forms the floor of the posttemporal fenestra and is medially connected to the prootic. The lateral extremity of this process is subdivided into two processes, namely an anterior quadrate process and a posterior mastoid process. The quadrate process is situated on the ventro-lateral edge of the paroccipital process. This process has largely broken off in the sectioned braincase, but is well-preserved in *Ptomalestes avidus* SAM 11942 (Figs 3C, 21). The other processes of the opisthotic are slightly damaged.

The mastoid process of the opisthotic contacts the mastoid process of the squamosal ventro-lateral to the posttemporal fenestra (Figs 11, 16). The mastoid process appears slightly larger than the quadrate process. In occipital view, it has an almost bowtie-shape with the lateral margin dorso-ventrally widened. Medially it forms a suture with the supraoccipital dorsally, the exoccipital medially and the basioccipital ventrally. In the sections of *Glanosuchus macrops* SAM K238a there are incomplete areas in the mastoid process (section 510). It is uncertain whether this is the result of unossified areas or damage to the fossil.

A deep triangular trough separates the mastoid process from the quadrate process. The mastoid and quadrate processes contact the medial surface of the quadrate and the squamosal (Fig. 3C). Section 498 shows the remaining portion of the quadrate process as a long, narrow ventrally directed structure separated from the body of the opisthotic by a deep slit. This slit widens and develops into the mastoid trough separating the mastoid and quadrate processes.

As described in Section 3.2, the anterior opening of the posttemporal fenestra is formed dorsally by the intermediate process of the squamosal, and laterally and ventrally by the anterior wall of the paroccipital process of the opisthotic and medially by the postero-dorsal process of the prootic. The medial edge is partly overlain by the prootic. The posterior opening of the posttemporal fenestra is surrounded dorso-medially by the squamosal, and dorsally, medially, posteriorly and ventrally by the postero-dorsal and mastoid processes of the opisthotic (sections 503-528). This differs slightly from the condition found in *Regisaurus* (Mendrez 1972 fig.8 p203, p204), where in posterior view, the squamosal forms the dorsal and lateral margins of the posttemporal fenestra.

The early therocephalians lack the paroccipital fossa present in later therocephalians, i.e. *Regisaurus* (Mendrez 1972 fig.8 p203). This fossa is situated between the anterior and posterior openings of the posttemporal fenestra in the dorsal surface of the paroccipital process of the opisthotic (Mendrez 1972 p206).

The opisthotic forms a deep fossa on the medial surface which housed the inner ear structures (Olson 1944 p26). The opisthotic of *Glanosuchus macrops* SAM K238a bears the vestibule on the medial surface. This is a deep fossa which

housed parts of the inner ear structures. It extends along the length of the opisthotic, and terminates within the paroccipital process as a rounded sac. The fenestra ovalis opens antero-laterally to the vestibule in *Glanosuchus macrops* SAM K238a (Fig. 5).

Within the antero-medial wall of the opisthotic are two fossae, originating immediately behind the antero-ventral margin of the fenestra ovalis. The first fossa (*of1*) is fairly deep and stretches across the anterior region of the opisthotic, along the upper ventral edge, formed by the lateral wall and a medial process of the opisthotic (section 486). The second fossa (*of2*) runs parallel to the first fossa (sections 487-491). It forms the jugular foramen (*juf*) (section 492).

In the sections of *Glanosuchus macrops* SAM K238a, the opisthotic originates anteriorly as a small, triangular bone (section 475) that presses closely against the basioccipital. The few sections following section 475 indicate that the opisthotic gradually increases in size to form a high lateral wall and a low medial process which contacts the basioccipital. The first fossa is situated between these walls (sections 483-486). The medial process forms the wall and floor of the first fossa. The lateral wall of the opisthotic is well-developed. The first fossa is situated lateral to the braincase cavity (section 489). The lateral wall is thicker than the medial process. The lateral wall meets the prootic dorsally in a horizontal suture. The upper edge of the opisthotic forms the base of the third fossa of the prootic. This fossa terminates a short distance behind the posterior ridge of the prootic. The third fossa of the prootic forms the anterior part of the vestibule. The vestibule is not completely closed off from the main braincase cavity. It opens into the braincase cavity via a wide opening referred to as the internal auditory meatus (Olson 1944 p31).

The medial process of the opisthotic develops anteriorly as a small protuberance on the medial margin of the first fossa (section 486). It develops from a short wide wall anteriorly, to a very long, slender process (section 492-496) posteriorly.

The first fossa (section 500) reduces to a small indentation, the base of which pinches off to form a small circular channel within the opisthotic (section 507). This channel opens onto the medial surface again at the same position one section

later (section 508) then persists in this form until it closes in section 513. This channel possibly housed the semicircular canal of the inner ear.

A groove (*pg*) leads from this fossa towards the jugular foramen. Olson (1938b p78) found a similar groove in the theropcephalians he sectioned. He suggests that the groove is the bony remnants of the perilymphatic duct of the inner ear. This duct opened into the jugular foramen as the fenestra rotunda. There is no indication of a fenestra rotunda in therapsids (Figs 6, 7).

Ventro-medial to the medial process is a second fossa, which is anteriorly very shallow and narrow (section 487-488). Posteriorly the fossa deepens. At the anterior end of the second fossa in *Glanosuchus macrops* SAM K238a, the suture is not situated at the centre of the fossa, but nearer the medial wall. The fossa consists of more opisthotic than basioccipital. Towards more posterior sections (section 489), the suture progressively extends medially towards the centre of the fossa and then towards the base of the medial process.

It therefore appears that the anterior portion of the second fossa is formed primarily by the opisthotic. More posteriorly, it is formed equally by the opisthotic and the basioccipital. Still more posteriorly, the fossa is formed primarily by the basioccipital. The exoccipital originates between the opisthotic and the basioccipital, and the opisthotic-exoccipital suture replaces the opisthotic-basioccipital suture (section 492).

Simultaneously, the opisthotic-exoccipital suture parts to form the anterior margin of the jugular foramen. The opisthotic forms the lateral wall of this foramen while the exoccipital forms the floor (sections 492-501). The wax model of *Glanosuchus macrops* SAM K238a indicates that the suture between the opisthotic and the exoccipital has loosened from section 502 onwards, elongating the jugular foramen into the foramen for cranial nerve XII. These two foramina should be separate, but the portion of bone between them is damaged.

The jugular foramen is large in proportion to the size of the sectioned *Glanosuchus macrops* skull, but it appears that this foramen was large in other therapsids as well. This could support Olson's (1938b) idea that the fenestra rotunda opened into the jugular foramen. The division of the jugular foramen and

the fenestra rotunda would possibly be cartilaginous, because no bony features remain in the jugular foramen. The conduction of the jugular vein and nerves IX, X and XI by this foramen requires a large aperture. This is discussed further in Sub-section 4.1.1.

Dorso-lateral to the first fossa is a third fossa (*of3*) which appears to be much wider than the first (sections 500-513). This shallow cup-shaped fossa projects postero-ventrally beyond and behind the lateral wall into the recess of the vestibule below the suture between the prootic and opisthotic and is the lateral pit (*lpit*) within the cochlear recess. This cavity, including the first and third fossae of the opisthotic, and the prootic with its fourth fossa, forms a large and well-developed cochlear recess which recedes into the paroccipital process (Figs 6, 7, 8). The cochlear recess has three pits and two grooves, forming a complicated structure. It is roughly circular in shape. This recess housed the hearing organ, the cochlea of the inner ear (Fig. 9). It is described further in Sub-section 4.3.6.

The anterior part of the roof of the cochlear recess is formed by the postero-dorsal process of the prootic. This process also forms the antero-medial edge of the posttemporal fossa (section 501). The medial wall of the recess is formed by a small, ventral kidney-shaped portion of the ventral process of the supraoccipital. The concave side of this process is directed into the recess. This medial wall separates the cochlear recess from the braincase cavity (Fig. 9). A small foramen opens between the braincase cavity and the anterior medial wall of the cochlear recess (section 503). It is situated between the suture of the prootic (postero-dorsal process) and the supraoccipital, and the small kidney-shaped portion of supraoccipital medial to the cochlear recess (Figs 5, 6, 7, 8, 9). This foramen is positioned in an antero-posterior direction (sections 500-502). It is possibly the internal auditory foramen for the vestibulo-cochlear nerve VIII. (See Sub-section 4.3.9.2). The supraoccipital process which forms the internal auditory foramen between the braincase and cochlear recess contacts the dorsal edge of the exoccipital over a short distance. The exoccipital contributes a small portion of the ventral side of the cochlear recess. These two bones, the supraoccipital and exoccipital, form a small vertical pit on the antero-ventral edge of the recess, which is termed the exoccipital pit (*epit*) (section 503). The base of the exoccipital pit is formed only by the exoccipital. Laterally it contacts the opisthotic and medially the supraoccipital (Fig. 9).

Situated laterally to the exoccipital pit against the dorso-medial side of the recess, is a second pit which lies in the hollow of the ventral process of the supraoccipital. The supraoccipital pit (*spit*) is a wide, shallow structure that extends downwards and posteriorly into the cochlear recess (section 500) (Fig. 9).

The third or lateral pit (*lpit*) lies against the lateral margin of the recess. It is very narrow and deep and the base extends laterally into the paroccipital process. It is formed by the third fossa of the opisthotic (section 500) (Fig. 9).

The fourth or posterior pit (*ppit*) is the deepest of all the structures in the opisthotic recess. It is cone-shaped, and is situated near to the dorsal side of the recess. The roof of the pit is formed by a small part of the postero-dorsal process of the prootic. The base of the recess is directed posteriorly into the paroccipital process and opens anteriorly into the cochlear recess (sections 515-522) (Fig. 9).

Two deep grooves are positioned within the cochlear recess. It is possible that the grooves are artificial and were created during the making of the wax model, as they have not been described in any other sectioned therapsid.

The first groove lies against the convex medial side of the supraoccipital pit. It is formed by the posterior margin of this pit (section 504). This dorso-medial groove curves upwards and around the cochlear recess and is situated posterior to the foramen between the cochlear recess and the braincase cavity (sections 505-506). The second groove lies dorsal to the exoccipital pit in the posterior ventral region of the recess. This is the ventro-lateral groove, which appears to curve around the outskirts of the cochlear recess and upwards towards the first groove (section 505). This gives these grooves the appearance of a slight spiralling pattern towards the centre of the recess (Fig. 9).

The cochlear recess is positioned lateral to the braincase cavity. It recedes diagonally upwards into the paroccipital process of the opisthotic (Figs 6, 7, 8). But *Glanosuchus macrops* SAM K238a is slightly distorted in this direction, and it is possible its position has been influenced to some extent by the distortion .

3.3.2 Comparative View

The paroccipital process of the opisthotic in *Dicynodon* is well-developed and is divided into a mastoid and quadrate process as in the early therocephalians. Agnew (1958 p101) states that the opisthotic in *Dicynodon* is fused to the prootic to form a periotic. Furthermore, the periotic is co-ossified to the bones surrounding it, and the sutures are not always definite.

Olson (1944 p13) claims that complete ossification of the periotic and fusion of the periotic to adjacent bones is characteristic of anomodonts. In one of the sectioned dicynodonts (Anomodont B), the periotic and supraoccipital are partly fused to the exoccipital. Olson (1944 p13) found complete ossification of the periotic and basioccipital in one specimen, Anomodont H, and partial fusion between the periotic and basisphenoid in Anomodonts F,G and H.

In *Lystrosaurus*, the opisthotic appears to constitute a very small part of the medial braincase wall (Cluver 1971 fig.9A p169). It forms the postero-dorsal edge of the fenestra ovalis, and the posterior portion of the inner otic capsule. The contribution of the opisthotic to the lateral wall of the braincase is very small, and it is situated between the supraoccipital, the exoccipital and the prootic. The mastoid and quadrate processes are, like *Dicynodon*, well-developed (Cluver 1971 fig.5 p166).

The opisthotic of *Regisaurus* strongly resembles that of early therocephalians (Mendrez 1972 fig.4 p197, fig.8 p203, fig.9 p204). In occipital view, it has three main processes, similar to *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 (Fig.11) and *Lycosuchus vanderrieti* GS M763 (Fig. 16). The postero-dorsal process forms the dorso-medial and ventral edge of the posttemporal fenestra. The internal process is situated below the jugular foramen and extends medially towards the foramen magnum. The paroccipital process is divided into an anterior quadrate process and a posterior mastoid process. The quadrate and mastoid processes are also very similar in shape to the early therocephalians (Mendrez 1972 p205, fig.9 p204). The opisthotic forms the postero-dorsal lip of the fenestra ovalis, which is characteristic of early therocephalians. It contacts the prootic anteriorly, the supraoccipital dorsally and the basioccipital ventrally.

In occipital view, the opisthotic of whatsiids appears similar to *Regisaurus* (Kemp 1972 fig.11B p30, fig.18a p32) but is relatively smaller (Fig.17D). The postero-dorsal process forms the medial and ventral edge of the posttemporal fenestra and a small portion of the dorso-medial edge, though not to the extent of the condition in *Regisaurus* (Mendrez 1972 fig.8 p203). The internal process extends medially to form a suture with the exoccipital, and also constitutes a small part of the floor of the jugular foramen.

In occipital view, the mastoid process of *Promoschorhynchus* varies in shape from the mastoid process of *Regisaurus* (Mendrez 1974b fig.4 p75). The lateral end of the mastoid process in *Promoschorhynchus* is overlapped by the mastoid process of the squamosal. This is unlike the condition in *Regisaurus* where the mastoid process of the squamosal is limited to the dorso-lateral rim of the mastoid process of the opisthotic (Mendrez 1972 fig.8 p203). The opisthotic of *Promoschorhynchus* forms the postero-dorsal margin of the fenestra ovalis, similar to *Glanosuchus macrops* SAM K238a, and forms the dorsal and dorso-medial edge of the posttemporal fenestra. Anteriorly it is covered completely by the intermediate process of the squamosal, in contrast to the situation in *Moschorhinus* (Mendrez 1974a) where this characteristic is absent.

The paroccipital process is well-developed in *Promoschorhynchus*, and like *Glanosuchus macrops* it has a deep and narrow mastoid trough. This trough separates the quadrate process from the mastoid process. In *Moschorhinus*, this trough is very broad and shallow. The mastoid process of *Promoschorhynchus* is slender, even though this area is damaged. The quadrate process is larger than the mastoid process. The difference between *Regisaurus* (Mendrez 1972 fig.8 p203), *Promoschorhynchus* (Mendrez 1974b fig.4 p75) and *Moschorhinus* (Mendrez 1974a fig.4 p84) is that the mastoid process in *Regisaurus* is much more robust than the specimens of the Moschorhinidae.

The opisthotic of *Promoschorhynchus* is marked antero-ventrally by a triangular groove into which the stapes probably fitted. A long and broad paroccipital fossa is present on the paroccipital process (Mendrez 1974b p74). The internal process is very similar to *Regisaurus* in shape and proportion.

The opisthotic of *Moschorhinus* (Mendrez 1974a p86) differs from *Promoschorhynchus* in occipital view, even more than in *Regisaurus*. The postero-dorsal process is very broad and elongated. It forms most of the dorsal margin of the posttemporal fenestra. The intermediate process of the squamosal covers much of the lateral end of the post-dorsal process of the opisthotic. The postero-dorsal process is visible in anterior view through the posttemporal fenestra.

The mastoid process of *Moschorhinus* is particularly large. It is situated posterior to a very large mastoid trough or paroccipital fossa. The fossa between the quadrate and mastoid process is broad and shallow. The mastoid process is marked by a ventral ridge originating approximately in the centre of the paroccipital process and terminating near the postero-lateral end of the mastoid process. This ridge adds to the robustness of the mastoid process, which is thickest near its distal end where the ventral ridge terminates. The shallow indentation which separates the two paroccipital processes is, according to Mendrez (1974a p86) and Durand (1991 p398), the roof of the middle ear ("toit de l'oreille moyenne").

The quadrate process of the opisthotic is narrower and longer than the mastoid process, and it becomes broader laterally, as does the mastoid process. The anterior portion of the paroccipital process contacts the postero-ventral process of the prootic medially. In occipital view, this combined structure forms the posterior wall of the pterygo-paroccipital foramen and the antero-dorsal border of the paroccipital fossa.

In *Moschorhinus*, the base of the central process of the prootic and the dorsal lip of the fenestra ovalis (also prootic) contact the antero-medial part of the opisthotic (Mendrez 1974a fig.6 p90). The internal process of the opisthotic is visible in ventral and occipital views. It expands ventro-medially to terminate as a boss between the jugular foramen and fenestra ovalis. This boss divides into a thin antero-lateral and a thicker postero-medial extension. The ventral projection forms the ventral lip of the jugular foramen and the anterior extension forms the postero-ventral part of the lip of the fenestra ovalis (Durand 1991 p399).

The sutures between the opisthotic, exoccipital and tabular are very similar to *Regisaurus*.

The paroccipital process of *Ictidosuchops* (Crompton 1955 fig.3 p156) is also divided into a definite mastoid and quadrate process. In occipital view, the opisthotic differs from *Moschorhinus* and *Regisaurus* because the mastoid process appears broader, and contact between the mastoid process of the squamosal and postero-dorsal edge of the mastoid process of the opisthotic has been lost. The mastoid process of the squamosal contacts the posterior tip of the tabular. The quadrate process is relatively larger in *Ictidosuchops* (Crompton 1955 fig.3 p156) than in *Regisaurus* and *Moschorhinus*.

The intermediate process of the opisthotic is much longer than in *Regisaurus* and forms the floor of the jugular foramen. The suture between this process and the basioccipital in *Ictidosuchops* (Crompton 1955 fig.6C p166) is situated in a similar in position to *Regisaurus*. The postero-dorsal process of the opisthotic of *Ictidosuchops* is laterally expanded and forms the medial corner of the posttemporal fenestra. The posttemporal fenestra is smaller and more laterally situated than in *Regisaurus*. Below the posttemporal fenestra on the occipital surface of the mastoid process is a deep groove or fossa (Crompton 1955 fig.6C p166). This fossa is cone-shaped and is open laterally. The ventral tip of the tabular protrudes onto the surface of this fossa and overlies its lateral end. The postero-lateral edge of the mastoid process appears to press against the quadrate, contacting the stapodial process of the quadrate (Crompton 1955 fig.6C p166). This fossa has not been noted in early thercephalians.

The position and shape of the opisthotic in *Thrinaxodon* (Fourie 1974 p379) appears similar to that of *Regisaurus*. Distinct sutures separate the opisthotic from all the bones surrounding it.

Medially, the opisthotic of *Thrinaxodon* contributes only a small portion to the braincase wall, and it forms the postero-dorsal part of the fenestra ovalis as in *Glanosuchus macrops* SAM K238a. It contacts the supraoccipital postero-dorsally, the exoccipital posteriorly, the prootic antero-dorsally and the basioccipital postero-ventrally.

The two processes of the paroccipital process are well-developed. The antero-dorsal facet of the paroccipital process is formed by the prootic, and it is excavated to form the middle ear cavity which accommodates the stapes. Furthermore, the facet possibly conducted blood vessels (Fourie 1974 fig.26 p370).

Midway between the posterior border of the fenestra ovalis and the antero-medial border of the jugular foramen, is a foramen that Fourie (1974 p379) claims have conducted the vena jugularis. However, this blood vessel does not penetrate the braincase through the jugular foramen (foramen lacerum posterium) with nerves IX, X and XI.

In occipital view, the opisthotic of *Thrinaxodon* appears to differ slightly from early theriocephalians. The posterior opening of the posttemporal fenestra is completely enclosed by the tabular. The mastoid process does not contribute to the borders of this fenestra. The mastoid process is a short, narrow rod placed between the squamosal and exoccipital below the tabular (Kemp 1972 fig.11B p30). The structure of the mastoid process is uncomplicated and simple. This is in contrast to the grooved surface of the mastoid process present in *Ictidosuchops* (Crompton 1955).

In occipital view, the mastoid process of *Procynosuchus* resembles that of *Thrinaxodon* because it is a small narrow bar. The posterior opening of the posttemporal fenestra is completely enclosed by the tabular (Kemp 1979 fig.3B p78). In ventral view, the mastoid trough is very shallow and broad, similar to that of *Moschorhinus* as described by Mendrez (1974a).

The opisthotic of *Procynosuchus* is not fused to the prootic, but articulates loosely with it. In ventral view, the suture between the opisthotic and basioccipital also appears very loose as does the articulation with the supraoccipital and exoccipital. Brink (1960 p132) claims these inadequately fused sutures suggest some measure of immaturity.

The paroccipital process is weakly developed for a cynodont (Brink 1960 p132). It forms an inadequate roof for the middle ear, a typical cynodont characteristic. The posttemporal fenestra is small and passes directly and sharply upward into

the temporal vacuity. The quadrate process is distinct (Brink 1960 p132). The mastoid process is not well-developed. In the procynosuchid specimen sectioned by Brink (1960 p132), the distal end of the paroccipital process is separated from the squamosal and tabular. In the other therapsid groups described in this study, these two bones are pressed closely together. According to Brink (1960), this condition is artificial and resulted from the sectioning process.

In *Procynosuchus*, the opisthotic forms much of the border of the jugular foramen. A distinct boss is present on the posterior border of the jugular foramen anterior to the sutures with the exoccipital and supraoccipital.

Olson (1938b p145, 1944 p14) uses the term "periotic" to describe a fused prootic and opisthotic in gorgonopsians. Sigogneau (1974 p53) indicates that a definite suture is present between these two bones. Olson (1938b) states that the braincase of gorgonopsians appear robust and stable. The fact that the periotic is further fused to the supraoccipital and exoccipital adds to its robustness.

Sigogneau (1974 p53) claims that *Gorgonops* has a complete ear region, but that the ossification in this region is "defective and renders its interpretation delicate and numerous uncertainties remain". Sigogneau (1974 fig.2 p55) indicates a definite suture between the supraoccipital and prootic on the left side of the braincase. The suture between the basioccipital and supraoccipital is only visible on the right ear capsule (Sigogneau 1974 fig.3 p57). She (Sigogneau 1974 fig.1 p54) indicates a definite suture between the opisthotic and exoccipital.

In one of the gorgonopsians sectioned by Olson (1938b fig.1 p143), the fenestra ovalis is divided into two by a dorsal spur of the opisthotic. Olson (1938b) claims the anterior opening of the fenestra ovalis represents the fenestra rotunda, situated anteriorly in the fenestra ovalis. This is also found in *Diademodon* described by Watson (1913 p218) and some cynodonts described by Simpson (1933 p288).

In occipital view, the opisthotic of *Leontocephalus* is smaller than that of therocephalians. The mastoid process is a narrow rod which laterally contacts the squamosal, and is dorso-laterally overlain by the tabular. The opisthotic forms the ventral margin of the posttemporal fenestra. The postero-dorsal process is very reduced and has almost disappeared. The internal process is well-developed and

forms a suture with the basioccipital at the base of the occipital condyle (Kemp 1969 fig.8 p18).

In occipital view, the mastoid process of *Arctognathus* (Kemp 1969 fig.3B p10) appears much larger than that of *Leontocephalus*. The extent to which the tabular overlies the opisthotic is not clearly defined, as are the sutures with the exoccipitals. The opisthotic forms the ventral border of the posttemporal fenestra, similar to the condition in *Leontocephalus*.

The medial surface of the inner ear is described in sectioned gorgonopsians by Sigogneau (1974) and Olson (1938b, 1944). The prootic forms the anterior portions of the otic capsule and the opisthotic forms the posterior portion. Below the floccular fossa is a ridge formed by the prootic upon which the horizontal semicircular canal was positioned.

The internal auditory meatus is large and open in gorgonopsians (Olson 1938b p151). The margins of the meatus are smooth in gorgonopsians and cynodonts, apparently indicating that no cartilage was present, unlike *Captorhinus* and *Dimetrodon* where the margins are irregular indicating the presence of cartilage (Olson 1938b p152). The smooth margins of the meatus are definite in *Glanosuchus macrops* SAM K238a, and there are indications of cartilage having formed the medial wall of the otic capsule (See Section 4.2).

Sections through the gorgonopsian opisthotic (Sigogneau 1974 fig.4B no.278A p61) show distinct similarities to the opisthotic of *Glanosuchus macrops* SAM K238a (section 488). There is a medial process present in *Gorgonops*, similar to the process in *Glanosuchus macrops* SAM K238a. The end of this process is also forked (sections 492-494). The first fossa present between the lateral wall and the medial process in *Glanosuchus macrops* SAM K238a is present as two fossae in *Gorgonops* (Sigogneau 1974 fig.4 no.278A p61).

The fossa medial to the medial process (Sigogneau 1974 fig.4B no.278A, 285A p61), is very similar to the second fossa in *Glanosuchus macrops* SAM K238a. The basioccipital-opisthotic suture runs down the centre of the fossa (section 490). More posteriorly in the skull, the basioccipital is replaced by the exoccipital (section 492). Sigogneau (1974 fig.4B p61) claims that the second fossa is the

recessus scala tympani. Posteriorly, this recess forms the jugular foramen. The inner ear of *Gorgonops* appears to closely resemble the ear of *Glanosuchus macrops* SAM K238a. Further comparisons of the inner ear structure are included in Chapter Four.

3.4 Frontal

3.4.1 Description

The frontals form the dorsal margins of the orbitals and the anterior part of the skull roof (Fig. 3A). The ventral surface of the frontals form oval recesses that according to Kemp (1979 fig.14 p106) and Van den Heever (1987 p102) housed the olfactory lobes of the brain (Fig. 4B).

The frontals contact each other medially in a straight suture. Anteriorly, the frontals contact the posterior end of the nasals in an interdigitating suture. The nasals overlap the anterior tips of the frontals in two posteriorly directed prongs. The frontals enlarge posteriorly and the nasals acquire a lateral position.

The lateral margins of the nasals are wedge-shaped, and are clasped by two narrow prongs of prefrontal. As the nasals reduce, the prefrontals form a suture with the lateral edges of the frontals that form lateral processes which contribute to the dorsal margin of the orbits. With the exception of gorgonopsians, cynodonts and some primitive whaitsiids, (*Moschowaitzia* Tatarinov 1974), the lateral process of the frontal always forms the dorsal margin of the orbit (Figs 4C,D).

Posterior to the orbits, the frontals are overlain by the postorbitals which form the posterior edges of the orbits. The part of the postorbital overlapping the frontal also overlaps the anterior portion of the parietal.

The posterior ends of the frontals contact the parietals in an interdigitating suture anterior to the pineal foramen. According to Van den Heever (1987 p102 fig.50k, 78b) the dorsal surface of the frontals are relatively smooth in early therocephalians although the orbital margin may be thickened and rugose, especially in older specimens where the suture between the frontals are often present as a low ridge.

The undersurface of the frontals are vaulted and form a large shallow single indentation. This is evident in the prepared skull roof of *Glanosuchus macrops* GS M796 (Fig.4D) as well as the sectioned *Glanosuchus macrops* SAM K238a (Fig. 4B). A single indent is present in *Procynosuchus* (Kemp 1979 fig.14 p106). As previously noted, this fossa probably contained the olfactory lobes of the brain, stated by Kemp (1979 fig.14 p106) for *Procynosuchus*, and Van den Heever (1987 p102) for early therocephalians. This fossa continues across the frontal-parietal suture onto the ventral surface of the parietal and is continuous with the parietal trough. The parietal trough possibly housed the cerebral hemispheres of the brain.

3.4.2 Comparative View

In *Lystrosaurus* (Cluver 1971 p201), the dorsal surface of the frontals are thickened to form a pair of raised bosses from which a system of grooves and ridges radiate. These bosses, ridges and foramina are reminiscent of those found on the horn-forming bony tissue of mammals.

This points to the possible existence of a thick horny pad covering the frontals. These pads perhaps formed a pair of knob-like projections over the bosses during life. Less well-developed tuberosities are also found on the anterior portions of the parietals and preparietal.

The inner surface of the frontal in *Lystrosaurus* is extended ventrally as a ventral ledge which makes contact with one of the two dorsally diverging wings of the orbitosphenoid. Anteriorly the ledge becomes a ridge which is continued on to the inner surface of the nasal and appears to have supported a sphenethmoidal commissure (Cluver 1971 p201, Agnew 1958 p103). Between the diverging flanges of the orbitosphenoid, the inner frontal surface is recessed to accommodate the olfactory hemispheres. The frontals continue forward in the midline between the nasals, as described for *Glanosuchus macrops* SAM K238a, emerging briefly on the anterior surface of the snout in front of the fronto-nasal ridge. According to Cluver (1971 p202), this condition was observed in only one other *Lystrosaurus* specimen.

In dorsal view, the lateral process of the frontal forming the dorsal margin of the orbit, is much broader in *Lystrosaurus* than in early therocephalians.

In *Dicynodon grimbeeki* (Agnew 1958 p84), the frontals appear to be fused along the midline. The ventral surface of the frontal is cupped to accommodate the brain lobes as described for the early therocephalians. As Cluver (1971) noted for *Lystrosaurus*, the frontals of *Dicynodon* (Agnew 1958 p85) house the wing-shaped orbitosphenoids in recesses. The frontals also contact the mesethmoid lying between the orbitosphenoids.

The frontals of *Regisaurus* (Mendrez 1972 fig.1 p194) are very similar to the frontals of the early Therocephalia.

In dorsal view, the frontals of *Moschorhinus* (Mendrez 1974a fig.1 p74) appear shorter and broader than in early therocephalians. The lateral process does not form the dorsal margin of the orbit, but forms the postero-dorsal edge. This is because the prefrontal is extended posteriorly to form the dorsal rim of the orbit. In the *Promoschorhynchus* specimen described by Mendrez (1974b), the frontals are missing and cannot be included in this comparison.

The frontals of *Ictidosuchops intermedius* (Crompton 1955 fig.1A p152) are elongated and similar to *Regisaurus*. The position of the lateral processes are similar to *Moschorhinus* in that they contact the edge of the orbit postero-dorsally. The prefrontals of *Ictidosuchus* are also enlarged along the dorsal edge of the orbit, similar to *Moschorhinus*.

The frontals of *Thrinaxodon liorhinus* (Fourie 1974 fig.2 p342) appear to be much shorter and narrower than those of early therocephalians. The frontals do not contribute to the dorsal edge of the orbit, as this is formed by the prefrontal and postfrontal. Anteriorly, the frontal is overlapped by the nasal and posteriorly by the parietal as found in the sections of *Thrinaxodon* by Fourie (1974 fig.11 p350, fig.17A p360).

The postorbitals overlap the frontals laterally (Fourie 1974 fig.15B p356). The frontal forms a wide trough on the ventral surface, similar to the condition found in early therocephalians (Fourie 1974 fig.17B,C p360). There is no ridge dividing the fossa into two parts, as is found in *Procynosuchus*.

In *Procynosuchus* (Kemp 1979 p106), the olfactory lobes occupied the ventral surface of the frontal bones. The fossa is double because a slight median ridge is present. It is bounded antero-medially by well-developed ridges which reduce in height anteriorly but meet in the midline in a rugose area. Kemp (1979 p106) believes that this area probably marks the attachment of an unossified mesethmoid.

Immediately anterior to these ridges are a pair of turbinal ridges which is a positive indication that this part of the braincase housed the olfactory lobes. The fossa that housed these lobes indicates that the lobes were bulbous, the height is not known and the length can only be approximated since there is no definite anterior boundary (Kemp 1979 p106).

Anteriorly the frontal-nasal suture of *Procynosuchus* (Brink 1960 p137) is level with the anterior borders of the orbits. According to the cynodont pattern, the frontal-prefrontal sutures extend to the postorbitals, therefore excluding the frontals from the dorsal edge. Brink (1960 fig.33 p130) could not define the sutures between the frontals and parietals in the procynosuchid he described. The ventral surface of the frontal is generally flat and smooth with no indication of fronto-nasal turbinals (Brink 1960 p137). There is no indication of turbinal attachment in this region in *Glanosuchus macrops* SAM K238a or *Glanosuchus macrops* GS M796 (Fig.4D).

As previously stated, the frontals of gorgonopsians do not contribute to the dorsal margins of the orbitals. The prefrontals extended posteriorly, to meet the postfrontals. The prefrontal forms the anterior and antero-dorsal margin of the orbit. The postfrontal forms the posterior and postero-dorsal margin of the orbit as in *Leontocephalus intactus* (Kemp 1969 fig.4 p14).

The fronto-nasal and fronto-parietal sutures are transverse, slightly interdigitating sutures. In dorsal view, the frontals appear roughly oval in shape.

3.5 Parietal

3.5.1 Description

The parietal forms the roof of the braincase and the central portion of the dorsal margin of the occiput. The parietal extends from the orbit, to the occiput (Fig. 3A). Anteriorly, it is present as two bones which fuse to form a single bone posterior to the pineal foramen. In section, the unfused parietals are thin slivers of bone, (for example section 433) and the fused parietal is triangular in shape (section 494). In the lychosuchid GS C60, the parietals do not fuse posterior to the pineal foramen as is found in *Glanosuchus macrops*, and a suture remains between the parietals (Van den Heever 1987 p141).

In dorsal view, the parietal is shaped like an hourglass (Figs 10,15B). Anteriorly, the parietal forms a suture with the frontal and with the postorbitals laterally. The ventral edge of the parietal forms a suture with the prootic antero-laterally and the supraoccipital ventro-laterally. The occipital end contacts the tabular postero-ventrally, and the squamosal both postero-laterally and postero-ventrally.

In dorsal view, the parietal overlaps the frontal in two lateral, anteriorly facing prongs, with a median V-shaped piece of frontal exposed in between. Anteriorly, the postorbital lies on the lateral edge of the parietal and frontal, but at the termination of the frontal, the postorbital migrates upwards to a dorso-lateral position on the parietal (sections 418-427) (Fig. 3A).

Dorsally, the sagittal crest of the parietal extends from the pineal foramen to the posterior margin of the parietal. This crest is damaged in *Glanosuchus macrops* GS M796, *Glanosuchus macrops* SAM K238a and *Ptomalestes avidus* SAM 11942, but it is widest at its origin and appears to increase in height posteriorly end of the parietal. At the posterior end it divides into two laterally directed lamboid crests which form the dorsal border of the occiput.

The parietal has a characteristic feature found in reptiles, namely the pineal foramen or parietal fenestra. The pineal foramen is situated on the midline of the parietal in early therocephalians, and is further discussed in Chapter Four, Sub-section 4.1.1.6. (Figs 3A, 4B,C,D, 10).

On the ventral surface of the parietal, is a small, elongated, ventral process situated on either side of a central shallow trough. This process extends from the posterior margin of the pineal foramen, and runs along the ventral ledge of the parietal contacting the dorsal edges of the epipterygoid and anterior processes of the supraoccipital (sections 445-456) (Fig. 4B).

The lateral sulcus (sections 445-456) which is formed between the parietal process and the lateral parietal margin is a deep venous groove, which according to Fourie (1974 p375), conducted the vena lateralis. This is called the venous channel by Kemp (1979 fig.13 p112). Van den Heever (1987 p105) states that the vena parietalis was probably positioned here.

In occipital view, the parietal of early therocephalians forms the dorsal portion of the occiput (Figs 11, 16). It contacts the interparietal ventrally and the tabular ventrolaterally. Two lateral flanges arise from the distal end of the parietal, and are wedged between the tabular and the dorsal process of the squamosal. They are referred to as the lamboid crests by Durand (1991) for *Moschorhinus*, and nuchal crests by van den Heever (1987) for early therocephalians.

The ventral surface of the parietal of *Glanosuchus macrops* forms a long central trough that continues across the frontal-parietal suture (sections 415-450) (Fig. 4B). This was possibly where the cerebral hemispheres were positioned. In the lycosuchid GS C60, the trough is flanked on either side by a low ridge, situated medial to the parietal process. This ridge runs across the frontal-parietal suture and the dorsal lamina of the epipterygoid is placed in a groove medial to this ridge. Both the ridges and grooves appear to be absent from *Glanosuchus macrops* GS M796 and *Glanosuchus macrops* SAM K238a. As mentioned in the discussion of the supraoccipital (Sub-section 3.7.2), these grooves may indicate an insertion area of cartilaginous extensions of the anterior processes of the supraoccipital (Fig. 4D).

Anterior to the ventral opening of the pineal canal the parietal trough deepens (sections 435-450). Posterior to the pineal foramen the trough gradually slopes upwards towards the supraoccipital and the interparietal to form a wide, deep cone-shaped fossa. This fossa then slopes gradually downward again towards the foramen magnum. The fossa is formed only by the supraoccipital.

This fossa is seen in *Glanosuchus macrops* SAM K238a (Figs 4B, 6 labelled as *cblc*). In *Ptomalestes avidus* SAM 11942, where the matrix in the interior of the braincase has been cleaned out, this cerebellar fossa is also evident. The fossa probably housed the cerebellar lobes of the brain. The constricted region posterior to the cerebellar fossa anterior to the foramen magnum may be the possible position of the medulla oblongata. This is similar to the structure described in *Procynosuchus* by Kemp (1979 fig.14 p106).

Postero-ventrally, the parietal contacts the single interparietal (postparietal) with an interdigitating suture, much like the contact between the supraoccipital and interparietal, but interdigitating to a lesser degree (sections 491-528).

3.5.2 Comparative View

In dorsal view, the parietal of dicynodonts is very broad, lacking the narrow intertemporal region of therocephalians. This broad skull roof is also characteristic of gorgonopsians and some cynodonts.

The two anterior prongs of the parietal overlapping the frontal in dicynodonts appears to be similar to *Glanosuchus macrops* SAM K238a. A preparietal is present between the prongs, and the anterior margin has a suture with the frontal. The pineal foramen is situated centrally on the midline of the parietal on the suture between the frontal and parietal, and the posterior end of the frontal forms the anterior edge of the pineal foramen.

The preparietal is a single median bone that varies in size and shape and is only found within the Dicynodontia and Gorgonopsia. It is situated between the frontal and the parietal. In some dicynodont specimens the preparietal is wide and blunt anteriorly (*Lystrosaurus* Cluver 1971 p202), and in others it forms a sharp process between the frontals and is diamond-shaped in dorsal view as in *Dicynodon* (Agnew 1958 p85). In all other aspects, the parietal appears to be the same.

The parietal of *Regisaurus jacobii* also resembles the early therocephalian parietal, except that in *Regisaurus* the anterior end of the parietal is as not wide (Mendrez 1972 fig.1B p194).

In whaitsiids, the intertemporal region is greatly constricted, and is much narrower than any specimen described in this study. In comparison to the dicynodont with its broadened braincase roof, the Whaitsiidae has a slender parietal, which widens very slightly at the posterior end (Kemp 1972 fig.1B p3). This is evident in the whaitsiid SAM K5512) (Fig. 17A).

The parietal of the *Promoschorhynchus* specimen described by Mendrez (1974b) is missing, and therefore will not be included in the discussion here.

In dorsal view, the parietal of *Moschorhinus* is shaped like an hourglass. The prongs of the parietal that overlap the frontal described for early therocephalians and *Regisaurus* are not present in *Moschorhinus*. The frontal and parietal meet in a slightly curved, transverse interdigitating suture (Mendrez 1974a p78, fig.1 p74). Unlike early therocephalians, *Moschorhinus* lacks a postfrontal (Mendrez 1974a p78).

Durand (1991 p404) claims that in *Moschorhinus*, the anterior third of the ventral border of the parietal does not make sutural contact with any bones, because this part of the braincase was unossified. No such unossified zone was identified in the parietal of the sectioned early therocephalian specimen. According to Olson (1944 fig.5 p12, fig.6 p14), there is no unossified zone in dicynodonts, or in the gorgonopsians and cynodont specimen he sectioned. Kemp (1969) found no unossified zone in the gorgonopsians he studied either. However, in *Procynosuchus delaharppae*, an unossified zone is present on the postero-ventral surface of the parietal where it meets the interparietal (Kemp 1979 fig.14 p106).

The parietal of *Ictidosuchops intermedius* is broad and flat, and the posterior end is very wide. The sagittal crest appears to be small and insignificant (Crompton 1955 p151, fig.1A p152). The two anterior prongs of parietal overlapping the frontal are similar to the early therocephalian specimens. The parietals do not contribute to the occipital surface, contrary to the condition described for *Regisaurus* (Mendrez 1974a p197) and early therocephalians (own observation).

The parietal of *Thrinaxodon liorhinus* is similar to *Regisaurus* in dorsal view, but the posterior end appears to be less widened. The postero-lateral flanges flaring from the posterior end of the parietal (the lamboid crests) are hardly visible, as the squamosal overlaps the parietal where these crests join the parietal body (Fourie 1974 p375, fig.2 p342).

In dorsal view, the parietals of *Procynosuchus delaharpae* (Kemp 1979 fig.1 p176) are similar to those of the lycosuchid GS C60. Posterior to the pineal foramen they are unfused, and in dorsal view appear similar to the parietals of whaitsiids. The parietal is very narrow in the intertemporal region and meets the frontal in a short interdigitating suture. Brink (1960 p134) indicates that the procynosuchid he sectioned does not have a narrow intertemporal region, in contrast to what Kemp(1979 p176) states.

As in *Ictidosuchus intermedius*, the parietal of *Procynosuchus* does not contribute to the occiput (Kemp 1979 fig.176). As mentioned above, an unossified zone is present on the ventral surface of the parietal where it meets the interparietal (Kemp 1974 fig.14 p106). Posterior to the pineal foramen the parietal forms a venous channel between the lateral margin and the ventral process.

The parietals of *Procynosuchus* (Brink 1960 p134) differ from whaitsiid parietals, which are characterized by prominent sagittal crests in that the crest of *Procynosuchus* is reduced and the parietal is flattened on the dorsal surface resembling *Ictidosuchus* (Crompton 1955).

Brink (1960 p134) indicates in the procynosuchid he sectioned that the pineal foramen is more anteriorly situated and the lamboid crests are much longer than the procynosuchid described by Kemp (1979). The anterior prongs of the parietal overlapping the frontal in *Procynosuchus* are not as sharp as the therocephalian specimens described above (own observation). The parietal does not contribute to the occiput.

Gorgonopsians have a completely different parietal structure to therocephalians. The main reason for this is the broad intertemporal region, much like *Dicynodon* (Agnew 1958). The parietal is very short and more posteriorly situated than in therocephalians. The pineal foramen is situated on the sagittal plane between the parietals, but is peculiar in that it is situated in a raised cone-like structure.

Antero-medially, the parietals have a short, transverse interdigitating suture with the frontals, as does *Moschorhinus*. The interparietal contacts the parietal posteriorly, and the parietal does not form part of the occiput, resembling the condition found in *Ictidosuchus* and *Procynosuchus*. The posterior lamboid crests are elongated and posteriorly directed in gorgonopsians (Kemp 1969 fig.4 p14).

The preparietal is present in all gorgonopsians and is a very small bone situated between the parietal and the frontal. There appears to be no unossified zone in the gorgonopsian parietals (Kemp 1969 fig.5 p15, fig.22A p67), in contrast to *Procynosuchus* and *Moschorhinus*.

3.6 Interparietal

3.6.1 Description

The interparietal, or postparietal, is a single median bone. It is wedge-shaped, and positioned between the parietal dorsally and the supraoccipital ventrally (Fig. 5). In occipital view, the interparietal is bounded laterally by the tabulars (Figs 11, 16). It forms a very small portion of the ventral surface of the skull roof (Fig. 4B).

In occipital view, the interparietal forms the dorsal portion of the median occipital fossa which extends from the base of the parietal onto the supraoccipital ventrally. The vertical occipital crest divides the median occipital fossa into two smaller fossae. Comparison of the scylacosaurid *Glanosuchus macrops* GS M796 and the lycosuchid GS C60 indicates that the median occipital fossa of the lycosuchid appears deeper and more prominent (Figs 11, 16).

According to Van den Heever (1987 p130), a small portion of the interparietal is present on the lateral wall of the braincase of *Glanosuchus macrops* GS M796. It is situated between the parietal, the antero-dorsal process of the squamosal and the anterior process of the supraoccipital. This is also visible in *Glanosuchus macrops* SAM K238a (sections 491-505). In *Glanosuchus macrops* SAM K238a, the interparietal is laterally visible as a small, elongated portion of bone between the parietal and the supraoccipital. However, the squamosal and tabulars are damaged in

this specimen, and in section 506 a small portion of the intermediate process of the squamosal covers the interparietal laterally. It is not known to which extent this bone covered the interparietal in the undamaged state.

In section 491, the interparietal appears as a flattened rectangular bone, whereas it is wedge-shaped in sagittal view. The anterior end is very small, and the bone progressively increases in height towards the occipital end (section 511).

The interparietal forms interdigitating sutures with the parietal and the supraoccipital, which increases in an anterior-posterior direction. In ventral view, the anterior edge of the interparietal overlaps the parietal. A very small area is exposed on the ventral surface of the braincase roof before it is overlain by the supraoccipital (sections 491-496). The cerebral trough of the parietal continues onto the ventral surface of the interparietal. The latter appears as a small central portion of the skull roof, posterior to the pineal foramen. It is surrounded by the parietal anteriorly and laterally, and the supraoccipital posteriorly. This is the only part of the interparietal that contributes to the interior surface of the braincase (Fig. 4B).

3.6.2 Comparative View

In *Lystrosaurus*, the interparietal lies in a similar position to that described in *Glanosuchus macrops* SAM K238a. In ventral view, it appears, however, that the exposed portion of interparietal forming the roof of the braincase is substantially larger than is found in the sectioned specimen. The ventral trough is prominent anteriorly in the exposed region of the bone. The interparietal of dicynodonts is triangular in shape when sectioned dorso-ventrally, unlike *Glanosuchus macrops* SAM K238a, where the interparietal has a roughly rectangular shape.

Cluver (1971 fig.13 p172) indicates that an important function of the interparietal in *Lystrosaurus* is the formation of "nutrient canals". Such nutrient canals were not found in the sectioned early therocephalian skull.

In the sagittal view, it does not appear as if the interparietal of *Dicynodon* (Agnew 1958 fig.37 p89) contributes to the internal surface of the braincase cavity. It lies

almost completely on the dorsal surface of the supraoccipital, and is rectangular in section.

In occipital view, the interparietal of *Regisaurus* is rectangular and positioned similar to early therocephalians. Mendrez (1972 fig.3 p196) gives no indication of the presence of the interparietal on the lateral wall of the braincase as was found by Van den Heever (1987 p130) in *Glanosuchus macrops* GS M796.

In *Whaitsia* (Mendrez 1974a Table.1 p96), a portion of interparietal is present on the lateral braincase wall, as in *Moschorhinus*. Kemp (1972) does not refer to the interparietal in whaitsiids.

The *Promoscorhynchus* specimen described by Mendrez (1974b fig.1 p71) is badly damaged on the dorsal surface and the interparietal is missing.

Mendrez (1974a fig.3 p80) indicates that a thin, elongated portion of the interparietal is present on the lateral walls of the braincase of *Moschorhinus*. This portion of the interparietal is situated in the lateral fossa between the supraoccipital ventrally and the parietal dorsally. The occipital view of the interparietal also appears rectangular, but is much smaller than the interparietal of early therocephalians (own observation).

According to Durand (1991 p403), the anterior portion of the interparietal of *Moschorhinus* is triangular in section, and contacts the anterior processes of the supraoccipital. It is not indicated whether the interparietal is visible in a ventral view of the skull roof.

In *Ictidosuchops intermedius* (Crompton 1955 fig.2A p154), the parietal is restricted to the dorsal aspect of the braincase and the interparietal forms the dorso-medial portion of the occiput. The interparietal appears to be very wide but low.

The interparietal does not contribute to the lateral wall of the braincase in *Ictidosuchops* (Crompton 1955 fig.4A p157), as is found in *Moschorhinus* and whaitsiids. Crompton does not indicate whether the interparietal accords to the interior roof of the braincase.

In *Thrinaxodon liorhinus* (Fourie 1974), the interparietal varies from the early therocephalians in position and shape. It is a short, square bone that abuts against the

parietal anteriorly and the supraoccipital posteriorly, forming a small section of the ventral surface of the skull roof. It sits in a pocket-like cavity of which the parietal forms the anterior walls and the supraoccipital forms the posterior walls.

There is no indication that the interparietal is exposed on the lateral surface of the braincase walls in *Thrinaxodon* (Fourie 1974 fig.6B p346). It forms the dorsal margin of the occiput, and in occipital view has a triangular shape.

The interparietal of *Procynosuchus* (Kemp 1979 fig.3 p78) forms the dorsal part of the occiput. It does not form part of the lateral braincase wall. The interparietal appears to be completely missing from the procynosuchid sectioned by Brink (1960 p134). In Brink's reconstruction, an opening is presented in the position of the interparietal. The interparietal apparently covered certain areas of the tabulars. There is no explanation as to the absence of the interparietal.

In occipital view, the gorgonopsian interparietal is a large rectangular bone which forms the dorsal part of the occiput. The internal view of the skull roof (Kemp 1969 fig.5 p15) indicates that the interparietal does not form part of the ventral surface of the roof in *Dixeya*, but is completely overlain by the supraoccipital (Kemp 1969 fig.21 p50). In *Arctognathus*, however, the interparietal appears to form a portion of the ventral surface of the skull roof (Kemp 1969 fig.18A p55).

There is no indication that the interparietal contributes to the lateral walls of the braincase. The interparietal is a robust wedge-shaped bone which is completely encased by the parietal and supraoccipital on all sides except for the occipital face.

The therocephalian occiput is vertical in contrast to the gorgonopsian condition where the occiput is slanted. According to Van den Heever (1987 p129), this has resulted from the expansion of the intertemporal region to accommodate the adductor musculature.

3.7 Supraoccipital

3.7.1 Description

The supraoccipital comprises the greater part of the dorso-lateral and postero-dorsal braincase walls (Figs 2A,B). This bone consists of a robust inverted U-shaped body and two antero-lateral processes (Fig. 8). The body portion is positioned ventral to the interparietal and postero-dorsal to the prootic (Fig. 5). The anterior processes extend antero-dorsally. They contact the parietal, prootic, and epipterygoid. This is evident in *Glanosuchus macrops* GS M793, *Glanosuchus macrops* SAM K238a and *Ptomalestes avidus* SAM 11942.

The dorsal notch is present between the suture of the supraoccipital and the prootic of *Glanosuchus macrops* SAM K238a, a juvenile specimen. It is also present in mature specimens such as *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942. This falsifies the observation of Boonstra (1968) that this notch is a juvenile characteristic. It has been noted that in various advanced theriocephalians and primitive cynodonts, the dorsal notch of the prootic is also present in a similar position as the dorsal venous foramen in *Moschorhinus* (Mendrez 1974a) and *Thrinaxodon* (Fourie 1974) (Figs 2A,B, 5).

The interdigitating suture between the supraoccipital and the interparietal originates anteriorly as an insignificant feature. More posteriorly the interdigitation becomes exaggerated (sections 490-513). The connection between these two bones appears to have been greatly strengthened by this interdigitation. In *Glanosuchus macrops* SAM K238a, the outer layer of bone of the supraoccipital is thickened to further strengthen this area, possibly for the attachment of muscles. A similar suture is present between the parietal and the interparietal. There is a definite suture present between the supraoccipital and the prootic. This suture runs laterally in an antero-posterior direction.

Olson (1944 p13 fig.5, p14 fig.6, p63) provides some information about the position, shape and extent of the supraoccipital in sectioned therapsids, but does not elaborate, claiming that the bone is sufficiently known.

As stated above, the supraoccipital appears to have two anterior processes (sections 442-496) and a single, sturdy posterior body, which is tripartite in occipital view (Figs 11, 16). The anterior ends of the processes project between the dorsal lamina of the prootic and the parietal. The body portion lies between the parietal and the interparietal (sections 497-512). It contacts the opisthotic, the exoccipital and the prootic. The interparietal is wedged between the supraoccipital and the parietal (sections 491-528) (Fig. 5).

In *Glanosuchus macrops* SAM K238a, these anterior processes are slightly fractured anteriorly. They appear to contact only the parietal, prootic, interparietal and the opisthotic (Fig. 5). The exoccipitals are very fragmented, and it is difficult to assess the sutures with the supraoccipital. Various authors, i.e. Kemp (1969 p69 gorgonopsians), Cluver (1971 p170 *Lystrosaurus*) and Hopson (1979 p57 fossil reptiles) have noted that the anterior processes of the supraoccipital were probably anteriorly elongated by cartilage, and extended under the inner parietal edge.

Hopson (1979 p57) states that these cartilaginous extensions are present in all reptiles, and often fail to ossify in living reptiles. He identified the cartilaginous extensions from protuberances on the surface of braincase endocasts of extinct reptiles.

Kemp (1969 p69) identified the same cartilaginous extensions in gorgonopsian specimens by the roughened surface on the anterior processes of the supraoccipital, and by ridges present on the interior surface of the parietals. He noted that cartilage fossilizes as a matrix with a crystalline texture, and used this as an identifiable characteristic for cartilage.

Any indication of cartilaginous extensions on these processes in early theriocephalians is not evident, and are in no way indicated in *Glanosuchus macrops* SAM K238a. It therefore cannot be determined whether this condition was present in *Glanosuchus macrops* or not from the specimens studied. In the lycosuchid GS C60, two grooves are present on the ventral surface of the parietal, on either side of the parietal trough, medial to the ventral processes of the parietal. These grooves may indicate the presence of cartilaginous extensions of the anterior processes of the supraoccipital (Fig. 4C).

In transverse section, the anterior processes of the supraoccipital appear highly porous with an outer layer of hard bone layer. At the point where the processes extend from

the body of the supraoccipital, the bone is less porous and the ventral margin of the outer hard layer is greatly thickened.

Posterior to the point where the anterior processes join the body of the supraoccipital, the ventral surface of the bone is excavated to form a deep trough in *Glanosuchus macrops* SAM K238a (Fig. 8). The body is situated dorsal to the two ventrally directed processes on either side of the trough. The anterior processes are broad at this position (section 496), and the supraoccipital has an increasing proportion of hard bone to soft bone. The ventral trough of the supraoccipital is continuous with the parietal trough. It probably housed the cerebellar portion of the brain (Fig. 4B). A foramen pierces the anterior margin of the cerebellar trough. It leads through the medial wall of the cochlear recess into the cerebellar region of the brain cavity (sections 500-502). This foramen is probably the internal auditory foramen which conducted the vestibulo-cochlear nerve VIII from the cochlea to the brain (see Sub-section 4.3.9.2) (Figs 5,6,7,8) (*iaf*).

In occipital view, the supraoccipital is tripartite, resembling an inverted T-shape (Fig. 11). It consists of a dorsal process and two postero-lateral processes. The dorsal process of the supraoccipital, the interparietal and the medial edges of the tabulars form a cup-shaped hollow, the median occipital fossa. The ventro-medial portion of the supraoccipital contributes to the dorsal edge of the foramen magnum. Broom (1936 plates 7,8,9) indicates in several therocephalian specimens i.e. *Lycedops scholtzi*, *Hofmeyria atavus*, *Priesterognathus minor* and *Hyenosaurus platyceps* that this vertical, dorsal process of the supraoccipital is either very small or absent.

The median occipital fossa present in many therocephalian groups including the early cynodonts, i.e. *Thrinaxodon* (Fourie 1974) and *Diademodon* (Brink 1955 fig.3A p7). The extent of this fossa varies from group to group. A crest divides the median fossa into two smaller fossae. In *Glanosuchus macrops* GS M796 the crest is short. It runs from the interparietal to the lateral extensions of the supraoccipital. This is also evident in many therocephalians, including whaitsiids (Kemp 1972 p37) and *Ictidosuchus* (Crompton 1955 fig.2A p154).

Occipitally, the lateral edges of the supraoccipital are overlapped by the tabular. This is shown clearly by sectioned specimens of Broom (1936 plate.5). Furthermore, the

supraoccipital overlaps the squamosal in *Lycedops scholtzi* (Broom 1936 plates 7,8,9), and the exoccipital closely contacts the supraoccipital.

The supraoccipital constitutes a large part of the occiput, which in early therocephalians is almost vertical. The dorsal part of the occiput slopes antero-posteriorly at a very slight angle between the supraoccipital shelf and the parietal. Below the supraoccipital shelf is a vertically directed portion that extends into the two postero-lateral processes. These processes originate above the foramen magnum and extend laterally above the postero-dorsal processes of the opisthotic which contribute to the posttemporal fenestra. These lateral supraoccipital processes have sutures with the opisthotic, the exoccipital and the tabulars. The supraoccipital forms the antero-dorsal part of the auditory capsule with the prootic, basioccipital, parabasisphenoid and the opisthotic.

The braincase of *Glanosuchus macrops* SAM K238a and the braincase cavity of *Ptomalestes avidus* SAM 11947 indicate that the ventral surface of the supraoccipital is smooth. The anterior region of the supraoccipital forms a deep, rounded cup-shaped fossa in the roof of the braincase which probably housed the cerebellum. Behind this cerebellar fossa, the supraoccipital slopes gradually downwards in a postero-ventral direction. It forms a small step before sloping towards the foramen magnum. The supraoccipital forms the roof of the braincase cavity at the level of the medulla oblongata.

3.7.2 Comparative View

In dicynodonts, the supraoccipital appears to differ in shape from that of early therocephalians. The anterior processes are much shorter, and they do not contact the epipterygoid. The contact with the interparietal is not as extensive as the contact found in the early therocephalians.

In *Lystrosaurus*, the supraoccipital forms a portion of the roof of the braincase and otic capsules, the dorsal margin of the foramen magnum and most of the dorsal part of the occiput. It meets the opisthotic in a straight suture. Dorsally it is overlain by the interparietal. Posteriorly, the supraoccipital is overlain by the tabular and the squamosal, and anteriorly it is overlain by the dorsal part of the prootic (Cluver 1971 P169-170).

The anterior processes of the supraoccipital in dicynodonts are abruptly truncated and terminate a distance posterior to the epipterygoid. The unfinished surface of the anterior edge of this process suggests that the supraoccipital was continued forward as cartilage beneath the inner parietal surface (Cluver 1971 p170).

Agnew (1958) claims that the occipital bones of dicynodonts (opisthotic, supraoccipital and exoccipital) are fused to such an extent that it is difficult to distinguish the sutures between the bones. Olson (1944) also found this condition to exist in the dicynodonts which he sectioned. Cluver (1971) found that this is not the case in *Lystrosaurus*.

The supraoccipital in *Regisaurus* is similar to that described for the early therocephalians. It has extended anterior processes which contact the epipterygoid. It is tripartite in occipital view and comprises most of the median occipital fossa. The supraoccipital forms the ventral portion of the occipital crest which divides the fossa into two parts (Mendrez 1972 fig.4 p197).

In occipital view, the supraoccipital is low and broad (Fig. 17D). The supraoccipital does not contribute to the border of the posttemporal fenestra (Kemp 1972 p29). In *Theriognathus* (Kemp 1972 fig.11B p30), the supraoccipital is a laterally expanded bone in occipital view, but not as wide as early therocephalians (own observation).

In lateral view, a dorsal venous foramen is present between the supraoccipital and the prootic in whaitsiids. This is formed by the dorsal notch which has closed off to form a foramen. It is referred to as the dorsal venous foramen, foramen veineaux and the venous notch by various authors and it conducted blood vessels through the wall of the braincase. Specimens with a dorsal venous foramen present other than whaitsiids, are *Moschorhinus* (Mendrez 1974a fig.6 p76, Durand 1991 p407), *Promoschorhynchus* (Mendrez 1974b fig.3 p74), *Thrinaxodon* (Fourie 1974 fig.22A p366) and *Ictidosuchops* (Crompton 1955 fig.4A p157).

The specimen of *Promoschorhynchus* described by Mendrez is missing the dorsal part of the skull roof including the dorsal occiput, but the ventral occipital part is present. The ventral portions of the postero-lateral processes of the supraoccipital are present and are similar to *Moschorhinus* in that they do not contribute to the posttemporal fenestra. The median occipital fossa is well developed ventrally.

In occipital view, the supraoccipital of *Moschorhinus* (Mendrez 1974a fig.4 p84) is smaller than that of early therocephalians (own observation). The dorsal process is not very large. The medial occipital fossa is very well developed and incorporates the entire dorsal part of the occiput. The occipital crest is well developed, and is narrow on the interparietal. The crest widens on the dorsal process of the supraoccipital.

The exoccipitals overlies the ventro-lateral and lateral margins of the supraoccipital, except for the part directly above the foramen magnum. The dorsal region of the occiput above the supraoccipital ledge is more anteriorly set than the ventral part. This is similar to the occiput of the early therocephalians.

In lateral view, situated on the suture between the parietal and the supraoccipital, is a deep fossa which Durand (1991 p402) refers to as the lateral supraoccipital fossa. This fossa is not prominent in *Glanosuchus macrops* GS M796 or *Ptomalestes avidus* SAM 11942 and is also not evident in *Glanosuchus macrops* SAM K238a. It is well-developed in *Lycosuchus vanderrieti* GS M793, but may be enhanced due to dorso-ventral distortion (Fig. 15A).

The supraoccipital of *Ictidosuchops intermedius* has an anterior process which overlaps the postero-dorsal process of the epipterygoid (Crompton 1955 fig.4A p157). The body region of the supraoccipital is overlapped by the intermediate process of the squamosal, similar to the condition in *Promoschorhynchus* (Mendrez 1974b fig.5 p75).

The supraoccipital and prootics of *Ictidosuchops* are fused (Crompton 1955 p158). There appears to be no sutural contact between the supraoccipital and the interparietal. This is unlike the sectioned *Glanosuchus macrops* SAM K238a, where the suture between these bones is interdigitating. The supraoccipital of *Ictidosuchops* appears to be fused to the tabulars (Crompton 1955 p158).

In the primitive cynodont *Thrinaxodon liorhinus* (Fourie 1974), the supraoccipital has a very different structure to that of early therocephalians. The anterior processes are very reduced, and do not extend anteriorly between the prootic and parietal. The body region of the supraoccipital is enlarged ventrally. In ventral view, the dorsal contact with the interparietal is very small. The interparietal forms a cup-shaped cavity between the parietal and supraoccipital on the ventral surface.

In sagittal section, the supraoccipital of *Thrinaxodon* (Fourie 1974 fig 6 p346) is thickened immediately below the interparietal. An unossified zone is present in the ventral surface of the braincase roof. It lies on the interparietal-parietal suture, and is not present in early theriocephalians. In occipital view, the tabulars overlie a great part of the lateral edge of the supraoccipital, similar to the situation in other early cynodonts.

In *Procynosuchus delaharpeae* (Kemp 1979 fig.3 p78, fig.20A,B plate 2), the supraoccipital also appears to be very different to that of theriocephalians. Kemp (1979) did not elaborate on the supraoccipital of *Procynosuchus*, but drawings and photographs of the specimen provides information as to its shape and position. In posterior view, the supraoccipital is a narrow, vertical bone. It is laterally constricted and the dorsal process is extended in height. The postero-lateral processes are absent. This appears similar to the whaitsiids, and the supraoccipital is overlain laterally by very enlarged tabulars (Kemp 1979 fig.20C,D plate 2) (Fig. 17D).

The supraoccipital forms the posterior inner braincase wall, and a definite unossified zone is present on the interior surface between the interparietal-supraoccipital suture (Kemp 1972 fig.3B p78). This unossified zone appears to be present in early cynodonts, and is also present in *Thrinaxodon*.

The supraoccipital does not contribute to the posttemporal fenestra, but forms the dorsal margin of the foramen magnum. The occiput of *Procynosuchus* does not appear as vertical as the early theriocephalian occiput, and slopes at a gentle angle (Kemp 1972 fig.3B p78). In lateral view, the lateral supraoccipital fossa is present, but Kemp (1979 fig.3A p78) refers to it as the venous channel. A dorsal venous foramen is absent.

The supraoccipital of cynodonts lacks the occipital crest, which was presumably for the attachment of the aponeurotic membrane in this region. This absence, according to Kemp (1972 p37), possibly suggested that "some temporalis muscle fibres originated from the otic process".

The supraoccipital of *Procynosuchus* sectioned by Brink (1960 p129) is not clear, especially the ventral margins. Brink (1960 fig.34 p131) interpreted it as a long bone extending between the parietals, and possessing a dorsal process in occipital view. It is

completely ossified in the posterior regions and is unlike the condition encountered in *Thrinaxodon* and *Procynosuchus* where an unossified region is present on the suture line between the interparietal and supraoccipital. Below this region there is an indication that cartilage was present in a "restricted section". Brink (1960 p129) used this, as well as the loose sutures, as a factor to indicate that the specimen is "not very juvenile". The validity of this argument is doubtful as it has already been shown by other authors that cartilage was present in juvenile and what appears to be adult therapsid specimens i.e. *Thrinaxodon* (Fourie 1974). It appears certain that the medial portion of most therapsid otic capsules were cartilaginous (see Section 4.2).

In gorgonopsians, the shape of the supraoccipital appears to differ from that of the early therocephalians. The anterior processes seem shorter and they appear to have had cartilage extensions. The occipital view indicates that the dorsal process of the supraoccipital is absent. Kemp (1969 p64, fig.18A p55) is not definite in his description of the supraoccipital of gorgonopsian skulls. It appears that the supraoccipital laterally participates in the formation of the foramen with the prootic, through which the trigeminal nerve V exited. In lateral view, there appears to be a dorsal venous foramen between the dorsal lamina of the prootic and the anterior process of the supraoccipital. The supraoccipital possesses a small anteriorly directed process which meets the prootic across the foramen and divides it into two openings. Kemp (1969 p64) states that such a process of the supraoccipital has not been described for gorgonopsians before. This process has not been noted in any of the early therocephalians considered for this study.

3.8 Tabular

3.8.1 Description

The tabular is a relatively large, flat rectangular bone that forms the dorso-lateral part of the occiput. The shape and size of the tabular varies greatly amongst therocephalians. It is pressed against the posterior face of the squamosal and overlies the lateral surface of the supraoccipital and interparietal, and the ventro-lateral edge of the parietal (Fig. 16). The tabular is broken off from the *Glanosuchus macrops* SAM K238a, and only the dorso-medial portion that contacts the squamosal is present.

In early therocephalians, the tabular overlies the intermediate and mastoid processes of the squamosal. This is similar to *Regisaurus jacobi* (Mendrez 1972 fig.8 p203) and the lycosuchid GS C60. The edges of the posttemporal fenestra are formed by the opisthotic and the squamosal, and the tabular does not contribute to this foramen (Figs 11, 16). The ventral edge of the tabular sends a short ventro-lateral spur along the inner face of the ridge forming the border of the squamosal sulcus (van den Heever 1987 p131). This is evident in *Ptomalestes avidus* SAM 11942 and *Glanosuchus macrops* GS M796.

According to the sections made by Broom (1936 plate 5 figs 68-76), the dorsal edge of the tabular is very thin, but towards its ventral edge, it thickens considerably. The lateral end is embedded into a pocket in the posterior wall of the squamosal (Broom 1936 plate.5 No.74,75).

3.8.2 Comparative View

The tabulars of *Lystrosaurus* are relatively small, oval bones which are situated high on the occipital surface. They lie lateral to the interparietal which forms the dorsal part of the occiput. They contact the squamosal laterally and the supraoccipital ventro-medially (Cluver 1971 fig.37 p203). The tabular does not form part of the posttemporal fenestra in *Lystrosaurus* (Cluver 1971 fig.37 p203) or *Dicynodon grimbeeki* (Agnew 1958 p100).

The tabulars of *Regisaurus* are broad, almost rectangular bones situated on the outer edges of the occiput (Mendrez 1972 p197). They are larger than those of *Ictidosuchops intermedius* (Crompton 1955 fig.2A p60), which form only the dorso-lateral corner of the posterior opening of the posttemporal fenestra. The tabulars of *Regisaurus* (Mendrez 1972 fig.8 p203) do not contribute to the edges of the posttemporal fenestra, similar to the early therocephalians. They contact the parietal dorsally, the interparietal medially, the supraoccipital ventro-laterally and the squamosal laterally (Mendrez 1972 fig.4 p197).

The tabulars of whatsiid therocephalians are relatively small and oval in shape, and contact the parietal and interparietal dorsally, the supraoccipital medially and the

squamosal laterally. The tabular forms the dorsal rim of the posttemporal fenestra (Kemp 1972 fig.11B p30) (Fig. 17D).

The tabulars of *Promoschorhynchus platyrhinus* are badly damaged and Mendrez (1974b fig.4 p75) does not indicate or discuss them.

In *Moschorhinus kitchingi* (Mendrez 1974a fig.4 p84) the large tabulars are similar in shape and size to those of *Regisaurus*. They cover the lateral edges of the supraoccipital to a greater extent, reducing the exposed portions of the dorsal process of the supraoccipital and the interparietal. This increases the area of the tabulars (Mendrez 1974a fig.4 p84, Durand 1991 fig.15 p395).

In *Thrinaxodon liorhinus* (Fourie 1974 fig.25 p369), the tabulars appear very similar to those of *Procynosuchus*. They are quite large in size and encircle the posttemporal fenestra. They press against the mastoid processes of the opisthotic ventrally and against the squamosals laterally.

The tabulars of *Procynosuchus* (Kemp 1979 fig.3B p78) are relatively large in occipital view, and form most of the lateral parts of the occiput. They contact the interparietal dorsally, the supraoccipitals medially, the squamosals laterally and the opisthotics ventrally. The posttemporal fenestrae are completely encircled by the tabulars. The portion of tabular forming the dorsal margin of the posttemporal fenestra is quite thick (Brink 1960 p134).

The tabulars of gorgonopsians (Kemp 1969 fig.8 p18) are relatively larger in proportion to the other occipital bones than those of whaitsiids, but relatively smaller than those of *Procynosuchus*. They have an almost diamond-shape and contact the interparietal dorso-medially, the supraoccipital ventro-medially, the squamosal laterally and the opisthotic ventrally. The tabular forms the dorsal and lateral and posterior edges of the posttemporal fenestra.

A ventro-lateral projection of the tabular extends far ventrally to cover most of the dorso-lateral part of the mastoid process of the opisthotic. This process also covers part of the suture between the mastoid process of the opisthotic and squamosal (Kemp 1969 fig.8B p18). Such a structure is not noted in any of the other therapsid groups compared in this study.

3.9 Exoccipital

3.9.1 Description

In *Glanosuchus macrops* SAM K238a, only the anterior part of the left exoccipital is intact and the description is based on other prepared early therocephalian specimens.

The paired exoccipitals are medium-sized tripartite bones, situated lateral to the foramen magnum. The medial sides of the exoccipitals form part of the floor and walls of the foramen magnum as well as the floor and the roof of the jugular foramen. They do not meet above or below the foramen magnum, but are separated by the supraoccipital dorsally and the basioccipital ventrally (Figs 11, 16).

The exoccipital contacts the opisthotic antero-laterally and the supraoccipital dorsally. They form the lateral parts of the occipital condyle for the articulation with the vertebral column, while the basioccipital forms the central part of the occipital condyle. Olson (1944 p84) claims that the exoccipitals of anomodonts and cynodonts form a double occipital condyle.

In posterior view, the exoccipital of the early therocephalians *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 appear to have three processes, namely a dorsal process, a ventral process and a lateral process. The ventral process forms the lateral portion of the occipital condyle. The dorsal process is a flat vertical sheet of bone which extends dorsally and around the dorso-lateral edge of the foramen magnum. The lateral process is quite large in *Ptomalestes avidus* SAM 11942, and it extends laterally towards the posttemporal fenestra (Fig.11). The lateral process of *Lycosuchus vanderrieti* GS M793 is very long, and forms the dorsal and medial edges of the jugal foramen (Fig. 16).

The ventral process of the exoccipital of *Ptomalestes avidus* SAM 11942 is simple, but in *Lycosuchus vanderrieti* GS M793 it is divided into a ventro-lateral and a ventro-medial process. The ventro-lateral process is the smaller of the two, and extends laterally below the lateral process to form the ventral edge of the jugular foramen. The ventro-medial process forms the lateral part of the occipital condyle and a part of the floor of the foramen magnum.

The hypoglossal canal which pierces the exoccipital is well-developed and large in *Glanosuchus macrops* SAM K238a. The foramen for nerve XII pierces the exoccipital on the inner margin of the foramen magnum on the suture between the exoccipital and the basioccipital. A portion of the exoccipital, connecting the posterior edge of the jugular foramen and the anterior edge of the foramen for nerve XII has broken off in *Glanosuchus macrops* SAM K238a. The foramina are not definite and appear as one large elongated aperture (sections 493-502) (Figs 5, 6, 7, 8).

In some therapsidians, i.e. *Regisaurus* (Mendrez 1972 fig.8: p203) and *Moschorhinus* (Durand 1991 p405), a second, smaller hypoglossal canal passes through the exoccipital and exits on the outer surface just below the jugular foramen. Olson (1944 p63) states that the number of hypoglossal canals vary between one and two in various therapsid groups, the number being of no particular significance. This second outer hypoglossal canal is not visible in *Glanosuchus macrops* SAM K238a.

The exoccipitals form a very small portion of the medial wall of the braincase (Fig. 5) and contribute a very small part to a recess of the inner ear (Fig. 9). This recess is formed mainly by the opisthotic, the supraoccipital and the prootic. Near the jugular foramen the posterior end of the exoccipital forms the base of a pit in the anterior margin of the cochlear recess. This structure is therefore referred to as the exoccipital pit (sections 503-509).

The exoccipital originates lateral to the basioccipital as a small bone that increases in height posteriorly. The medial walls of the exoccipitals have two shallow fossae, one anteriorly and one posteriorly. These fossae are positioned diagonally in a dorso-ventral plane and with the central fossa of the basioccipital, possibly accommodated structures relating to the medulla oblongata (Fig. 5). A suggestion for these fossae, is that they accommodated a blood sinus, similar to the one in vertebrates that produces cerebrospinal fluid.

3.9.2 Comparative View

The size of the exoccipitals in other therapsids varies greatly. Olson (1944 p13) states that fusion of the "exoccipitals to the periotics and the supraoccipital is characteristic in

anomodonts", and claims that the exoccipitals are fused to the basioccipital (Olson 1944 p62). This is also found in *Dicynodon grimbeeki* (Agnew 1958 p97).

According to Cluver (1971 p163), the suture between the exoccipitals and opisthotics in *Lystrosaurus* is very obscure. The exoccipitals meet ventrally in the midline, forming the floor of the foramen magnum. The exoccipital forms a part of the jugular foramen, together with the opisthotic and the basioccipital. The lateral processes of the exoccipitals are very small and do not extend laterally as far as the posttemporal fenestra (Cluver 1971 fig.10 p170).

In *Regisaurus*, the exoccipital contributes neither to the floor of the foramen magnum nor the occipital condyle (Mendrez 1972 fig.8 p203). It forms the roof of the jugular foramen. The exoccipitals are laterally placed to the foramen magnum, as in *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942.

The exoccipitals of *Promoschorhynchus* (Mendrez 1974b fig.4 p75) are tripartite. The lateral process is long and slender, more so than in *Moschorhinus*. A characteristic given by Mendrez for both *Promoschorhynchus* (1974b p16) and *Regisaurus* (1972 p206), is a well-developed tuberosity on the dorsal process. This is for the articulation between the exoccipital and the proatlas. It is damaged in *Promoschorhynchus* but appears to have been large (Mendrez 1974b). The ventral edge of the foramen magnum is formed by a triangular piece of basioccipital, below which the exoccipitals meet and form a suture. Further inside the foramen magnum, beyond the apex of the triangle of basioccipital, the exoccipitals also meet and the suture between them runs into the foramen magnum (Mendrez 1974b fig.4 p75).

In *Moschorhinus* (Mendrez 1974a p87 and Durand 1991 p405), the foramen magnum is formed mainly by the exoccipitals. They are small bones, with small ventrally-curved, lateral processes. A small part of the supraoccipital forms the dorsal margin of the foramen magnum on the dorsal midline and a small part of the basioccipital forms the margin on the ventral midline. The ventro-lateral processes are also well developed, forming a deep opening for the jugular foramen. The exoccipitals contribute to the occipital condyle.

In occipital view, the exoccipitals of *Ictidosuchops* (Crompton 1955 fig.2A p154, fig.6C p166) are triangular in shape. The definite processes present in *Moschorhinus* and *Promoschorhynchus* are absent.

Similar to other therocephalians, the exoccipitals of *Ictidosuchops* form the dorsal walls of the jugular foramina. In the exoccipital below the jugular foramen, is a small opening for the hypoglossal nerve XII (Crompton 1955 fig.5A p164).

The exoccipitals of *Thrinaxodon* (Fourie 1974 fig 25A p369) differ from those of therocephalians discussed in this study. In *Thrinaxodon*, these bones do not extend dorso-laterally as far as in therocephalians. They only form the medial wall of the jugular foramen, in contrast to early therocephalians where the exoccipital forms the dorsal and medial walls. In *Thrinaxodon*, the supraoccipital has extended laterally to form the dorsal walls of the jugular foramina. Lateral to the foramen magnum and below the supraoccipital-exoccipital suture on each exoccipital, is a foramen for the hypoglossal nerve XII (Fourie 1974 fig.25A p369). The size of the jugular foramen is exceptionally large.

In occipital view, the exoccipitals of *Procynosuchus* appear greatly enlarged (Kemp 1979 fig.3B p78). They are laterally expanded, and contact the tabular and squamosal.

A peculiar feature found on the exoccipitals of *Procynosuchus* (Kemp 1979 fig.3B p78), is the venous notch present on each lateral margin of the foramen magnum. The notches are situated between the supraoccipital-basioccipital suture. Kemp (1979 fig.3B p78, p105) assumes that each notch conducted a vertebral vein. The exoccipitals of *Procynosuchus* (Brink 1960 p129, fig.33 p130) do not surround the foramen magnum ventrally, but only form the lateral margins. They form the two main condyles for articulation with the atlas. According to Brink (1960 p129) this condition is typical of cynodonts, where the condyles articulate with the separate left and right halves of the atlas, while the loose intercentrum articulates with the basioccipital facet. This arrangement demands a trilobed odontoid process (atlas centrum) on the axis.

The small exoccipitals of gorgonopsians are more or less oval in shape. In *Leontocephalus* (Kemp 1969 fig 8B p18) the dorsal part of the exoccipitals appear to have articulation surfaces. This is similar to *Moschorhinus*, *Promoschorhynchus* and *Procynosuchus* where the exoccipitals form the two main articulation surfaces which

articulate with the proatlas. In *Leontocephalus*, a smaller more prominent process called the exoccipital process is present on the lateral process of the exoccipital. This has not been noted in any of the therocephalians.

3.10 Squamosal

3.10.1 Description

This bone has been extensively described by Van den Heever (1987), and only a brief description is presented here.

The squamosal is the largest bone in the occipital region of the skull. It contributes to the occiput and the postero-lateral part of the braincase and is paired. Even though they do not contribute to the interior wall of the braincase, the squamosals are important bones because they form the postero-lateral portion of the temporal fenestra, the pocket containing the quadrate and the jugal arch (Figs 11, 12, 16).

The terms used here are those introduced by Mendrez to describe the structures in *Regisaurus* (1972) and *Moschorhinus* (1974a). The squamosals have broken off in *Glanosuchus macrops* SAM K238a, except for a small fragment of the intermediate process on the left side of the skull (sections 506-528).

The squamosal of early therocephalians consists of five processes, one dorsal, one ventral and three anterior. This is similar to the squamosal in *Regisaurus* (Mendrez 1972 p199), *Ictidosuchops* (Crompton 1955 p151, fig.2B p154, p156, fig.4A p157), and *Thrinaxodon liorhinus* (Fourie 1974 fig.24C p368).

The dorsal process projects upwards and overlaps the lateral edge and lamboid processes of the parietal. Its dorsal edge overlies the dorsal edge of the tabular (Fig. 12).

The first anterior process is the intermediate process, and it passes inwards directly below the dorsal process. Medially, the intermediate process contacts the prootic ventrally and the supraoccipital dorsally. In *Glanosuchus macrops* SAM K238a this process forms the dorsal edge of the anterior opening of the posttemporal fenestra (Fig.

12). In *Regisaurus* (Mendrez 1972 p199), this process forms the dorsal and lateral edge.

The second anterior process, the antero-ventral process, connects the central process of the prootic in a short suture, to form a bar which is situated anterior to the posttemporal foramen in early therocephalians. This is also found in *Regisaurus* (Mendrez 1972 p199) and whaitsiid therocephalians (Kemp 1972). This bar is absent in lychosuchids. The opening above and below the posttemporal bar forms the pterygo-paroccipital foramen.

The intermediate process of the squamosal forms the roof of the anterior portion of the posttemporal fenestra (sections 501-528). The roof is flat and not arched as in *Ptomalestes avidus* SAM 11942 (Fig. 11), *Regisaurus* (Mendrez 1972 fig.7 p201) and *Moschorhinus* (Mendrez 1974a fig.6 p90).

The zygomatic process is the third anterior process, and is a lateral flange formed by the mastoid process of the squamosal. This horizontal process is long and narrow and forms a suture with the posterior process of the jugal, to form the jugal arch. This jugal arch forms the lateral edge of the temporal fenestra which is damaged in *Glanosuchus macrops* SAM K238a (Fig. 3B).

The quadrate process of the squamosal contacts the mastoid process of the opisthotic ventro-laterally, the quadrate antero-ventrally and the tabular dorso-laterally. The quadrate fits into a pocket in the ventral surface of the quadrate process of the squamosal. This process forms a large lateral flange anteriorly which gives rise to the zygomatic process.

3.10.2 Comparative View

The large triradiate squamosal of *Lystrosaurus* is well-developed (Cluver 1971 p203). It appears to have a slightly different structure to that of therocephalians. In occipital view, the lateral flanges are very robust, but do not extend far laterally as they do in therocephalians.

The squamosals of *Dicynodon grimbeeki* (Agnew 1958 fig.34 p86) are similar to those of *Lystrosaurus*. The angle between the dorsal and intermediate processes are not as sharp as they are in *Lystrosaurus*.

The antero-ventral process of the squamosal is absent from dicynodonts and gorgonopsians, therefore, the bar in front of the posttemporal fenestra is absent (Kemp 1979 p27, 1972, Van den Heever 1987).

The squamosals of *Regisaurus* (Mendrez 1972 fig.1 p194, fig.7 p201) are very similar to those of *Ptomalestes avidus* SAM 11942. In occipital view, the posttemporal fenestra is formed laterally by the quadrate process of the squamosal.

Kemp (1972 p27) describes the whaitsiid squamosal as having four processes not five. The processes are the ventral process (quadrate process) which runs down behind the quadrate, the zygomatic process, the parietal process (dorsal process), which forms the lamboid crests and the otic process (antero-ventral process), which forms part of the posttemporal bar. The intermediate process is considered by Kemp (1972 p27) to be part of the dorsal process.

The antero-ventral process joins the central process of the prootic in a convex edge. Simultaneously, it is directed antero-ventrally as a free process and contacts the quadrate ramus of the pterygoid. It is not certain how the squamosal contacts the quadrate ramus of the pterygoid in *Glanosuchus macrops* GS M796, *Glanosuchus macrops* SAM K238a or *Ptomalestes avidus* SAM 11942, as this region is damaged in all of these fossils.

In *Moschorhinus*, the quadrate process joins the pterygoid process of the quadrate. The squamosal of *Moschorhinus* possesses similar processes as *Glanosuchus macrops*, except for an additional process. This process is anteriorly directed, and is called the epipterygoid process of the squamosal. It contacts the postero-ventral process of the epipterygoid (Mendrez 1974a fig.6 p90). This process is not present in the early therocephalians, whaitsiids or *Regisaurus*, but is also present in *Promoschorhynchus* (Mendrez 1974a fig.5 p75).

The dorsal portion of the skull of *Promoschorhynchus* described by Mendrez (1974b fig.5 p75) is damaged. The dorsal process cannot be incorporated into this comparison.

The general structure of the lower part of the squamosal of *Promoschorhynchus* is similar to *Moschorhinus*, although in *Moschorhinus* this area is more robust.

The squamosal of *Ictidosuchops* appears very similar to that of early therocephalians and *Regisaurus* (own observation). The portion of the body which forms the postero-lateral corner of the skull is slightly concave. This is, according to Crompton (1955 p185), probably indicative of the course of the external auditory meatus. The squamosal supports the quadrate, a vertical plate which fits into a pocket in the squamosal (Crompton 1955 p158).

In dorsal view, the squamosals of gorgonopsians are very large. The dorsal process which overlaps the lamboid processes of the parietal are antero-posteriorly widened. These processes are dorso-ventrally flattened in some gorgonopsians and are positioned parallel to the midline of the skull (Kemp 1969 fig.4 p14 fig8A p18).

In occipital view, the squamosal is wide ventrally but very narrow dorsally (Kemp 1969 fig.8A p18). The antero-ventral process is absent from the squamosal, resulting in the absence of the posttemporal bar in gorgonopsians.

3.11 Pterygoid

3.11.1 Description

This bone has also been extensively described by Van den Heever (1987), and only a short description is necessary in this discussion.

The pterygoid is a paired bone that forms the anterior part of the basicranial axis of the braincase. The body consists of an elongated shaft extending from the posterior edge of the palate to the parabasisphenoid. The medial sides of the pterygoids are pressed firmly together, except at the posterior end. Here the edges separate to form the interpterygoid vacuity (Figs 3B, 10).

The anterior ends of the pterygoids contact the palatine laterally and the vomer medially. The posterior end contacts the parabasisphenoid, and the suture between these two bones runs through the position of the external openings for the internal carotids.

These openings are situated midway on either side of the parabasisphenoid keel (Fig. 4A).

The epipterygoid is situated on the dorsal margin of the quadrate process of the pterygoid, and the prootic is situated on the postero-dorsal margin of the parabasisphenoid (Figs 12, 13).

Each pterygoid bone has two lateral processes, one anterior (transverse processes) and one ventral (quadrate process). The transverse process contacts the ectopterygoid laterally and forms the posterior edge of the suborbital fenestra. The quadrate process supports the epipterygoid, and contacts the quadrate posteriorly (Fig. 3B).

Ventrally, the medial edges of the pterygoids are pressed closely together to form a centrally situated crest, the ventro-medial crest. On either side of this crest is a shallow, elongated fossa. The lateral edges of the pterygoids form ventro-lateral crests (Fig. 3B). This is very similar to the ventral aspect of the pterygoids of *Regisaurus* (Mendrez 1972 fig. p).

At the posterior limit these ventro-lateral crests expand towards the ventro-medial crest to form raised pterygoid bosses, one on either side (Van den Heever 1987 p156). Embedded in these bosses are a few small pterygoid teeth, conical in shape. Mendrez (1972 p200) refers to these bosses as dentigerous tuberosities in *Regisaurus*.

Lateral to these tuberosities are the transverse processes. These are large and well-developed. They are positioned almost perpendicular to the bodies of the pterygoids. The lateral tip of each transverse process is antero-posteriorly widened (Fig. 3B).

The rostrum of the parabasisphenoid in *Glanosuchus macrops* SAM K238a is positioned level to the postero-ventral edge of this widened end. The dorso-lateral side of the transverse process is extended upwards to form a short ridge. This ridge and the antero-lateral edge contacts the ectopterygoid.

The ventro-lateral crest of the pterygoid forms the medial edge of the suborbital fenestra. The anterior margin of the transverse process forms the posterior edge of the suborbital fenestra (Fig. 3B).

Postero-medial to the transverse processes, the pterygoids form the interpterygoid vacuity. On either side of this vacuity, are the basisphenoid processes of the pterygoid. The posterior ends of these processes clasp the parabasisphenoid anterior to the ventral parabasisphenoid keel. These processes are quite large in early thercephalians and in *Regisaurus* (Mendrez 1972 fig.3 p196).

On either side of the basisphenoid processes are the quadrate processes of the pterygoid. The bases of these processes, contact the basisphenoid process laterally and are very broad and horizontal (section 390). This lamina of bone lying between the pterygoid and quadrate process is also found in *Moschorhinus* (Mendrez 1974a) and *Promoschorhynchus* (Mendrez 1974b). The quadrate processes progress laterally away from the body of the pterygoids. The vertical stem of the quadrate process progressively increases in length. This increases the depth of the gutter between the lateral and medial edges. The quadrate process is important because it supports the epipterygoid on its dorsal surface. The epipterygoid is embedded within the pterygoid process of the quadrate.

In section, the quadrate process of *Glanosuchus macrops* SAM K238a appears to be a sickle-shaped splint of bone, with a short horizontal portion supporting the epipterygoid dorsally, and a long thin lateral ventral part extending below it. On the medial side of this lateral portion, is a deep gutter. The quadrate process has been discussed in detail with the epipterygoid (Sub-section 3.1.1).

The parabasisphenoid keel is anteriorly elongated and is clasped by the basisphenoid processes (sections 393-397).

At the level of section 393, the pterygoid has reduced to thin splints of bone pressed against the ventral surface of the parabasisphenoid body. The parabasisphenoid increases laterally in size in a posterior direction. The dorsal surface of the quadrate process is firmly pressed against the ventral edge of the antero-ventral process of the epipterygoid and the parabasisphenoid body (sections 395-402). At sections 403 through 414, the lateral edges of the parabasisphenoid support the medial edges of the epipterygoid.

At section 415, the quadrate process is directed posteriorly towards the quadrate, progressively moving away from the body of the parabasisphenoid.

3.11.2 Comparative View

The pterygoids of *Dicynodon grimbeeki* do not contact the vomer. Anteriorly, they contact the palatine and ectopterygoid, and postero-laterally the parabasisphenoid. An extensive interpterygoid vacuity is present (Agnew 1958 p88). The quadrate ramus of the pterygoid is a long thin bar of constant thickness, which terminates posteriorly against the pterygoid process of the quadrate.

The base of the epipterygoid rests on the dorsal surface of the quadrate ramus (Agnew 1958 fig.40 no.5 p92), and is not embedded into it, as is found in *Glanosuchus macrops* SAM K238a.

In *Dicynodon*, the pterygoid contacts the ectopterygoid, which in *Lystrosaurus* is absent. In *Lystrosaurus*, the pterygoid differs slightly from early theropcephalians in shape (Cluver 1971 fig.24 p187). Each pterygoid has two processes, namely a palatine process and a posterior quadrate process. The latter process is a broad median plate-like bone which meets its counterpart behind the interpterygoid vacuity. The quadrate ramus is a flat bar that extends laterally and is inserted between the paroccipital processes of the opisthotic and the quadrate. A smooth surface is present on the quadrate at this connection (Cluver 1971 p200).

The interpterygoid vacuity is positioned anteriorly in *Lystrosaurus*, and does not extend to the anterior edge of the parabasisphenoid keel, as it does in *Glanosuchus macrops* GS M796. The anterior palatine process is inserted between the palatine medially and the posterior pterygoid process of the maxilla laterally (Cluver 1971 p200). Between the palatine and pterygoid is a canal which runs from the palate to the posterior edge of the labial fossa.

The median pterygoid processes meet to form a strong pterygoid plate that closely clasps the ventral surface of the parabasisphenoid. This plate encloses a canal which conducted the palatine branch of the facial nerve VII (Cluver 1971 p200).

The pterygoid of *Regisaurus* (Mendrez 1972 fig.2 p195) is very similar to *Glanosuchus macrops* SAM K238a.

According to Kemp (1972 p23), the pterygoids of whatsiids resemble cynodonts, especially in the manner in which they are associated with the parabasisphenoid and the reduction of the interpterygoid vacuity. Kemp (1972 p32) notes that the loss of the pterygoid teeth is solely a whatsiid characteristic. Mendrez (1965 p1044-1045) disagrees with this observation, since pterygoid teeth are also absent in *Promoschorhynchus* and *Moschorhinus*.

The pterygoids of whatsiids form a deep narrow keel behind the palate and they clasp the equally deep keel of the parabasisphenoid posteriorly (Kemp 1972 fig.9A p20) (Fig. 17). A feature of whatsiids is the reduction or absence of the suborbital fenestrae. The only other therocephalian taxon lacking these fenestrae is *Euchambersia mirabilis* (Mendrez 1975 fig.9 p394).

The ventro-medial crest formed by the medial edges of the pterygoid is not present in *Theriognathus*. The ventro-lateral crests have been laterally enlarged to meet the ectopterygoid. Two wide fossae are positioned in this area. Anteriorly, the ventro-lateral crests are rudimentary (Mendrez 1974b fig.5 p389).

The pterygoids of *Promoschorhynchus platyrhinus* differ from *Regisaurus* and early therocephalians. The anterior portion forming the medial edges of the suborbital fenestrae has widened and the fenestrae are reduced in length. The ventro-medial crest is well-developed. However, the ventro-intermediate crests are not as well-developed as they are in the early therocephalians.

The pterygoid bosses are present as elongated crests in *Promoschorhynchus*, and pterygoid teeth are absent. The interpterygoid foramen is wider than in *Regisaurus*, and the basisphenoid processes are poorly developed (Mendrez 1974b fig.2A p72, 1975 fig.8 p393, fig.13 p402).

The transverse processes of *Promoschorhynchus* do not lie perpendicular to the longitudinal axis of the pterygoid body, as they do in *Glanosuchus macrops* GS M796 and *Glanosuchus macrops* SAM K238a, but are slightly posteriorly directed. The troughs situated between the interpterygoid foramen and the quadrate process are wider than the early therocephalians, and the posterior edge of the transverse process appears to be continuous with the edge of the quadrate process (Mendrez 1974b p74).

The basisphenoid process extends backwards beyond the external openings of the internal carotids in the parabasisphenoid keel, differing from the more anterior position of the early therocephalians.

The anterior portion of the pterygoid lying in front of the tuberosities is broader in *Moschorhinus* than in *Promoschorhynchus*. This part of the pterygoid does not contribute extensively largely to the medial edges of the suborbital fenestra (which are quite small), as it does in *Regisaurus* and *Promoschorhynchus* (Mendrez 1974a fig.2 p76, 1975 fig.6 p391) and *Glanosuchus macrops* SAM K238a (own observation).

In *Moschorhinus*, the ventro-medial crest extends from the palatine suture to the anterior edge of the interpterygoid foramen. This differs from the condition in *Promoschorhynchus*, where the anterior portion of the crest is reduced. The ventro-intermediate crests are very large. They extend towards and over the tuberosities which are toothless and underdeveloped.

In *Moschorhinus* (Mendrez 1974a fig.2 p76, 1975 fig.5 p389), the quadrate and transverse processes are linked by a thin lamina of bone on the lateral margin of the pterygoid body. This lamina is absent in whaitsiids (Kemp 1972 fig p), but present in *Glanosuchus macrops* SAM K238a (own observation) (Fig. 3B listed as *ptl*).

In all the therocephalian groups described thus far, the interpterygoid foramen is single, but in *Moschorhinus* it is paired. The interpterygoid foramen is very different from *Glanosuchus macrops*, *Promoschorhynchus* and *Regisaurus* (own observation). The foramina in *Moschorhinus* are very narrow and elongated, and are situated on either side of the parabasisphenoid rostrum. The rostrum extends forwards and is clasped by the small basisphenoid processes of the pterygoid (Mendrez 1974a fig.5 p88, p83). The anterior edges of the interpterygoid foramina are continued forwards as two deep fossae to the centre of the tuberosities. The quadrate processes appear more robust in *Moschorhinus* than they do in *Glanosuchus macrops*.

The pterygoids of *Ictidosuchops* resemble those of *Procynosuchus*, except that the suborbital fenestrae of *Ictidosuchops* are present in a similar position to that of *Regisaurus* (Mendrez 1975 fig.10 p369, fig.13 p402). Of particular importance is the connection of the pterygoid to the basiptyergoid process of the parabasisphenoid. Except for a very small strip of bone posteriorly, the entire basiptyergoid processes are

covered by pterygoid. The connection between the posterior end of the pterygoids and the parabasisphenoid differs from the condition found in *Regisaurus* described above. The ends of the pterygoid posterior to the interpterygoid vacuity do not meet. The basisphenoid flares out laterally to form two large basiptyergoid processes (Crompton 1955 fig.1B p152).

The posterior ends of the pterygoid are positioned in close proximity to each other, closely hugging the ventral surface of the basiptyergoid processes on either side of the parabasisphenoid keel. The rostrum protrudes between these processes into the interpterygoid vacuity.

The quadrate processes are very slender vertically orientated processes which pass backwards to the quadrate, but their orientation and angle to the parabasisphenoid are similar to early therocephalians.

The interpterygoid vacuity is large and pear-shaped. Anterior to this vacuity is a small vacuity which separates the pterygoids for a short distance (Crompton 1955 p153). This is a feature not indicated in *Ictidosuchops* by Mendrez (1975 fig.10 p396).

The transverse processes are sturdy and very similar in shape to early therocephalians. The angle of the processes to the body of the parabasisphenoid is also similar to the early therocephalians. The anterior laminae also resemble those of *Glanosuchus macrops* and they form the medial edge of the suborbital fenestrae. The tuberosities are present but pterygoid teeth are absent, similar to the condition in *Promoschorhynchus*, *Moschorhinus* and whaitsiids.

A prominent characteristic in cynodonts is the absence of suborbital fenestrae. This is evident in *Procynosuchus*, as well as the lack of tuberosities and pterygoid teeth. The interpterygoid vacuity is large and the rostrum extends forwards into the foramen (Kemp 1979 fig.2 p77). The transverse processes are orientated perpendicular to the longitudinal axis of the pterygoids, but the lateral ends are not widened as they are in *Glanosuchus macrops* SAM K238a.

A large interpterygoid vacuity is present in *Procynosuchus*. Lateral to this vacuity, the pterygoids are continued posteriorly as deeply concave ventro-lateral surfaces. The pterygoids posterior to the interpterygoid vacuity do not meet, and are situated against

the ventral surface of the parasphenoid, on either side of the rostrum. The rostrum protrudes down the midline of the interpterygoid vacuity. The ventro-medial borders contributing to the edges of the interpterygoid vacuity are very broad in contrast to the dorso-lateral edges which are very narrow. The quadrate processes originate and continue posteriorly to the point where the external openings of the internal carotid foramina are situated on the parabasisphenoid keel, similar to therocephalians (Brink 1960 p144-145).

The quadrate processes maintain a constant thickness throughout their length. The quadrate processes in *Procynosuchus* do not lend any significant support to the eipterygoids (Brink 1960 p145). This condition differs in early therocephalians, where these two bones are closely connected.

The quadrate processes do not contact the quadrate, but turn towards the prootic, level with the quadrate and cover the prootic dorso-laterally. This has not previously been observed in any other therocephalian (Brink 1960 p145).

The pterygoids meet one another anterior to the interpterygoid vacuity, with broad areas of contact. The anterior tips of the pterygoids extend forward over the vomer. Their joint dorsal margin contains a groove which continues with the groove in the vomer anteriorly (Brink 1960 p145). This groove continues posteriorly into the interpterygoid vacuity.

The suborbital fenestrae are absent in the Gorgonopsia. The transverse process is very large due to the anterior extension into the position of the suborbital fenestra in therocephalians (Kemp 1969 fig.6 p16).

In ventral view, the pterygoid is cross-shaped. The anterior portion of the pterygoid forms a large flat plate-like bone contacting the palatine anteriorly. The ectopterygoid is medially enlarged. The ventro-lateral crests found in early therocephalians and *Regisaurus* are absent.

Posteriorly, the pterygoid overlies the anterior portion of the parabasisphenoid keel. A longitudinal groove runs along the anterior part of the dorsal surface and opens anterior to the interpterygoid vacuity as a laterally facing recess. The dorsal surface of the pterygoid slopes up towards the midline for the length of the groove, but behind the

groove the dorsal surface is horizontal. The width of the pterygoid increases gradually to the basipterygoid process. The pterygoids are closely connected along the midline, except for the minute interpterygoid vacuity immediately in front of the basipterygoid process.

In gorgonopsians, the quadrate ramus is positioned similar to the early theropcephalians. The epipterygoid is positioned on top of the ramus, and is not embedded into it as in *Glanosuchus macrops* SAM K238a (Kemp 1969 fig.12X,Y,Z p28).

Tuberosities and pterygoid teeth are absent from gorgonopsian pterygoids (Kemp 1960 fig.2 p8, fig.6 p16).

3.12 Parabasisphenoid

3.12.1 Description

The parabasisphenoid consists of two fused bones, the parasphenoid and the basisphenoid (Romer 1956 p64). It is situated anteriorly in the base of the braincase, and is roughly triangular in ventral view (Figs 3B,C). It has an anterior suture with the pterygoid, a posterior suture with the basioccipital, and a dorsal suture with the basal area of the prootic. The latter extends from the base of the prootic directly below the origin of the antero-ventral process, to where the prootic forms the antero-dorsal lip of the fenestra ovalis (Fig. 5).

The parabasisphenoid forms the antero-ventral part of the basal tubera and the parabasisphenoid keel. The anterior region of the parabasisphenoid is clasped on either side by the basisphenoid processes of the pterygoids. The slightly interdigitating suture between the parabasisphenoid and the basioccipital runs through the external opening of the internal carotid canals situated anteriorly on the parabasisphenoid keel.

The cultriform process or rostrum of the parabasisphenoid is V-shaped, and extends anteriorly between the interpterygoid vacuity (sections 370-380). This process is clear in *Glanosuchus macrops* GS M796 but is damaged in *Ptomalestes avidus* SAM 11942. In reptiles, the sphenethmoid originates within the dorsal V-shaped inset of the process

as a thin sheet of bone that forms the interorbital septum (Romer 1956 p68). There is no indication that such a bony septum existed in early Therocephalia.

The parabasisphenoid keel is a single, median plate. It is directed ventrally. The ventral edge protrudes below the ventral surface of the braincase. The keel is extended in an anterior direction and the antero-ventral edge protrudes beyond the parabasisphenoid-pterygoid suture (sections 390-440) (Figs 3B,C, 21). This structure is present in therocephalians, gorgonopsians and cynodonts (although reduced) but is absent in dicynodonts.

Anteriorly, the dorsal surface of the parabasisphenoid forms the rounded pituitary fossa of which the posterior wall rises vertically as the dorsum sellae. The base of the fossa forms the sella turcica and the dorsum sellae is formed by the parabasisphenoid and the base of the prootics. The dorsum sellae also contributes to the floor of the brain cavity (Romer 1956 p67, 1986 p243). In sagittal section, the dorsum sella in *Glanosuchus macrops* SAM K238a rises upwards steeply, and then declines abruptly to the braincase floor, at roughly the same level as the sella turcica. This area is fractured in *Glanosuchus macrops* SAM K238a but is well-preserved in *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942 (Figs 5, 12, 13, 14, 15, 18).

In ventral view, the external openings for the internal carotids lie on either side of the parabasisphenoid keel (Fig. 3B). These canals penetrate the body of the parabasisphenoid below the pituitary fossa. In the sectioned *Glanosuchops macrops* SAM K238a, they run anteriorly through the parabasisphenoid body for a short distance before opening as a single foramen, the internal openings of the internal carotids, in front of the pituitary fossa (sections 402-407) (Fig. 5). Furthermore, the carotid canals extended posteriorly in the parabasisphenoid body, parallel to the midline, and are referred to as the vidian canals (sections 407-428). The destination of these canals is not definite in the sectioned *Glanosuchus macrops* SAM K238a because they end abruptly in section 428. The parabasisphenoid does not appear to be well-preserved in this area.

A shallow, circular fossa is present on the ventral surface of the braincase (Figs 3B,C, 21) immediately behind the parabasisphenoid keel. It extends to the level of the posterior edges of the basal tubera. The transverse parabasisphenoid-basioccipital suture is positioned in the centre of this fossa. It lies across the anterior portion of the

basioccipital. Laterally, on either side of this fossa, are the basal tubera surrounding the fenestra ovalis (Fig. 3C).

3.12.2 Comparative view

The rostrum is prominent in *Dicynodon grimbeeki* (called the rostromparasphenoid by Agnew (1958 p97)). It is a thin process which curves antero-dorsally from behind the interpterygoid vacuity pointing towards the tip of the snout. The anterior half of the rostrum is situated in a shallow groove in the dorsal edge of the vomer. In *Dicynodon*, the dorsal edge of the rostrum has a longitudinal groove for the presphenoid ossifications, and has a U or V shape in section (Agnew 1958 p97).

The parabasisphenoid possesses no posterior expansions representing the wings of the parasphenoid. This agrees with Olson's (1944 p69, p73) description. It is pierced by a single internal canal which runs almost vertically through the bone. In *Glanosuchus macrops* GS M796, two internal carotid canals pierce the parabasisphenoid either side of the keel. Agnew (1958 p98) claims that since most anomodonts possess paired carotid canals, this appears to be a variable feature in this group. The single canal in *Dicynodon grimbeeki* may have resulted from the fusion of the two canals.

The sella turcica of *Dicynodon* is positioned posterior to the carotid canal in the floor of the basisphenoid, and forms a shallow depression. A distinct dorsum sellae is absent (Agnew 1958 p98). In early theriocephalians, the pituitary fossa is deep and a definite dorsum sellae is present.

There is a definite unossified zone present between the parabasisphenoid and the basioccipital in *Dicynodon* (Agnew 1958 p98) and *Lystrosaurus*, but this zone is not visible in ventral view, as found by Olson (1944 p64) for dicynodonts.

On either side of the rostrum, a basipterygoid process is present on the parabasisphenoid process. In *Dicynodon*, it supports the base of the epipterygoid as a small but distinct structure (Agnew 1958 p97-98), but in *Lystrosaurus* it appears larger and better developed (Cluver 1971 fig.4 p165).

The basicranial pit, situated between the basisphenoid and basioccipital, lies in the same position as the unossified zone described above. In *Lystrosaurus*, this structure is continued ventrally for some distance. The parabasisphenoid keel is absent in dicynodonts (Olson 1944 p69, Agnew 1958 p98).

The parabasisphenoid of *Regisaurus* is very similar to that of early therocephalians. In ventral view it is triangular, with very well-developed basal tubera (Mendrez 1972 fig.2 p195). The keel is well-developed and prominent. The basicranial fossa on the ventral surface of the basicranial axis is deepest posterior to the keel. It extends onto the basioccipital, shallowing progressively.

In whatsiid therocephalians, the parabasisphenoid keel is well-developed and the basipterygoid processes are large and prominent. The rostrum is short and it seems unlikely that it played a role in the ventral support of the orbitosphenoid (Kemp 1972 p25). The parabasisphenoid is exempted from the border of the fenestra ovalis (Mendrez 1974b Table.1 p97).

The morphology of the parabasisphenoid of *Promoschorhynchus* is typical of therocephalians (Mendrez 1974b p74). The basipterygoid process is not completely covered by the pterygoid. In her specimen, the keel is damaged. The external openings of the internal carotid canals are situated on the suture between the pterygoid and the parabasisphenoid either side of the keel (Mendrez 1974b fig.2A p74).

The basal tubera (the tubercula sphenoccipitalia of Mendrez 1974b p74) are well-developed. The parabasisphenoid and the basioccipital each form less than one quarter of the border of the fenestra ovalis, differing from early therocephalians and *Regisaurus* in this respect.

In ventral view, the parabasisphenoid of *Moschorhinus* is relatively broader than in *Regisaurus*, but retains the triangular shape. The basal tubera of *Moschorhinus*, like that of *Promoschorhynchus*, are well-developed (Mendrez 1974b fig.2 p76). The parabasisphenoid keel is present but smaller than in *Regisaurus*. The basipterygoid processes of the parabasisphenoid are covered by the pterygoids (Mendrez 1974b p83).

Mendrez (1974b p83) observed a lateral parabasisphenoid process either side of the the interpterygoid fossa in the pterygoid. These processes are also present in the early Therocephalia.

In *Ictidosuchops*, the parabasisphenoid keel is present but somewhat reduced. A narrow space separates the basioccipital from the parabasisphenoid (Crompton 1955 p163), a condition not noted in sections of *Glanosuchus macrops* SAM K238a. A short rostrum projects into the interpterygoid vacuity. Anteriorly the basisphenoid flares laterally to form two large basipterygoid processes (Crompton 1955 p163). Anterior to the basipterygoid processes, the basisphenoid is a thin horizontal plate. The parasphenoid is fused to the ventral surface of this plate (Crompton 1955 p165).

In ventral view, the parabasisphenoid of *Ictidosuchops* has a relatively less robust form than *Moschorhinus*, and the basal tubera are not as distinct as those of early therocephalians (own observation). The parabasisphenoid does not contribute to the ventral edge of the fenestra ovalis in *Itidosuchops* (Crompton 1955 fig.5A p164).

In *Thrinaxodon*, an unossified zone is present between the basioccipital and the basisphenoid (Fourie 1974 fig.20 p364). Ventrally the wings of the parasphenoid do not extend as far laterally towards the fenestra ovalis as figured by Parrington (1946 fig.3 p185).

In *Thrinaxodon*, the dorsum sellae is virtually non-existent. Therefore the sella turcica is very shallow and narrow (Fourie 1974 p364). The internal carotid canals emerge almost directly above their points of entry into the parasphenoid-basisphenoid. Parasphenoidal teeth, described for *Thrinaxodon* by Estes (1961) have not been noted in any other group in this study.

A small foramen (Estes 1961) is present in both wings of the parasphenoid, medial to the fenestra ovalis (Fourie 1974 fig.25A p369). This foramen is positioned precisely where the Eustachian tube opens in mammals (Fourie 1974 p366).

In ventral view, the parabasisphenoid of *Procynosuchus* has the typical triangular shape found in early therocephalians, but is slightly enlarged antero-laterally. The parasphenoid-pterygoid suture does not run through the internal carotid canals as in

early therocephalians, but appears level with the posterior margin of the interpterygoid vacuity (Kemp 1979 fig.2 p77).

The basiptyergoid processes are very well-developed. A small round process is present on the ventral surface of the parasphenoid immediately behind the ventral openings for the internal carotids. The significance of this structure is unclear (Kemp 1979 p100). The rostrum is a long thin rod, positioned between the pterygoids and contacts a delicate anterior mid-ventral septum. The interpterygoid fenestra is present but is reduced in later cynodonts (Kemp 1979 p100).

Posterior to the interpterygoid vacuity, the dorsal surface of the parabasisphenoid possesses a pair of irregular ridges. These ridges originate posterior to the cultriform process and diverge to form a long and shallow sella turcica.

The dorsum sellae is short and squat. It appears slightly better developed than in *Thrinaxodon* (Fourie 1974 p364), where it is practically non-existent.

Two medial depressions are situated anterior to the dorsum sellae, with the anterior fossa being wider and shallower. The floor of each has a series of very small nutritive foramina (Kemp 1979 p102). It seems that the pituitary gland had two ventral lobes and was not deeply inserted into the braincase floor (Kemp 1979 fig.12 p101).

The paired internal carotid canals are situated immediately in front of the sella turcica and from each canal a short groove traverses in an anterior direction (Kemp 1979 p102). In *Thrinaxodon*, an unossified zone lies on the suture between the parabasisphenoid and basioccipital, as in the dicynodonts and later therocephalians.

In the procynosuchid sectioned by Brink (1960 p146), the suture between the basioccipital and basisphenoid is indistinct. Brink (1960) does not describe the presence of an unossified zone in the base of the braincase. The parabasisphenoid is narrow anteriorly but expands laterally across the internal carotid foramina to form two separate swollen bosses. These bosses contact the antero-ventral process of the eipterygoid and the basisphenoid processes of the pterygoids.

In *Procynosuchus*, the rostrum passes dorsally and anteriorly above the interpterygoid vacuity between these processes. It is well-developed and its anterior portion is V-

shaped in section (Kemp 1972 p25, Brink 1960 p146). Posteriorly, the groove along the dorsal surface deepens and widens, and the rostrum becomes U-shaped. The parabasisphenoid keel is short, pointed and reduced compared to the early therocephalians (Brink 1960 fig.34 p131).

The dorsum sellae of *Procynosuchus*, as in *Thrinaxodon*, is small and inconspicuous. There is a gradual rise in the floor of the braincase in the position of the dorsum sellae. More posteriorly, the braincase floor flattens where it widens to the level of the vestibules (Brink 1960 p146). The prootics loosely contact this part of the basisphenoid.

Brink (1960) and Kemp (1972) give no indication of an unossified zone in the floor of the braincase as is suggested by Olson (1944) for cynodonts.

In Gorgonopsia (Olson 1938b), the basiptyergoid processes are narrow and jut from the basisphenoid at right angles (Olson 1938b fig.4 p162). A well-developed keel is present, similar to that of early therocephalians, and is clasped anteriorly by the pterygoids. The prootics form the anterior portion of the dorsum sellae.

The sella turcica in gorgonopsians is quite large and does not form an anterior wall. This depression in the dorsal surface of the basisphenoid is divided longitudinally by a median septum. The septum is composed mainly of basisphenoid and partially prootic.

Anteriorly, the base of the sella turcica possesses a single large foramen for the internal carotids. More posteriorly, this canal divides to form two postero-laterally directed canals which emerge posterior to the basiptyergoid (Olson 1938b p163). These canals are the vidian canals that are also evident in *Glanosuchus macrops* SAM K238a. An unossified zone is present posterior to the sella turcica in gorgonopsians, similar to the zones described in other therapsids by Olson (1944 p65).

The rostrum is quite long and almost its entire dorsal length is grooved. It arises immediately above the basiptyergoid processes and runs antero-dorsally. The posterior extremity of the parabasisphenoid forms the anterior portion of the floor of the sella turcica, which is broad and bears a low median ridge.

Anteriorly, the rostrum becomes continuous with the pterygoid septum ventrally and a dorsal median ossification dorsally (Kemp 1969 p64). Here the dorsal surface of the rostrum is a smooth trough, and the rostrum rests on the dorsal edge of the pterygoid septum.

In Gorgonopsia, the dorsum sellae is formed by the bases of the antero-ventral processes of the two prootics. Between the dorsal edge of the dorsum sellae and the orbitosphenoid, ossification is lacking in the braincase floor (Kemp 1969 p64,65). In its place is a deposit of crystalline material that according to Kemp (1969), is a remnant of cartilage.

A median ridge at the base of the dorsal surface of the rostrum indicates that a septum extended to the anterior edge of the sella turcica (Kemp 1969 p65). The posterior part of this crystalline structure extends a short distance above the floor of the sella turcica and contacts the dorsum sellae. There is no foramen preserved in the sella turcica to show exactly where the stalk of the pituitary gland penetrated it. The rest of the braincase floor extending to the foramen magnum slopes gradually downwards (Kemp 1969 fig.25A p72).

The interpterygoid vacuity is restricted to the anterior portion of the pterygoids. The vacuity is not longitudinal as in therocephalians, but pear-shaped (Kemp 1969 fig.2 p8). Kemp (1969 fig.6 p16) does not indicate an interpterygoid vacuity for the gorgonopsian *Leontocephalus*.

3.13 Basioccipital

3.13.1 Description

In ventral view, the basioccipital is a stout, triangular bone which forms the posterior part of the skull base. The bone makes sutural contact with the parabasisphenoid anteriorly, and these two bones form the base of the braincase (Figs 3B,C, 21).

The basioccipital and parabasisphenoid form the ventral part of the basal tubera surrounding the fenestra ovalis in early therocephalians (Fig. 5). The basioccipital forms the posterior part of the tubera and the parabasisphenoid forms the anterior part.

In a ventral view, a deep fossa is situated between the basal tubera of *Glanosuchus macrops* GS M796 and *Ptomalestes avidus* SAM 11942.

The ventral rim of the basal tubera are broken off in *Glanosuchus macrops* SAM K238a, and their original position is not clearly defined in the sections. The remains of the tuberas are present as oval structures situated below the basioccipital (section 467-480). The basioccipital also forms the ventral edge of the foramen magnum and the ventral portion of the occipital condyle (Figs 11, 16, 19).

At section 474, the lateral edge of the basioccipital in the fenestra ovalis contains a fossa that appears to correspond to the shape of the footplate of the stapes. The stapes is present, but is laterally displaced.

Anteriorly, the basioccipital meets the parabasisphenoid in an interdigitating suture that expands transversely between the lower lip of the basal tubera (sections 466-488). The suture between the parabasisphenoid and the basioccipital is difficult to identify in the sectioned early therocephalian, as the two bones appear very similar in shape and size (sections 463-468).

On the ventral surface of the skull base the parabasisphenoid-basioccipital suture forms a small unossified zone. In *Glanosuchus macrops* SAM K238a, this zone is in the form of a deep pit (section 466). This zone has been well documented in nearly all other sectioned therapsids (Olson 1938a, 1938b and 1944, Fourie 1974 and Crompton 1955) (Fig. 5).

In the lycosuchid GS C60, a small area of calcareous bone is present on the ventral midline of the basioccipital-basisphenoid suture which corresponds to the unossified zone mentioned above. This zone is not generally present in therapsids. A pair of small foramina also appear to be present posterior to the calcareous region (Van den Heever 1987). These foramina are present in some therapsids and Olson (1944 p62) refers them as the nutrient foramina.

Mendrez (1972 p207) states that in *Regisaurus*, a part of the floor of the jugular foramen is formed by the basioccipital. The outer edge of the jugular foramen is also formed by the basioccipital in *Glanosuchus macrops* GS M796. The sections indicating the participation of the basioccipital to the floor of the jugular foramen are missing

from *Glanosuchus macrops* SAM K238a. The occipital view of *Ptomalestes avidus* SAM 11942 also indicates the contribution of the basioccipital to the jugular foramen.

Antero-laterally, the basioccipital contacts the opisthotic (sections 475-491). The exoccipital is situated between the lateral opisthotic and the medial basioccipital (sections 492-499). The basioccipital contacts the exoccipital on the posterior, dorsal and lateral surfaces. At section 492, the jugular foramen is formed between the opisthotic and the exoccipital.

In occipital view, the basioccipital forms the medial portion of the condyle, and is situated between the ventro-medial portion of the exoccipitals. The exoccipitals form the ventro-lateral parts of the condyle. Lateral to the occipital condyle, the medial portion of the mastoid processes of the opisthotics meet the basioccipital in a suture on either side of the condyle.

In dorsal view, the basioccipital has an oblong shape. The anterior portion is reasonably broad, but towards the posterior edge of the fenestra ovalis, the bone is reduced in width. This appears to compensate for the laterally situated opisthotics, which expands outwards. The basioccipital is narrowest at the level of section 476.

Between the anterior and posterior edges of the fenestra ovalis the lateral edges of the basioccipital slope downwards (sections 466-473). Behind the unossified zone in the centre of the basioccipital, level with the anterior edge of the jugular foramen, the basioccipital forms a wide shallow fossa. The base of the medulla oblongata was probably situated in this fossa.

The central trough on the dorsal surface of the basioccipital is similar to that described for other sectioned therapsids (Olson 1944 fig.18 p62) (Fig. 5). Behind this fossa, the dorsal surface of the basioccipital becomes level. It remains level up to the ventral lip of the foramen magnum (sections 500-502). This area is well preserved in *Ptomalestes avidus* SAM 11942. Beyond section 502, the basioccipital has broken off from *Glanosuchus macrops* SAM K238a.

3.13.2 Comparative View

The basioccipital of *Lystrosaurus* (Cluver 1971 fig.4 p165) resembles that of early therocephalians. The dorsal surface is saddle-shaped, and has a raised median crest. This crest is low posteriorly and rises anteriorly to form the posterior lip of a cup-like depression, the basicranial pit, lying between the basioccipital and basisphenoid (Cluver 1971 p164). The basioccipital in *Lystrosaurus* is deepest in the region of the auditory canal. This corresponds to the shallow fossa in the basioccipital of *Glanosuchus macrops* SAM K238a which probably accommodated the medulla oblongata.

On the ventral surface between the two lateral tubera, a transverse intertuberal ridge is formed, comparable to that found in *Moschorhinus* (Mendrez 1974a). This is unusual for dicynodonts as this area is usually flat.

In *Lystrosaurus*, the basicranial pit in the braincase floor is situated similar to the position of the unossified zone mentioned by Olson (1944) and Boonstra (1968). Olson (1944) states that the unossified zone is a rudimentary basicranial fenestra and therefore a primitive characteristic.

Medial to the fenestra ovalis in dicynodonts, the dorsal opening of the auditory canal is enlarged to form an auditory vestibule. Posterior to the vestibule, a groove traverses from the basioccipital to the jugular foramen. The direction indicates that the groove passes medial to the vestibule. The groove does not enter the jugular foramen as it does in dicynodonts and therocephalians sectioned by Olson (1938b, 1944 p24) and *Glanosuchus macrops* SAM K238a. The only difference in the therocephalians is that the groove is located in the opisthotics, not in the basioccipital as it is in dicynodonts. The contact between the basioccipital and the prootic, opisthotic, basisphenoid and the exoccipitals in dicynodonts appear to resemble the condition in the early therocephalians.

In section, the basioccipital of *Dicynodon grimbeeki* (Agnew 1956 fig.42 p95) shows that the central portion of the dorsal surface is sided laterally by a sacculo-cochlear recess, which is similar to the vestibule mentioned by Cluver (1971) in *Lystrosaurus*.

The basioccipital of *Regisaurus* is very similar to that of early therocephalians. The opening of the hypoglossal nerve XII is situated at the junction between the basioccipital and exoccipital bones (Mendrez 1972 p206).

In *Promoschorhynchus*, the contact between the basioccipital and surrounding bones is similar to that of early therocephalians (own observation). The basioccipital of *Promoschorhynchus* forms slightly more than one third of the occipital condyle (Mendrez 1974b p72, p76). It also forms the postero-ventral part of the fenestra ovalis, as in early therocephalians. In *Promoschorhynchus*, it contributes the smallest part to the lip of the fenestra ovalis of the four bones. In occipital view, the basioccipital forms the smallest part of the ventral lip of the foramen magnum. In dorsal view this ventral lip portion protrudes very far out, and appears triangular, with the apex directed inwards (Mendrez 1974b fig.1 p71). This is contrary to *Regisaurus* where the basioccipital forms a much wider portion of the foramen magnum (Mendrez 1972 fig.1 p194).

The basioccipital of *Promoschorhynchus* is laterally overlain by the exoccipitals, as in *Regisaurus* (Mendrez 1972 p197). In ventral view, it forms the large basal tubera, which Mendrez (1974b p76) refers to as the tuberculum speno-occipitale. The basioccipital-basisphenoid suture runs transversely between the tubera. As in early therocephalians, a fossa is present in this position. It is deepest anteriorly (on the basisphenoid) and becomes shallower posteriorly (on the basioccipital). On either side of this ventral basioccipital-basisphenoid fossa, is a smaller, posteriorly situated fossa on the basioccipital (Mendrez 1974b p72).

The basioccipital of *Moschorhinus* (Mendrez 1974a fig.2 p76) is very broad but it forms less than half of the posterior portion of the basal tubera. The basisphenoid forms the anterior portion. The ventral fossa between the tubera is deep and pit-like, but the secondary fossae inside this fossa, as described for *Promoschorhynchus* (Mendrez 1974b fig.2 p76), is absent in *Moschorhinus*.

In *Moschorhinus*, the basioccipital forms a very small portion of the ventral lip of the fenestra ovalis. In dorsal view, the basioccipital is an elongated strip between the exoccipitals extending into the foramen magnum (Mendrez 1974a fig.1 p74). The contribution of the basioccipital to the postero-ventral portion of the fenestra ovalis is

much smaller than in *Promoschorhynchus* (Mendrez 1974a p86), *Regisaurus* or *Glanosuchus macrops* (own observation).

Posterior to the basal tubera, the internal process of the mastoid process protrudes onto the ventral surface of the basioccipital. The suture between this portion of opisthotic and the basioccipital is directed medially and then posteriorly onto the centre of the ventral lip of the jugular foramen. Between the posterior border of the internal process of the opisthotic and the postero-ventral edge of the occipital condyle, is a short parasagittal flange which separates the ventro-lateral border of the basioccipital and the ventro-medial border of the occipital boss from the exoccipitals (Durand 1991 p406).

The posterior portion of the basioccipital forms the occipital condyle, which in ventral view appears knob-like and broad. The occipital condyle is tripartite, as in the therocephalians compared in this section and the exoccipitals press against the dorso-lateral part of this condyle (Mendrez 1974a fig.2 p76).

In ventral view, the basioccipital of whaitsiids is much like that of early therocephalians. The fossa on the ventral surface is exceptionally deep (Fig. 17B).

In ventral view, the basioccipital of *Ictidosuchops intermedius* is roughly triangular, and according to Crompton (1955 p163), no sutures were found between the basioccipital and exoccipitals. Crompton (1955) records that a narrow space is present between the basioccipital and basisphenoid, a feature not found in any of the therocephalians compared in this study. There is no evidence of the unossified zone on the basisphenoid-basioccipital suture in *Ictidosuchops* (Crompton 1955 p163).

The exoccipitals overlie the postero-ventral portion of the basioccipital. The internal process of the opisthotic is situated antero-laterally against the basioccipital, and not onto the ventral surface (Crompton 1955 fig.5B p165). This condition is also found in *Moschorhinus*.

In *Thrinaxodon*, an antero-ventral extension of the exoccipital lies on the latero-dorsal surface of the posterior part of the basioccipital where it forms the inner wall of the jugular foramen (Fourie 1974 p376). In dorsal view the basioccipital is more or less triangular. The basal tubera appear smaller than in therocephalians.

In *Thrinaxodon*, a very small foramen is present immediately below the fenestra ovalis, on the ventral surface of the basioccipital. This foramen was possibly for a branch of the hypoglossal nerve XII or a blood vessel (Fourie 1974 fig.1 p341, fig.25 p369, p377).

Posterior to the suture between the basioccipital and basisphenoid, an unossified zone is present in the dorsal surface of the basioccipital (Fourie 1974 fig.20 p364). This structure is described in most sectioned therapsids, i.e. Olson (1944 p67), and is also present in *Glanosuchus macrops* SAM K238a.

In sagittal view, a very shallow fossa appears to extend lengthwise along the midline on the dorsal surface of the basioccipital in the region of the fenestra ovalis (Fourie 1974 fig.29 p376). The lateral margins of the basioccipital are slightly raised, and the bone is very thin in the centre of the fossa.

In the region of the sacculo-cochlear recess, where the jugular foramen is situated between the exoccipital and opisthotic, a thin sheet of the exoccipital clasps the basioccipital. The exoccipital curves over and covers the lateral raised edges of the basioccipital (Fourie 1974 fig 29B p376). Posterior to this and nearer the foramen magnum, the basioccipital lacks prominent bosses or fossae (Fourie 1974 fig.27A,B p370).

In ventral view, the basioccipital of *Procynosuchus delaharpeae* is very robust. Kemp (1979 fig.2 p77) does not indicate whether the basioccipital forms the postero-ventral lip of the fenestra ovalis or if the ventral sutures between the opisthotic and the basioccipital, or the sutures between the exoccipital and the basioccipital are present. The unossified zone on the basioccipital-parabasisphenoid suture is present (Kemp 1979 p102).

In dorsal view, the basioccipital in *Procynosuchus* is similar to that of *Thrinaxodon*. The dorsal surface of the basioccipital has a wide shallow fossa. This is further confirmed by a sagittal section (Kemp 1979 fig.13 p102). There is no indication of the basisphenoid-basioccipital suture, therefore it is not possible to assess the contribution of the basioccipital to the fenestra ovalis (Kemp 1979 fig.12 p101). The exposure of the basioccipital is restricted in occipital view, with a very small portion lying between the enlarged exoccipitals. The size of the basioccipital in this view may be due to damage,

as the occipital condyle is not indicated, but only what appears to be the articulation surfaces of the exoccipitals (Kemp 1979 fig.3 p78).

According to Brink (1960 p128), the basioccipital of the specimen of *Procynosuchus* he sectioned is "of typical therapsid build". The occipital condyle has developed a crescent shape as the result of a degree of reduction of the basioccipital. This condition has been described for cynodonts by Broom (1938 p279). In *Laevachia* (Brink 1960 p128), the condition appears to be more primitive since it has a trilobed condyle.

The basioccipital does not contribute to the walls of the jugular foramen in the procynosuchid sectioned by Brink (1960). The walls of this foramen are formed entirely by the exoccipital and the opisthotic. The basioccipital forms reduced basal tubera which extend laterally and not ventrally (Brink 1960 p128). The ventral surface of the basioccipital has a small median ridge, with a foramen on either side, some distance posterior to the basisphenoid-basioccipital suture (Brink 1960 fig.33B p130).

The anterior margin of the basioccipital is largely fused to the basisphenoid. Brink (1960 p129) uses this as an indication that the specimen is "not quite as juvenile as other features tend to suggest". Anterior to the jugular foramen, the opisthotic is loosely connected to the basioccipital. The exoccipitals lie close to the postero-lateral sides of the basioccipital.

In sagittal view, the dorsal surface of the basioccipital of *Procynosuchus* has a similar structure to that of *Thrinaxodon*. The central part of the basioccipital bears a slight cavity and slopes towards the foramen magnum (Brink 1960 fig 43B p131).

In ventral view, the basioccipital of gorgonopsians (Kemp 1969 fig.2 p8) is short, broad and roughly triangular, as in *Ictidosuchops*. The bones forming sutures with the basioccipital are similar to those in the early theropcephalians. The basioccipital is contacted by the parabasisphenoid anteriorly, the opisthotic dorsally and ventrally, the prootic anteriorly and the exoccipitals postero-ventrally.

According to Olson (1938b p142) the exoccipitals of gorgonopsians are ventrally fused to the basioccipital. The basioccipital forms the entire occipital condyle. Passing between the basioccipital and the exoccipital is a small foramen for the hypoglossal

nerve XII (Olson 1938b p143) as mentioned for *Thrinaxodon*. This foramen opens lateral and independent to the jugular foramen.

In dorsal view, the basioccipital of gorgonopsians is similar to that of the therocephalians. The portion of the basioccipital posterior to the fenestra ovalis has an elongated fossa extending along the length of the basioccipital (Kemp 1969 fig.5 p15), also described by Olson (1944 fig.18 p62, fig.19 p63).

The basioccipital of "Gorgonopsian B" has steep walls on either side of what appears to be a large flat braincase floor. "Therocephalian B" (a gorgonopsian) is slightly different. The left side of the diagram appears to illustrate the anterior end of the basioccipital. The fossa in the dorsal surface of the basioccipital originates half way along the length of the bone.

According to Olson (1944 p62), the vestibule of the inner ear is formed by a shallow recess in the basioccipital, dorsal to the fenestra ovalis.

CHAPTER 4

THE INTERNAL BRAINCASE STRUCTURES

This chapter will discuss in depth the internal structures of the braincase in the early Therocephalia. These structures are formed mainly by the prootic, opisthotic, supraoccipital, basioccipital and exoccipital. The discussion of the otic structures emphasizes the inner ear structure and an explanation of the various cavities, ridges and grooves on the medial walls of the braincase. The early therocephalian inner ear is compared to that of other sectioned therapsids. Further discussions include the shape of the cranial cavity. This is followed in Chapter Five by a reconstruction and discussion of the possible shape of the brain in the early Therocephalia.

The ear is an important structure in the living animal, for its function of hearing and balance. It is divided into the external, middle and internal ear. Very little is known of the external ear in mammal-like reptiles, but the middle and inner ear are quite well documented. Therefore, the middle ear of early therocephalians is not described in detail in this study (see Van den Heever 1987). However, the inner ear of early therocephalians is less well known and will be discussed in this chapter.

To facilitate the discussion of the inner ear, a brief comparison of the reptilian and mammalian inner ears are given. The paired internal ears in vertebrates are built upon a relatively uniform pattern (Romer 1986 p523) and this basic pattern is expected to continue within the mammal-like reptiles.

4.1 The Shape of the Cranial Cavity

This section is concerned with the overall shape of the cranial cavity in the early Therocephalia, including the fossae on the medial surfaces of the bones and the foramina in the braincase (it excludes the foramina in the inner ear, which is discussed in Sub-section 4.5.9). This discussion is based on sections of *Glanosuchus macrops* SAM K238a and is compared with gorgonopsians, other therocephalians and

cynodonts. The braincase cavity of dicynodonts is well documented, but as they are morphologically very different, this taxon is omitted from this discussion.

4.1.1 The Foramina in the Braincase

These foramina include those conducting blood vessels and nerves, as well as those foramina that housed particular structures, such as the pineal organ.

4.1.1.1 The Jugular foramen

The jugular foramen is large and opens onto the occipital surface of the skull below the lateral projection of the exoccipital, and above the internal process of the opisthotic. The external lip is formed by the exoccipital, and the floor consists of the opisthotic laterally and the basioccipital medially. Its size indicates that more than one cranial nerve, such as IX, X and XI, may have passed through it.

When viewed sagittally, the internal roof of the jugular foramen is formed by the exoccipital medially, and a very small portion of opisthotic laterally. The floor is formed by the opisthotic and the basioccipital. This foramen is situated in a deep groove inside the braincase, medial to the high, broad ridge formed by the opisthotic. This ridge forms the medial wall of the sacculo-utricular recess anterior to the opisthotic recess. The medial surface of this ridge is concave and faces towards the braincase cavity.

Olson (1944 p32, 1938b p77) states that the jugular foramen in theriocephalians and cynodonts opens directly into the vestibule, at the junction of the sacculus and utriculus. In *Glanosuchus macrops* SAM K238a and the gorgonopsians studied by Olson (1944 p32), this foramen does not open into the ossified part of the vestibule, but postero-medial to it.

The jugular foramen is positioned adjacent to the medial ridge formed anteriorly by the basioccipital and posteriorly by the exoccipital. Medial to the position of the foramen is the medulla oblongata portion of the braincase (Figs 5, 6, 7, 8). Crompton (1955

fig.6C p166) does not indicate the jugular canal on the medial surface of the braincase of *Ictidosuchops*.

In the cynodont ear region (Simpson 1933 fig.3 p289), the large jugular foramen is situated posterior to the vestibule. In the later cynodonts *Massetognathus* and *Probelesodon* (Quiroga 1979 fig.2 p181, fig.1 p180) the jugular foramen is situated in a similar position. It opens postero-ventrally to the vestibule and the floccular fossa, and posterior to the position of the ampulla of the posterior semicircular canal.

In *Procynosuchus* (Kemp 1979 fig.12 p101), the jugular foramen is large and positioned posterior to the fenestra ovalis, as in *Probelesodon* and *Massetognathus*. In the procynosuchid described by Brink (1960 fig.34 p131), the jugular foramen is situated different to the other cynodonts in this comparison. It is formed by the exoccipital posteriorly and the opisthotic anteriorly. The jugular foramen is situated a distance from the vestibule, as in *Glanosuchus macrops* SAM K238a, and is not connected to the inner ear structures.

Olson (1938b p78) notes that the fenestra rotunda may have opened into the jugular foramen, although this foramen is situated posterior to the vestibule. Cluver (1971 p169) presumes that this was also the case in *Lystrosaurus*. The function of the jugular foramen in theriocephalians was to conduct nerves from the braincase to the neck, and if the fenestra rotunda opened into it, its function would be extended to relieving the pressure in the perilymphatic system of the inner ear. Fourie (1974 fig.25 p369) indicates a very large foramen situated is between the fenestra ovalis and the foramen magnum in *Thrinaxodon* and refers to this foramen as the fenestra rotunda (labelled *FNA*). This is the only therapsid in this study which has a reference to this foramen, for in all the other specimens there is no indication of a fenestra rotunda.

4.1.1.2 The Foramen for Nerve XII

The foramen for nerve XII lies between the jugular foramen and the foramen magnum in *Glanosuchus macrops* SAM K238a (Figs 5, 6, 7, 8). It is formed mainly by the exoccipital and the basioccipital. The exoccipital forms the roof and walls, while the basioccipital forms the floor of the foramen. In later theriocephalians and early cynodonts, this foramen is formed by the exoccipital only. In *Glanosuchus macrops*

SAM K238a, the foramen for nerve XII and the jugular foramen are present as a single elongated opening, because of damage to the bone separating the two foramina. A peculiar condition concerning the jugular foramen is described by Olson (1944 p29, fig.12 p40) in one of the cynodonts he sectioned. He refers to this jugular foramen as not being very distinct, but is part of the "elongate open metotic fissure". This appears similar to the condition found in the sectioned early therocephalian.

In *Regisaurus* (Mendrez 1972 fig.8 p203) and the therocephalian sectioned by Olson (1938b p76), there are two foramina for nerve XII, namely the internal opening of nerve XII and the external opening. The internal opening lies within the exoccipital, on the inside lip of the foramen magnum. The external opening of the jugular foramen is situated on the basioccipital-exoccipital suture.

If the two openings for nerve XII are present in *Glanosuchus macrops* SAM K238a, it was not detected in the reconstructions. The only foramen present is the internal opening of nerve XII, situated above and slightly posterior to the jugular foramen, and is formed by the basioccipital and exoccipital as described above. The number of foramina present in therapsids varies widely (Olson 1938b). Two foramina are also present in a later cynodont (Simpson 1933 fig.3 p289) and *Procynosuchus* (Kemp 1979 fig.12 p101).

4.1.1.3 The Foramen Magnum

This foramen is similar in gorgonopsians, cynodonts and therocephalians. It conducted the spinal cord out of the braincase cavity into the vertebral canal. In early therocephalians, it is formed by three bones, namely the supraoccipital dorsally, the exoccipital laterally and the basioccipital ventrally. The exoccipital and basioccipital form the single occipital condyle which is situated on the ventral lip of the foramen. The basioccipital forms the basal section, while the exoccipitals form the lateral sections of this condyle.

4.1.1.4 The Foramina for the Internal Carotids

The external foramina for the internal carotids are paired in most therapsids (Fig 3B). An exception is *Dicynodon grimbeeki* (Agnew 1958 p98), where only one foramen is present. These canals open ventrally in the parabasisphenoid on either side of the keel. They penetrate the braincase floor at a point below the pituitary fossa and run forwards through the body of the parabasisphenoid either side of the midline for a short distance before opening in front of the pituitary fossa as a single foramen (Fig 5). These carotid canals in the parabasisphenoid also extend backwards as the paired vidian canals.

4.1.1.5 The Vidian Canals

The paired vidian canals are posteriorly directed extensions of the carotid canals and are also situated parallel to the midline (Romer 1986 p243).

The destination of the vidian canals in *Glanosuchus macrops* SAM K238a is uncertain, for they dissipate abruptly. This appears to be due to poor ossification of this area in the parabasisphenoid. Except for Olson (1944 p74), the canals are not readily described in the sectioned therapsids which are compared here. Olson does not explain the destination of the canals, only notes their position in the parabasisphenoid.

4.1.1.6 The Pineal Foramen

The pineal foramen is an opening in the parietal bones of most therapsids but is found in many extinct reptilian groups as well. Moreover, in extant groups, it is restricted only to *Sphenodon* and particular lizards. In *Regisaurus* and later cynodonts, the pineal foramen is lost. When a pineal foramen occurs in either living or extinct reptiles, it is median and single, and varies in size, shape and acquires an antero-posterior position (Quay 1979 p290). In early therocephalians, the foramen is oval, whereas in *Moschorhinus* (Mendrez 1974 p79, Durand 1991 p404) it is spindle-shaped.

The pineal foramen housed the pineal organ, which Romer (1956 p32) refers to as the parapineal body in reptiles. Quay (1979 Table.10 p304) provides information on the pineal foramen in the Therapsida, and indicates that it varies greatly within this taxon.

The function of this structure in therapsids is uncertain. Perhaps it functioned as in living reptiles where the pineal foramen houses a photo-receptive parietal eye organ.

From experiments performed on the iguanid *Scaloporus* (Underwood 1977), it was noted that the pineal organ is an important component of the circadian system, and that it possibly imposes frequency onto other biorhythmic systems. This would aid reptiles in accumulating details about the seasonal changes which influence their biorhythms.

The persistence of the pineal foramen in so many genera of the mammal-like reptiles suggests that its presumed content, the parietal eye-pineal organ, remained functionally significant. The sagittal crest may have served as muscle-attachment zones and for protection of the parietal eye (Quay 1979 p302).

In some later theriocephalian groups, for example *Regisaurus*, and more advanced cynodonts, the pineal foramen is lost. These advanced groups, the Tritylodontoidea, Bauriamorpha and Ictidosuchidae, may form the basis for the loss of the parietal foramen in ancestral mammals in the Upper Permian to Lower Triassic (Quay 1979 p302).

4.1.2 The Fossae on the Medial Walls of the Braincase

Information concerning the therapsid brain must be derived either from cranial casts or from reconstructions of the cranial cavities. Studies of the therapsid brain yield interesting but often inaccurate results. Even comparisons of the brains of reptiles and mammals with those of therapsids can be unyielding, because there are significant differences between the mammalian and reptilian brain, and the therapsid brain (Olson 1944 p106) (see Chapter 5).

Cranial casts of reptiles do not give satisfactory insight into the basic morphology of the brain because the cranial cavity is considerably larger than the brain (Starck 1979 fig.10 p21). However, cranial casts of mammals yield a fairly accurate reproduction of the shape of the brain. Therapsid brains appear to be intermediate in form with respect to these two groups. It is evident from the internal surfaces of the therapsid braincases that certain parts of the brain are impressed on the walls and floor of the cranial cavity, while other parts have left no record.

The reconstruction of the braincase of *Glanosuchus macrops* SAM K238a indicates that many fossae are present on the medial walls of the braincase. These indicate close contact between the medial wall of the braincase and the brain in the posterior region of the braincase. The anterior portion of the braincase bears either a few shallow, indefinite fossae, or none, possibly implying that there were wide cavities between the brain and skull. The lack of detail on the internal surface of the anterior portion of the braincase may leave much room for speculation on the shape of this part of the brain.

4.1.2.1 The Braincase Roof

There is a single wide fossa present on the ventral surface of the frontals in early therocephalians, such as *Glanosuchus macrops* SAM K238a and *Glanosuchus macrops* GS M796. The frontal lobes or olfactory lobes of the brain were possibly situated in this fossa. Based on the length of the fossae in the frontals in *Glanosuchus macrops* SAM K238a, these olfactory lobes appear to have been quite short, in comparison to those of extant reptiles (Figs 4B,C).

It is assumed that there were two olfactory lobes present in early therocephalians, even though it is not indicated by the fossa in the bones. These lobes are paired in living mammals and reptiles. These lobes are also paired in cynodonts as shown by the endocast of *Trirachodon kannemeyri* SAM K4801 (Hopson 1979 fig.29 p134) and *Diademodon* (Watson 1913 fig.2 p223) In *Procynosuchus* (Kemp 1979 fig.14 p106) the fossa is divided into two parts by a low ridge.

The fossa for the olfactory lobes continues across the parietal-frontal suture onto the ventral surface of the parietal. It is continuous with the parietal trough which in early therocephalians is also unpaired. This fossa supposedly supported the cerebral hemispheres from above. These hemispheres were also probably paired, as in living mammals and reptiles. The parietal trough leads towards the ventral opening of the pineal foramen on the ventral surface of the parietal. This foramen probably housed the epiphysis or pineal organ (see Sub-section 4.1.1.6). The parietal trough then extends across the parietal-interparietal suture, and is continued on the small area of exposed interparietal in the braincase roof. The cerebral fossa continues across the interparietal-supraoccipital suture onto the supraoccipital.

A short distance behind the internal auditory foramen in the medial wall of the otic capsule, the cerebral fossa develops into a deep, cone-shaped fossa in the supraoccipital. It is probable that the cerebellum of the brain occupied this fossa. From the shape of the fossa, one can see that the cerebellum was unpaired and well-developed in early therapsids such as *Glanosuchus macrops* SAM K238a and *Ptomalestes avidus* SAM 11942) (Fig 4B). The cerebellar fossa recedes upwards and backwards into the supraoccipital in the braincase roof. This condition is also found in *Thrinaxodon* (Kemp 1974 fig.28 p372), but the fossa is smaller and is positioned in the interparietal, not the supraoccipital. This fossa is clearly evident in the sagittal view of the skull of *Glanosuchus macrops* SAM K238a (Fig 5). It gradually slopes downwards towards the dorsal rim of the foramen magnum.

Olson (1944 p108) claims that very little about the nature of the medial lobe of the cerebellum can be determined from the roof of the braincase in therapsids. He (1944 fig.6 p14) does not indicate a deep fossa in any of the therapsids he sectioned, except for "Cynodont B". Other cynodonts displaying this deep fossa is *Procynosuchus* (Kemp 1979 fig.13 p102) and *Thrinaxodon* (Fourie 1974 fig.6 p346). The procynosuchid sectioned by Brink (1960 fig.34 p131) does not display this deep fossa.

4.1.2.2 The Medial Walls

The medial surface of the braincase walls, namely the prootic, the opisthotic and the exoccipital, bear many fossae, indicating a close contact between the brain and braincase (Fig 5).

The prootic is a vital element in forming the otic capsule (see Section 4.5) and bears evidence of the inner ear structures on the medial wall. The floccular fossa, positioned postero-dorsally on the medial surface of the prootic, possibly supported the lateral lobes of the cerebellum. According to Olson (1944 p108), the most striking feature of the cerebellum is the development of the flocculus. The floccular fossa is evident in most therapsids, especially cynodonts where it appears relatively larger in size (Fourie 1974 p374, Simpson 1933 fig.2 p288, Quiroga 1979 fig.1 p180, fig.2 p181). This contradicts Olson's (1944 Table.12 p37) proposal that the floccular fossa does not

increase in size from primitive to advanced therapsids. He states that the floccular fossa of cynodonts is smaller than in gorgonopsians.

In reptiles, the lateral lobe of the cerebellum is called the cerebellar auricles or auriculum cerebelli. The auricles are present in all vertebrate groups and are especially concerned with maintaining balance and is closely connected with the inner ear (Romer 1986 p581). The well-developed floccular fossae in cynodonts and early therocephalians could signify that the auricles were large and that hearing in these animals was reasonably acute (Fig 24).

In *Glanosuchus macrops* SAM K238a, the medial wall of the opisthotic, situated medially to the cochlear recess, bears a long, diagonal fossa that originates posterior to the fenestra ovalis, and terminates antero-ventral to the internal auditory foramen. This fossa possibly housed parts of the cerebellum (Fig 5).

The exoccipital forms a small portion of the braincase wall anterior to the foramen magnum. The medial wall of the exoccipital has two deep fossae which possibly supported the medulla oblongata (Fig 5). This may indicate that the medulla oblongata of therocephalians was not a simple swollen tube as it is in reptiles, but that it had lateral protrusions. Another suggestion is that this area accommodated a pons, a structure similar to the mammalian pons or that a blood sinus or other tissue was situated here. In *Gorgonops* (Sigogneau 1974 fig.1 p54), a single fossa is present in the exoccipital above the foramen for nerve XII.

4.1.2.3 The Braincase Floor

The dorsal surfaces of the pterygoid and the anterior portion of the parabasisphenoid do not possess any fossae. The parabasisphenoid forms a deep rounded sella turcica posterior to the suture with the antero-ventral process of the prootic. The posterior wall or the dorsum sellae rises steeply and is formed by the parabasisphenoid and laterally by the bases of the antero-ventral process of the prootic. Together the sella turcica and dorsum sellae form the pituitary fossa. This pit is well formed in early therocephalians, such as *Glanosuchus macrops* GS M796, *Glanosuchus macrops* SAM K238a and *Ptomalestes avidus* SAM 11942 (Figs 5, 12, 13). The size of the pit implies that the pituitary was quite large in early therocephalians. The pit is well-developed in

gorgonopsians (Sigogneau 1974 fig.1 p54, Olson 1938a fig.3 p161 and 1944 fig.20A p66, Kemp 1969 fig.7 p17). It is quite wide and shallow in *Procynosuchus* (Kemp 1979 fig.12 p101) but appears to be reduced in *Thrinaxodon* (Fourie 1974 fig.6 p346).

A wide shallow fossa is present in the dorsal surface of the basioccipital of *Glanosuchus macrops* SAM K238a and *Ptomalestes avidus* SAM 11942, below the exoccipital-basioccipital suture (Fig 5). This fossa possibly supported the ventral surface of the medulla oblongata which is bulbous and rounded in both mammals and reptiles. This fossa is indicated by Olson (1944 fig.18 p62, p109) in gorgonopsians and cynodonts, and by Sigogneau (1974 fig.1 p54) in *Gorgonops*.

4.2 The Reptilian and Mammalian Inner Ears

The purpose of this sub-section is to establish a basis to discuss the inner ear of both reptiles and mammals, and to make a comparison between reptiles, mammals and early theriocephalians possible. The membranous labyrinths of these three groups are represented in Fig 22. The inner ear morphology of reptiles and mammals is discussed with little reference to histological detail as this is not relevant in fossil material. The membranous labyrinth is included in the discussion, because certain structures in the fossil, such as the ampullae and the semicircular canals are imprinted on the medial wall of the braincase wall. Discussions of the mammalian and reptilian membranous labyrinth may provide insight to those structures in early theriocephalians.

The inner ear in both reptiles and mammals is a complicated structure, consisting of both soft tissue (the membranous labyrinth) and the corresponding ear structures in the braincase wall (the bony labyrinth) (Cunningham 1937 p1113). The bony labyrinth is slightly bigger than the membranous labyrinth, and in the fossil this is the part that is preserved in the medial walls of the prootic and opisthotic.

4.2.1 The Membranous Labyrinth

The membranous labyrinth, also known as the vestibular apparatus (Kardong 1994 p691), consists of a closed system of sacs and canals which form a set of cavities. These cavities are lined by epithelium and contain endolymph. The cavity between the

epithelium and bony labyrinth is surrounded by perilymph (Tortora and Anagnostakos 1987 p389, fig.17.10B p389). The endolymph and perilymph never mix with each other, nor with the lymph in the lymphatic system. Both the endolymphatic and perilymphatic systems end in a sac-like structure. The endolymphatic sac is positioned within the braincase cavity below the dura mater (Cunningham 1937 p1116). The perilymph sac penetrates the medial braincase wall through the foramen for nerve X in reptiles and amphibians and terminates against the dura mater.

The membranous labyrinth is surrounded by the bony labyrinth contained within the otic capsule formed by the temporal bone. It consists of a dorsal and a ventral part. The dorsal part includes the semicircular canals, the ampullae and the utriculus. The ventral part consists of the sacculus, the endolymphatic sac and the cochlear duct, which is the cochlea in mammals and the lagena in reptiles (Wever 1978 p64). The endolymphatic duct connects the endolymphatic sac to the sacculus and utriculus (Cunningham 1937 fig.959 p1116).

In reptiles, the lagena forms the main hearing apparatus. It is postulated that the lagena lengthens and coils up to form the cochlea in mammals (Romer 1986 fig.388 p534). Kardong (1994 p685) refers to the cochlea and the lagena as the same structure in mammals. Romer (1986 p524) and Wever (1978) differ from Kardong (1994) and state that the lagena is a separate structure in the form of a depression in the floor of the sacculus of mammals. This lagena contains a smaller lagena macula, consisting of sensory cells called neuromasts (Romer 1986 p524).

In the following discussions, the mammalian description forms the basis of each subsection, and the reptilian condition is compared at the end of each mammalian description.

4.2.1.1 The Semicircular Ducts

The function of the semicircular ducts are to maintain balance and evaluate movement of the head (Romer 1986 p526). The three ducts are the horizontal duct, the anterior vertical duct and the posterior vertical duct. Each is a narrow tube that begins and ends in the utriculus and is expanded at the ampullary end. These ducts contain sensory cells and branches of the vestibular nerve. The anterior and posterior semicircular ducts join

to form a thin tube, the crus communis. The crus extends downwards, connects the semicircular ducts and then joins the utriculus (Wever 1978 fig.3.3 p65). The posterior vertical canal runs postero-laterally from the crus communis and ends in a posterior ampulla.

Each of the three ducts lies in a plane at right angles to the other two, so that one is present for each of the three dimensions of space (Romer 1986 p525). The anterior vertical canal is angled antero-laterally from the upper surface of the utriculus at the crus communis and ends in an anterior ampulla.

The semicircular ducts of both mammals and reptiles appear to be very similar, except that in reptiles the posterior semicircular duct seems to be shorter (Kardong 1994 fig.17.34 p693, fig.17.36D p695).

4.2.1.2 The Ampullae

At the position where each semicircular duct rejoins the utriculus, there is a spherical expansion called the ampulla. The three ampullae are the posterior ampulla adjoined to the posterior duct, the anterior ampulla adjoined to the anterior duct and the external or horizontal ampulla, adjoined to the horizontal duct. The vertical ducts bear these ampullae at their distal ends, but the ampulla of the horizontal duct is proximally placed. The posterior ampulla is situated on the medial side of the utriculus, and the external and anterior ampullae are situated on the lateral side of the utriculus and lie in close proximity to one another (Romer 1986 p525). Within each ampulla is a sensory area containing hair cells or neuromasts (Romer 1986 fig.381 p525). The ampullae of reptiles and mammals are very similar (Kardong 1994 fig.17.34 p693).

4.2.1.3 The Utriculus

The utriculus and the sacculus are contained within the vestibule (a bony chamber above the bony cochlea) that connects the semicircular canals. The utriculus occupies the postero-dorsal portion of the vestibule. It consists of a narrow tube below the crus communis that extends into a broad ventral sac. This ventral region is situated above the point of origin of the sacculus (Kardong 1994 fig.17.36D p695). The sacculus and

the utriculus are connected by a narrow utriculo-sacculus duct. The most dorsal part of the utriculus lies in the ellipsoid fossa in the vestibule, and the anterior and horizontal ampulla open into it. The non-ampullated end of the horizontal canal opens into the central part of the utriculus which is elongated upwards into the crus communis (Cunningham 1937 p1116).

The walls of both the utriculus and sacculus contain small, flat plate-like regions called maculae, which are the receptors concerned with static equilibrium. They provide sensory information regarding the orientation of the head and are also essential for maintaining balance (Tortora and Anagnostakos 1987 p392). The utriculus of reptiles consists of a main part which is a broad tube extending from the crus communis to the junction of the paired ampullae. First it gives off a branch of the horizontal semicircular duct, and then forms the ventral part situated medial to the sacculus. This ventral part is not bulbous as it is in mammals, but consists of two branches, the posterior sinus and an expanded anterior end, the utricular recess (Wever 1978 fig.3.3 p65, fig.3.4 p63).

4.2.1.4 The Sacculus

The sacculus in mammals is much smaller than the utriculus. It is a finger-like projection situated at the base of the utriculus. It occupies the spherical recess in the anterior part of the vestibule. A small tube, the endolymphatic duct, originates from the posterior part of the sacculus and elongates into a blind structure, the endolymphatic sac. The upper end of the sacculus is directed dorsally and posteriorly to contact the utriculus. At the ventral end of the sacculus, a short duct descends and gradually widens into the vestibular end of the cochlear duct (Cunningham 1937 p1116). The endolymphatic duct is joined to the utriculo-sacculus duct. The sacculus of lizards is placed rather high in the vestibule. It differs from the sacculus in mammals because it is greatly enlarged, and is postero-ventrally situated to the utriculus.

4.2.1.5 The Endolymphatic Duct and Sac

The endolymphatic duct is connected to the base of the sacculus. This duct traverses the vestibule and terminates at the endolymphatic sac which is usually situated within the

braincase (Romer 1986 p526). In some bony fish, amphibians and reptiles, the endolymphatic sac may be of great size and contains calcareous matter. In reptiles, the endolymphatic duct arises from the medial wall of the sacculus and swings beneath the main part of the utriculus. It extends dorsally alongside the crus communis where it finally expands into the endolymphatic sac (Wever 1978 fig.3.3 p65).

4.2.1.6 The perilymphatic Duct and Sac

The perilymphatic system expands into a perilymphatic sac, similar to the endolymphatic system. In mammals, the perilymphatic sac lies below the cochlea, and penetrates through a foramen in the medial wall of the braincase into the braincase cavity. This foramen lies posterior to the foramen for nerve VIII. The perilymphatic duct is conducted through the foramen and the sac contacts the arachnoid membrane surrounding the brain.

In reptiles, this condition differs from mammals. This foramen, through which the perilymphatic system is conducted, is the jugular foramen, situated anterior to the foramen for nerve XII (Wever 1978 p72). The jugular foramen is ventrally situated to the cochlear organ and in reptiles even opens into the cochlear cavity (Wever 1979 p66).

4.2.1.7 The Cochlea and Lagena

In mammals, the cochlea forms the largest portion of the inner ear, and is an intricate organ of hearing. It is a long tubular structure, tightly coiled to form a cone.

In most reptiles, the lagena is lengthened into a sac-like structure. The relative size of the lagena varies greatly amongst the reptiles. In crocodiles, it is a short blunt tube, but in a few lizards and nearly all snakes, the lagena is very enlarged (Wever 1978 p66).

According to Romer (1986 p534, fig.388 p534), it appears that the cochlea of mammals has developed from the lagena of reptiles. In both crocodiles and birds, the cochlea has become a straight, elongated finger-like tube. This tube appears to be the intermediate condition and elongated further to become coiled and give rise to the

mammalian cochlea. The embryonic development of the inner ear of mammals indicates that the cochlea is a sac-like structure similar to the lagena of reptiles. The cochlea only coils at a later stage of development (Romer 1986 fig.382 p527).

4.2.2 The Bony Labyrinth

The bony labyrinth consists of a series of canals and cavities which closely surround the membranous labyrinth. This capsule, in which the hearing organs are contained, is generally known as the otic or auditory capsule. It has three divisions, namely the vestibule, the cochlea and the semicircular ducts. The labyrinth of reptiles is located towards the posterior end of the skull, lateral to the brain (Wever 1978 p64). In mammals, the labyrinth is anteriorly situated, when compared to the position in reptiles.

4.2.2.1 The Vestibule

The vestibule is the chamber that forms the middle portion of the bony labyrinth. It is connected to the semicircular canals dorsally and the cochlea ventrally. It houses the sacculus and utriculus. In mammals, a posterior vestibular ridge on the medial wall of the vestibule divides into two branches. These branches diverge to form a small fossa called the cochlear recess. Above and behind the vestibular ridge in the roof and medial wall of the vestibule is an oval depression called the elliptical fossa, which houses the utriculus (Cunningham 1937 p1113). Antero-ventrally in the medial wall of the vestibule, the sacculus is housed in a circular fossa called the spherical recess (Cunningham 1937 p1113).

4.2.2.2 The Semicircular Canals

The semicircular canals of mammals and reptiles are similar in structure, except that the postero-vertical canal in reptiles appears shorter than in mammals. The three semicircular canals of the bony labyrinth correspond closely to the structure of the membranous semicircular ducts. The canals are arranged in three planes, anterior, posterior and horizontal. They open into the vestibule through five apertures only,

since the medial opening of the anterior canal joins the upper end of the posterior canal in the common canal, the crus communis (Cunningham 1937 p1114). The crus then opens into the vestibule as a single canal.

4.2.2.3 The Bony Cochlea

The lagena of reptiles (Sub-section 4.2.1.7) is an elongated, uncoiled sac that varies in length (Kardong 1994 fig.17.34 p693, fig.17.41B p701). In mammals the cochlea is very elongated, but coiled (Kardong 1994 p691, fig.17.36D p695, fig.17.44B p704). It is positioned anterior to the vestibule in mammals and postero-laterally in reptiles.

4.2.2.4 The Fenestra Rotunda

A release mechanism, the fenestra rotunda, is situated at the end of the perilymphatic system to release vibrations. It is sealed by a flexible membrane, and is positioned below the fenestra ovalis between the internal auditory meatus and the middle auditory meatus in both mammals and reptiles.

4.2.2.5 The Fenestra Ovalis

The oval window which receives the footplate of the stapes, is situated in the wall of the vestibule in both mammals and reptiles. The vibrations from the footplate induce waves in the perilymph and endolymph of the inner ear structures. As stated above in Sub-section 4.2.2.4, the vibrations originated by the stapes through the fenestra ovalis are released by the fenestra rotunda.

4.3 The Therocephalian Inner Ear

The following sub-section discusses the inner ear of the early Therocephalia and other sectioned therapsids, and compares it to the reptilian and mammalian inner ears. It is hoped that this discussion will help to clarify the evolutionary position of the early therocephalian inner ear with respect to those of reptiles and mammals.

An important factor taken into account in the interpretation of the inner ear of *Glanosuchus macrops* SAM K238a, is that it is a juvenile specimen. This implies that the lack of ossification in the otic region (see Section 3.2 and 3.3) may be a juvenile characteristic. Comparison between the inner ears of *Glanosuchus macrops* K238a and other sectioned gorgonopsians, therocephalians and cynodonts may help clarify the question whether cartilage in the braincase is a juvenile characteristic or whether it is a permanent feature of adult specimens.

The main inner ear structures on the medial wall of the otic bones are:

The floccular fossa.

The vestibule.

The ampullary fossae.

The ridges supporting the semicircular ducts.

The sacculo-utricular recess.

The cochlear recess.

4.3.1 The Floccular Fossa

The floccular fossa is positioned on the postero-medial wall of the prootic (Fig. 5). In *Glanosuchus macrops* SAM K238a, it appears as a well-developed, cup-shaped fossa of reasonable depth. Olson (1938a p80) appears to agree with this, saying that the floccular fossa or subarcuate fossa is deep in therocephalians. According to him, the fossa is partially encircled by the anterior vertical semicircular canal, as is found in *Glanosuchus macrops* SAM K238a. A portion of the anterior vertical semicircular canal is embedded in the dorsal portion of the prootic above the floccular fossa (sections 493-499).

Olson (1944 fig.9 p25) produced casts of the inner ear region of all the therapsids he sectioned, and subsequently shows the floccular fossa as a finger-like projection. These projections are the lateral lobes of the cerebellum. He reconstructed the inner ear over these braincase structures, incorporating the floccular fossa into the inner ear. The floccular fossa protrudes between the semicircular canals. This is similar to the ear of *Glanosuchus macrops* SAM K238a, the cynodont described by Simpson (1933 fig.2

p288) and the cynodonts *Massetognathus* and *Probelesodon* (Quiroga 1979 fig.1 p180, fig.2 p181). In the reconstruction of the inner ear of *Thrinaxodon*, Fourie (1974 fig.28 p372) places the ear below the floccular fossa. In most other therapsid inner ear reconstructions, the antero-vertical semicircular canal passes above the floccular fossa.

According to Fourie (1974 p372), the function of the floccular fossa is to accommodate the lateral lobe of the cerebellum. If the inner ear was positioned over the floccular fossa, the cerebellar lobes would have to protrude past the inner ear canals to rest in the fossa in the medial wall of the braincase. The inner ear would have to be protected from the brain by the bony or cartilaginous otic capsule. A complete separation of the brain and the membranous inner ear is vital to protect the latter from damage.

This condition is completely absent in mammals and reptiles, as the bony labyrinth completely surrounds the membranous inner ear structure. Therefore, there is no contact between the inner ear and the brain of mammals or reptiles, unlike the early therocephalian condition described above, and the capsule surrounding the membranous inner ear is completely ossified.

The floccular fossa in *Gorgonops* (Sigogneau 1974 p54), is well-developed, and appears similar to *Glanosuchus macrops* SAM K238a. It opens into the cerebral cavity as it does in *Glanosuchus macrops* SAM K238a. This fossa in *Gorgonops* is formed on three sides by the prootic (anterior, dorsal and ventral) and by the opisthotic posteriorly, similar to the early therocephalians. Sigogneau (1974 p54, fig.3 p57) states that the floor of the floccular fossa in *Gorgonops* is formed by the posterior process of the prootic. Olson agrees with this condition in the therocephalian he sectioned (1938b fig.4G,H p81). In *Glanosuchus macrops* SAM K238a, the anterior portion of the floor of the floccular fossa is similar to that of *Gorgonops*, but it becomes horizontal over a shorter distance and remains so until its termination (sections 486-496).

Posteriorly, the supraoccipital forms both the roof and floor of the floccular fossa in gorgonopsians (Olson 1944 fig.6A,B,C p14 and Sigogneau 1974 fig.4A p60), but in the *Glanosuchus macrops* SAM K238a, the supraoccipital forms only a very small portion of the roof. The reconstructions of the sagittal view of the braincases of the three gorgonopsians ("Gorgonopsian A" and "B" and "Therocephalian B") sectioned by Olson (1944 fig.6 p14), show the floccular fossae as deep V-shaped structures on the posterior wall of the prootic. In "Gorgonopsian A", the floccular fossa is very high up

on the prootic, and lies immediately below the supraoccipital. The gorgonopsian "Therocephalian B" shows a deep groove within the floccular fossa, for the anterior vertical semicircular canal.

Glanosuchus macrops SAM K238a differs slightly from these specimens, in that the floccular fossa appears to have a much wider opening and is not angled to the same extent as Olson indicates. The anterior vertical semicircular canal is not positioned inside the fossa, but lies above it. A possible explanation for the similarity between the reconstruction of *Gorgonops* by Sigogneau (1974 p53) and the early therocephalian, is that *Gorgonops* is at "an evolutionary higher level" than the gorgonopsians used by Olson (1944) (Sigogneau 1974).

An interesting feature is found in a more "primitive" gorgonopsian sectioned by Olson (Olson 1938a fig.3 p161). In sagittal view, the floccular fossa appears no different to that described by Olson (1944). But in a particular dorso-ventral section through the braincase (Olson 1938a fig.7D p173), the floccular fossa appears as a foramen in the medial wall of the prootic (labelled as *fsubarc*). It appears that the skull has been sectioned at the posterior end of the floccular fossa and that the anterior opening of the cochlear recess has been cut through. A similar occurrence is found in *Glanosuchus macrops* SAM K238a in sections 500 through 503. The ventral process of the supraoccipital forms the medial wall of the cochlear recess and overlies the posterior extremity of the floccular fossa. When this region of the fossa is sectioned, the ventral process of the supraoccipital is also cut through and appears to form a foramen.

In a different section cut more anteriorly through the skull of a gorgonopsian, Olson (1938a fig.7E p173) shows the subarcuate fossa as an open fossa below the anterior vertical semicircular canal. This phenomenon could be similar to that described by Sigogneau (1974) for *Gorgonops* and *Glanosuchus macrops* SAM K238a (own observation).

A reconstruction of the sectioned *Ictidosuchops intermedius* (Crompton 1955 fig.6A) shows a very elongated fossa above a well-developed process. This appears to be the floccular fossa situated above the posterior process of the prootic, but Crompton (1955) does not elaborate on the structures on the medial surface of the prootic.

Thrinaxodon liorhinus has a very well-developed floccular fossa, which Fourie (1974 p372) also refers to as the subarcuate fossa. He notes that this fossa extends backwards "into a large space above the anterior opening of the posttemporal fossa". The large "space" Fourie (1974) refers to appears to correspond to the cochlear recess in *Glanosuchus macrops* SAM K238a. A major difference between the position of the recess and the early therapsid, is that in *Thrinaxodon* it is situated above the posttemporal fenestra. In the sectioned therapsid, this recess lies below the posttemporal fenestra.

Fourie (1974 fig.28 p372) reconstructs the inner ear of *Thrinaxodon* as a very low, small structure that lies below the floccular fossa. The presence of the antero-vertical semicircular canal above the floccular fossa in *Glanosuchus macrops* SAM K238a indicates that the inner ear structure was situated over the fossa, as presented by Olson (1944), Quiroga (1979) and Simpson (1933).

In Brink's (1960 fig.34B p131) reconstruction of *Procynosuchus*, the medial surface of the prootic shows a very well-developed, deep floccular fossa situated above a prominent posterior process. As described for *Glanosuchus macrops* SAM K238a and *Gorgonops* (Sigogneau 1974), the anterior, dorsal and ventral sides of the fossa are formed by the prootic and the posterior surface by the opisthotic. An interesting feature found in *Oligokyphus* (Crompton 1964 fig.3 p71, fig.7 p74), is the presence of a vascular canal piercing the floccular fossa. This has not been documented in the description of any other sectioned therapsid used for comparison in this study.

The floccular fossae of the cynodonts *Massetognathus* and *Probelesodon* (Quiroga 1979 fig.1 p180, fig.2 p181) are well-developed and large. Quiroga (1979) reconstructs the membranous inner ear over the floccular fossa, so that the lateral lobes of the cerebellum protrude through the semicircular canals. This is similar to the reconstructions by Olson (1944 fig.9 p25). The difference in the relationship between the inner ear and floccular fossa of *Thrinaxodon* (Fourie 1974 p372) and the two later cynodonts, is that in *Thrinaxodon* Fourie (1974) reconstructs the inner ear below the floccular fossa, not over it as Quiroga (1979), Simpson (1933) and Olson (1944) have done.

Olson (1944 Table.12 p37) holds the view that the floccular fossa decreased in depth and importance through the course of therapsid evolution. It appears that the cynodonts

discussed above contradict this statement and that the situation is precisely the opposite. The floccular fossa develops into a much better defined structure than that found in *Glanosuchus macrops* SAM K238a, or any of Olson's (1944) specimens. An example of such a condition in cynodonts is documented by Simpson (1933 fig.2 p288).

4.3.2 The Vestibule

The central part of the bony labyrinth, or the bone-cartilage capsule in theriocephalians will be referred to as the vestibule in this study.

The vestibule is the middle portion of the bony labyrinth situated between the semicircular canals and the cochlea (Cunningham 1937 p1113). It contains the membranous sacculus and utriculus in fossae within its medial walls. The vestibule opens into the endocranial cavity via the internal auditory meatus. Simpson (1933 p289) and Quiroga (1979 p179, p181) use this term in later cynodonts for the area stretching from the anterior edge of the fenestra ovalis to the opening of the cochlear recess, and from the lower rim of the posterior process of the prootic to the basioccipital. Olson (1944 fig.6 p14, p31-32, 1938a p146, 1938b p79) does not properly define the term "internal auditory meatus" in his text or diagrams, and this leads to some confusion concerning the position of this structure.

Cunningham (1937) describes the internal auditory meatus as being a canal between the medial wall of the otic capsule and the brain membranes. In contrast to Olson (1944), Sigogneau (1974 p53) claims that a definite internal auditory meatus does not exist on the medial wall of the otic capsule, but "merely a vast opening" which leads into the braincase cavity. This is also the condition in all sectioned therapsids compared in this section, due to the absence of the medial wall of the otic capsule. The author agrees with Sigogneau (1974) that the internal auditory meatus cannot be indicated if the structure is not present. It is for this reason that the structure is not described in *Glanosuchus macrops* SAM K238a.

Olson (1944 p24) noted that in the therapsids he sectioned, the vestibule is formed by the prootic, opisthotic, supraoccipital and basioccipital. He further states that the vestibule contained the utriculus, sacculus and the cochlea. The vestibule opens freely into the cranial cavity and into the ampulla of the semicircular canals. But even greater

confusion is created by Olson (1944 fig.6 p14), as the vestibule is not labelled in any of the diagrams, and the internal meatus appears to be labelled as what the author expects to be the vestibule. No attempt is made to clarify this aspect. However, the vestibule as described by Olson (1944) appears to be the cavity stretching between the basioccipital and the posterior process of the prootic, the anterior edge of the internal opening of the fenestra ovalis and the anterior margin of the cochlear recess.

Sigogneau (1974 p54) renounces the use of the term "vestibule" in the description of the inner ear of *Gorgonops*. This is because she believes the vestibule to refer to the bony portion immediately surrounding the membranous sacculus and utriculus, which is incomplete in therapsids. Therefore, Sigogneau claims a that vestibule is absent. In therapsids, the otic capsule labyrinth consisted of a bone and cartilage capsule. This is formed directly by the wall of the braincase, not by a separate bony structure, and there does not appear to be a proper bony labyrinth, as is found in mammals and reptiles.

In all therapsids sectioned thus far, there is no indication of a completely ossified vestibule, similar to the one found in mammals. This is probably because the medial walls of the vestibule of all therapsids remained unossified. The cartilage and bone vestibular structure possibly resembled and functioned like the mammalian vestibule in living therapsids (Kardong 1944 fig.17.36 p695).

The vestibule in *Glanosuchus macrops* SAM K238a appears to originate above the anterior inner edge of the fenestra ovalis. It extends dorsally past the opening for nerve VII to the prootic-supraoccipital suture (Fig. 5). Posteriorly, the vestibule terminates against the anterior opening of the cochlear recess, and ventrally above the medial ridge of the opisthotic, forming the roof of the jugular foramen and nerve XII. This region designated as the vestibule includes the utriculus and the sacculus. The vestibule, as mentioned above, consists of bone laterally and cartilage medially. The position of the endolymphatic sac is uncertain. The cochlea is contained within the opisthotic recess, and is separated from the rest of the ear.

The reconstruction of *Glanosuchus macrops* SAM K238a indicates that in the medial wall of the vestibule, between the posterior process of the prootic and the fenestra ovalis, is a shallow rounded fossa. It appears that the anterior part of the utriculus was situated in this fossa (Fig. 5).

In all the gorgonopsians, such as *Gorgonops* (Sigogneau 1974 fig.1 p54), therocephalians, such as *Ictidosuchops* (Crompton 1955 fig.6A p166) and cynodonts, such as *Thrinaxodon* (Fourie 1974 fig.28 p372) compared in this section, the vestibule appears very similar. Firstly, a cavity medial to the fenestra ovalis is present in all sectioned therapsids, representing the capsule. Secondly, the medial wall of the capsule is incomplete, indicating that cartilage was a permanent feature, even in mature specimens.

The conclusion can therefore be drawn that the otic capsule in therapsids was complete, and that the inner ear was protected from the brain by this capsule. The presence of cartilage in the otic region of *Glanosuchus macrops* SAM K238a is not a juvenile characteristic, but a permanent one, found in adult specimens as well. The development of a complete, ossified otic capsule must have developed in the early mammals, because even in later cynodonts the otic capsule contained cartilage.

4.3.3 The Semicircular Canals

In *Glanosuchus macrops* SAM K238a, the semicircular canals are supported by the prootic and opisthotic. It seems that a very small part of the posterior canal was supported by the ventral portion of the supraoccipital forming the medial wall of the cochlear recess.

Sigogneau (1974 p54) found that the absence of ossification in the inner ear of *Gorgonops* is such that the canals are open medially, and appear continuous with the vestibule. In gorgonopsian braincases there is a greater lack of ossification than in other sectioned therapsids (Kemp 1969). Olson also found that the canals were not medially enclosed by bone in therocephalians (1938b p80).

The presence of the semicircular canals within the medial wall of the braincase is specifically evident in the posterior vertical canal and the anterior vertical canal. The horizontal canal is situated in the medial surface of the inner ear, and extends beneath the ventral ledge of the prootic anteriorly to the posterior ledge below the floccular fossa posteriorly. This canal penetrates the prootic, for a very short distance only.

As described for the prootic (Section 3.2), the fossa housing the horizontal canal (*pf3*) is quite deep when sectioned dorso-ventrally. Approximately at sections 491 through 495, the fossa closes around the canal to partially cover it medially, before opening up into a fossa again. This indicates that almost the entire horizontal canal must have been enclosed by bone and cartilage.

The posterior vertical canal lies against, but does not penetrate the opisthotic or supraoccipital. However, it does penetrate the prootic. The foramen for this canal lies in the dorsal part of the prootic below the postero-dorsal process of the prootic. In section 496 all three semicircular canals are present within the wall of the prootic. This enclosure of the canals by bone may be significant by implying that ossification is occurring around the canals but is incomplete.

A similar occurrence is evident in the anterior canal as well. It appears to arise from the utriculus anterior to the cochlear recess and partially within the opisthotic, partially on the prootic. It follows an arc above the floccular fossa, terminating in the anterior ampulla above the dorsal ledge on the prootic. Above the floccular fossa, the anterior canal is another canal formed by the prootic (sections 493-499). The prootic is damaged on its lateral surface in *Glanosuchus macrops* SAM K238a (section 499) is second canal is exposed on the postero-dorsal process of the prootic.

The posterior canal and the anterior canal arise at the same position on the utriculus, forming a short common canal, the crus communis. This crus may have been positioned on the medial surface of the prootic, anterior to the suture with the opisthotic, for no such structure is evident in *Glanosuchus macrops* K238a. The posterior canal runs medially towards the braincase cavity, supported posteriorly by the anterior rim of the cochlear recess.

In *Thrinaxodon* (Fourie 1974 fig.19C p363), the dorso-ventral section of the braincase in the otic region indicates that the anterior vertical canal lies below the floccular fossa. The canal is situated in a deep, dorsally directed fossa in the prootic, and not in a foramen, like the sectioned early therocephalian. This is similar to the canal in the medial wall of the prootic in the early therocephalian that conducted the horizontal semicircular duct.

Posterior to the floccular fossa in *Thrinaxodon* (Fourie 1974 fig.19B p363), the presence of a foramen is indicated in the prootic. The foramen features in the posterior sections of the braincase of *Thrinaxodon* as well (Fourie 1974 fig.29A p376). This indicates that the membranous labyrinth is partially enclosed in cartilage, and partially in bone as in the early therapsid. In *Thrinaxodon* (Fourie 1974 p384), the posterior vertical canal joins the utricular recess, as in *Glanosuchus macrops* SAM K238a.

With evidence of foramina within the prootic for the semicircular canals, it may be concluded that these canals were probably partially surrounded by bone and partially by cartilage. It is certain that cartilage was a permanent feature in the otic capsule of all therapsids, because this condition persists in all sectioned therapsids, gorgonopsians and cynodonts discussed in this study.

4.3.4 The Ampullary Fossae

The ampullary fossae in the medial wall of the braincase of *Glanosuchus macrops* SAM K238a are present but not very definite. The structure of the inner ear of the early therapsid has thus far followed the basic pattern found in mammals and reptiles, and the presence of the ampullae is certain. Olson (1938b p79) states that the ampullae of therapsids must have been large, based on the size of the ampullary fossae.

The three ampullae present were the anterior, horizontal and posterior ampullae. The anterior ampulla situated at the distal end of the anterior canal and the horizontal ampulla situated at the proximal end of the horizontal canal must have been positioned very near to the internal opening of the nerve VII at the base of the antero-ventral process of the prootic. The position of the anterior ampulla appears to be similar to *Thrinaxodon* (Fourie 1974 fig.27A p371).

The second small fossa, presumably for the external ampulla, appears to be positioned immediately above the foramen for nerve VII and the anterior ampulla. This fossa in the prootic is quite deep and forms the posterior edge of the foramen for nerve VII (sections 474-467). The fossa for the anterior ampulla is above and slightly posterior to the external ampullary fossa, above the dorsal ledge of the prootic (described in detail in the prootic, Section 3.2).

The position of the third ampulla, the horizontal ampulla, is not evident. It is situated on the posterior end of the horizontal canal where the posterior vertical canal meets the sacculus. This area did not leave an impression on the medial wall of the braincase. The bony labyrinth forming the ampulla presumably consisted of cartilage.

In the other sectioned therapsids discussed in this section, the ampullary fossae are not indicated on the medial surface of the braincase, except for Fourie (1974) in *Thrinaxodon* and Olson (1944 fig.6C p14). Olson (1944) indicates a single fossa for the anterior ampulla in "Therocephalian B", situated above the jugular foramen. This position is unrealistic, because it is situated far posteriorly at too great a distance from the inner ear structures. The ampullary fossae indicated in *Thrinaxodon* (Fourie 1974) are well-developed.

4.3.5 The Sacculo-Utricular Recess

In *Glanosuchus macrops* SAM K238a, there are two main recesses in the inner ear, a small posterior cochlear recess and a large anterior sacculo-utricular recess. The large anterior recess is divided into two smaller recesses, the utricular recess and the saccular recess (Figs 6, 7, 8).

The sacculo-cochlear recess does not appear to be present in early therocephalians, because of the presence of a large cochlear and a sacculo-utricular recess in the sectioned specimen. Therefore, a recess for the sacculus and cochlea is absent in the early therocephalians. Because the saccular recess appears to lead into the utricular recess, a sacculo-utricular recess is suggested here.

In mammals, the vestibule houses the utriculus and the sacculus (Cunningham 1937 p1113). In *Glanosuchus macrops* SAM K238a, this implies that the sacculo-utricular recess is situated in the vestibule.

The anterior portion of the sacculo-utricular recess is a deep pocket, and it extends down into the opisthotic, anterior to the mastoid process. This deep recess is formed antero-ventrally by the opisthotic and the basioccipital, and postero-ventrally by the ventral portion of the prootic, and the opisthotic. It housed the utriculus antero-

ventrally, slightly above and behind the inner opening of the fenestra ovalis. The utriculus is ventro-laterally situated against the medial wall of the vestibule, extending in a posterior direction. The sacculus lies postero-ventrally to the base of the cochlea.

The shape of the utricular recess indicates that the utriculus is a slightly flattened finger-like projection (Fig. 7). Due to the shape and depth of the recess, it can be deduced that the utriculus in *Glanosuchus macrops* SAM K238a is considerably larger than that found in reptiles, and only slightly larger than that found in mammals (Kardong 1994 fig.17.34 p693). The utriculus in reptiles appears to be a thickened tube, with a very slight widening at the posterior end (see Sub-section 4.2.1.3). In mammals, the utriculus has a considerably larger volume than in reptiles with a tube-like dorsal portion, and a ventrally widened sac. A wide shallow fossa, situated on the medial wall of the prootic between the posterior process and the fenestra ovalis, possibly accommodated the anterior part of the utriculus.

Above the dorsal rim of the utricular recess, at the posterior end of the sacculo-utricular recess, is a smaller more rounded recess. This pocket appears to be the saccular recess. It is positioned anterior to the base of the cochlear recess (Figs 6, 7, 8). It is also possible that the lateral pit in the anterior rim or the exoccipital pit of the cochlear recess could have housed the sacculus.

Because the shape of the opisthotic recess suggests coiling of the cochlea, and the ventro-lateral groove is slightly anterior to the lateral pit, it can be presumed that the cochlea filled the entire cochlear recess. Therefore, no space would remain for the sacculus in the cochlear recess, and would have to be positioned immediately anterior to the recess. This corresponds with the postero-dorsal sacculo-utricular recess. This concurs with the condition that the sacculus is situated posterior to the utriculus, as described by Sigogneau (1974 p58) for *Gorgonops*. Similar to the early therocephalian, the horizontal canal opens into the sacculo-utricular cavity in the gorgonopsian.

In reptiles, the sacculus is greatly enlarged and situated below the horizontal canal, with the utriculus present as a small lobe. This is the reverse of the condition in mammals, where the utriculus is large and the sacculus is reduced. The condition in *Glanosuchus macrops* SAM K238a and *Gorgonops* (Sigogneau 1974 p59), appears to comply with the mammalian condition.

In the other sectioned therocephalians (*Ictidosuchops* Crompton 1955 fig.6A p166, Olson 1938b) and cynodonts (*Procynosuchus*, Kemp 1979 fig.13 p102, Brink 1960 fig.34 p131) there is no indication or discussion of a saccular or utricular recess. This makes comparison between these groups and the early therocephalian impossible. There, however, a suggestion of a cochlear recess by a few authors, like Fourie (1974 *Thrinaxodon*) and Olson 1938a.

4.3.6 The Cochlear Recess

The cochlear recess is discussed in Section 3.3, but the structures within it are elaborated upon in this sub-section. This recess appears to correspond with the cochlear recess of the mammalian bony labyrinth. The similarity lies in the contents of the recess, the cochlea, and not the shape, which differs greatly. The terms used to name the grooves and pits in this recess have not been described in fossils before. The structures have been specifically identified to facilitate to their description in this study (Fig. 9).

The cochlear recess is situated between the dorsal suture of the prootic (below the postero-dorsal process), the exoccipital, the basioccipital and the supraoccipital. The roof of the recess is formed by a part of the postero-dorsal process of the prootic which forms the antero-medial edge of the posttemporal fenestra. The recess opens into the posterior end of the vestibule and is directed in a postero-lateral direction, slightly diagonally upwards. The braincase of *Glanosuchus macrops* SAM K238a is slightly distorted in this direction. It could be that distortion aggravated the orientation of this recess (Figs 6, 7, 8).

The medial wall of the cochlear recess is formed by a small kidney-shaped portion of the ventral process of the supraoccipital, with the concave side directed into the recess. This medial wall separates the cochlear recess from the braincase cavity. More anteriorly, the recess is not completely closed off from the main braincase cavity. Dorsal to the medial wall of the opisthotic recess, a small foramen is present between the braincase cavity and the anterior medial wall of the cochlear recess (section 503). This foramen is referred to in this study as the internal auditory foramen because of its position. It is highly probable that it conducted the vestibulo-cochlear nerve VIII (Fig. 5).

The lateral and ventro-lateral sides of the cochlear recess are formed by the paroccipital process of the opisthotic. The supraoccipital portion forming the auditory nerve foramen between the braincase and cochlear recess forms the medial wall. The supraoccipital briefly contacts the dorsal edge of the exoccipital, which contributes a small ventral portion to the recess. The cochlear recess has two grooves and four pits. The grooves are the dorso-medial groove and the ventro-lateral groove. The pits are the exoccipital pit, the supraoccipital pit, the lateral pit and the posterior pit (Fig. 9).

A small vertical depression, the exoccipital pit, is present on the antero-ventral edge of the cochlear recess. The base of this pit is formed only by the exoccipital, the lateral wall by the opisthotic and the medial wall by the supraoccipital. Situated laterally to the exoccipital pit against the dorso-medial side of the recess, is a second pit that lies in the hollow of the supraoccipital process. This supraoccipital pit is a shallow structure that extends postero-ventrally into the recess.

As explained in Section 3.3, it is not certain whether the grooves present in the cochlear recess are artifacts created by the wax model reconstruction process, or whether they are true structures. Another factor influencing this certainty, is the poor ossification in this area of the opisthotic. No grooves or pits are described in other sectioned therapsids, and the cochlear recess is usually cone-shaped and lacking markings on the interior surface. Description of this area in another sectioned early theriocephalian will certify whether any grooves are present in the cochlear recess or not.

The first groove lies against the medial wall of the supraoccipital pit. It curves upwards and around to form a deep dorso-medial groove situated posterior to the internal auditory foramen of VIII, between the cochlear recess and the braincase cavity.

The second groove lies dorsal to the exoccipital pit at the back of the cochlear recess. This ventro-lateral groove is deep and seems to curve around the outskirts of the cochlear recess and then turn dorsally towards the first groove. The grooves evince a slight spiralling pattern towards the centre of the cochlear recess.

The third depression, the lateral pit, lies against the lateral edge of the recess. It is very narrow and deep and the base extends laterally into the paroccipital process.

The fourth pit, or the posterior pit, is the deepest of all the structures in the cochlear recess. It is cone-shaped and situated near the roof of the recess. The anterior part of the roof of the pit is formed by the prootic and the posterior part by the opisthotic. The base of the pit is directed posteriorly into the paroccipital process. The pit opens anteriorly into the posterior wall of the recess with a wide opening.

If the spiralling within the cochlear recess is real, it will appear that the cochlea of early therocephalians could have possessed one or two poorly developed coils. This can be based on the position and direction of the grooves and pits on the inner surface of the cochlear recess towards the central posterior pit. If the therocephalian cochlea possessed coils, it could be that the inner ear of the therocephalian leaned itself towards an intermediate stage between the reptiles, with their underdeveloped postero-lateral lagena, and mammals, with their spiralled anterior cochlea. Olson proposed that the cochlea of therapsids was similar to primitive living mammals. The cochleas of these mammals (Olson 1944 fig.11 p40) do appear similar to the early therocephalian cochlea proposed here. The cochleas of these mammals appear to be very poorly developed, having one, two or three coils (Fig. 22B).

In support of this assumption, one has to consider to what extent the structure of the inner ear can be utilized in phylogenetical analysis. Diversity of lifestyle within a specific group of animals can be wide, and probably affects the hearing apparatus.

The length of the cochlea appears to have an effect on the frequency of sound wave detected. It seems that the more the cochlea duct elongates, the more sensitive the ear is to high frequency sounds. The increase of the length of the cochlea is evident in living reptiles through birds to mammals. Therefore, there is an increasing sensitivity to high-pitched sounds in mammals. Reptiles are less sensitive to quiet sounds, and are most sensitive to low frequencies. McGowan (1992 p80) claims that the heavy stapes in therapsids is suited to low frequency terrestrial sounds.

Olson (1938b p78) mentioned a structure found in his sectioned therocephalian that appears to be the same as the cochlear recess discussed in *Glanosuchus macrops* SAM K238a. He states that the vestibule is "double in character", with two parts; an antero-medial portion of the vestibule which is the part containing the dorsal inner ear structures and "a smaller latero-posterior portion". This latter portion appears to be the

cochlear recess. He states that these two cavities are separated by a spur or rim of opisthotic. This is similar to the early therocephalian, where the anterior rim of the mastoid separates the cochlear recess and the floccular fossa.

Furthermore, Olson recognized this recess in gorgonopsians as well (1938a p155), naming it "a long recess into the opisthotic". Previously to this, Olson (1938a p148) states that "the lagena-cochlea must have been poorly developed". He apparently did not realize that the cochlea may have been developed in therocephalians and gorgonopsians to fill this cavity, and ascribes no function to it. "The posterior opening leads dorsally into the latero-ventral margin of a deep, blind recess which passes back and somewhat laterally into the opisthotic portion of the periotic. This deep recess housed the posterior ampulla and a portion of the horizontal semicircular canal, but, since it continues for some distance back of these structures, is much too large to be completely filled by them, and opens into the posterior fenestra of the vestibule, it must have enclosed some other soft structure as well" (Olson 1944 p78).

The only clues that provide information regarding the function of the cochlear recess in the sectioned early therocephalian, is the relationship between the position of the semicircular canals, the utricular and the saccular recess. The spiral design created on the inside of the recess by the grooves and pits, gives the impression of coils. The only organ in the inner ear that possesses coils, is the cochlea of the mammalian inner ear. Hence, the idea that the recess housed the cochlea. Because there is no supportive evidence as to the presence of a coiled cochlea in therapsids, the grooves in the cochlear recess cannot be indicative of a coiled cochlea.

A few other authors, such as Fourie (1974 p371) name the recess but make no suggestions as to its contents. In *Thrinaxodon*, Fourie (1974 fig.27A p371) describes a cone-like recess for the cochlea, inside the sacculo-cochlear recess, as Olson (1944) does. This sacculo-cochlear recess is separated from the jugular foramen by a bony ridge of opisthotic and the sacculo-cochlear ridge is further separated from the utricular recess by another bony ridge. This differs from the early therocephalian condition with the presence of a sacculo-utricular recess, and a cochlea recess leading into it. The division between the saccular and utricular recess is a very small bony ridge surrounding the saccular recess to form a round shallow fossa. The sacculo-utricular recess is separated from the jugular foramen by a single bony ridge.

Another very important difference between the mammalian and early therocephalian cochlea, appears to be its position. In mammals, the cochlea is positioned so that it points anteriorly. In the early therocephalian, it points postero-laterally, as it does in reptiles.

4.3.7 The Endolymphatic System

The endolymphatic tube arises from the medial surface of the utriculus, and swells to form the endolymphatic sac, as described in Sub-section 4.2.1.5. In both reptiles and mammals, the endolymphatic sac is positioned dorso-medially to the utriculus. Since this portion of the otic capsule is not preserved in the early therocephalian, detail concerning the endolymphatic system is lacking. Olson (1938a p158) states that in gorgonopsians the endolymphatic sac lies in a small fossa on the suture between the prootic and supraoccipital above the dorsal margin of the vestibule and posterior to the floccular fossa. He also notes that the endolymphatic sac must have passed into the cranial cavity via the internal auditory meatus in gorgonopsians.

In conclusion, the endolymphatic system would probably penetrate the medial wall of the otic capsule and lie within the braincase cavity as in reptiles and mammals. This opinion is also shared by Sigogneau (1974 p58) for *Gorgonops*, where the endolymphatic system is poorly represented.

4.3.8 The Perilymphatic System

As mentioned in Sub-section 4.2.1.6, the perilymphatic system is situated between the membranous labyrinth and the bony labyrinth (Romer 1986 fig.387 p533, p533) and terminates against the fenestra rotunda. According to Wever (1978 p72), this sac bulges into the cranial cavity through the jugular foramen in the medial wall of the otic capsule (Wever 1978 fig.3.12 fig.3.13 p73).

In the cranial cavity, the perilymph sac contacts the arachnoid membrane surrounding the brain. This appears to be similar to the mammalian condition (Cunningham 1937 p1116). Romer (1986 p533) notes that the sac also leaves the otic capsule through the jugular foramen in mammals.

It is possible that the internal auditory foramen for nerve VIII in the *Glanosuchus macrops* SAM K238a may have conducted the perilymphatic duct into the cranial cavity. Because of the small size of the foramen and its position to the cochlear recess, this is unlikely. The other possible position for the perilymphatic sac in the early therocephalian skull, is in the groove suggested in a sectioned therocephalian by Olson (1938b). This groove runs from the anterior edge of the fenestra ovalis to the jugular foramen. Olson (1944 p32, 1938b p77) claims that this groove is the bony remnant of the perilymphatic system (see Sub-section 4.2.1.6), and is present in *Glanosuchus macrops* SAM K238a (Figs 6, 7).

As stated in Sub-section 4.1.1.1, there is no indication of a separate fenestra rotunda in the sectioned therapsids compared in this study. Only one early cynodont, *Thrinaxodon* (Fourie 1974 fig.28 p372), displays a foramen that could be the fenestra rotunda. It is quite large and is situated between the fenestra ovalis and the foramen magnum, but is not present in any other cynodont compared in this study.

Sections through the ear region of *Iguana iguana* (Wever 1979 fig 3.12 fig 3.13 p73) indicate the close connection between the vagus nerve X, the jugular foramen and the inner ear structure. A frontal section through the otic capsule indicates the closeness between the medial wall of the otic capsule and the brain tissue (Wever 1978 fig 3.11 p72). The cartilaginous wall of the otic capsule in therocephalians was expected to exhibit a similar condition.

A little further through the otic capsule of *Iguana iguana* (Wever 1978 fig.3.12 p73), the jugular foramen appears to contact the medial wall of the otic capsule. Within this foramen is a second foramen, the perilymph foramen, in which the perilymph sac and nerve IX have contact with the cochlear duct.

A more posterior section through the otic capsule of *Iguana iguana* (Wever 1978 fig.3.13 p73) indicates the jugular foramen in the medial wall of the otic capsule, with the formation of the fenestra rotunda membrane laterally. This could give an indication why Olson (1944 p32) claims that the fenestra rotunda in therapsids is confluent with the jugular foramen.

In some of the sectioned therapsids, Olson (1944 p32) describes the fenestra as having a double character, and that the fenestra rotunda is a lateral extension of the fenestra ovalis. In other specimens, Olson claims that a sliver of bone separates the two fenestrae. He also discusses a similar fenestra rotunda in gorgonopsians (Olson 1938a p154).

If a fenestra rotunda, which opened into the fenestra ovalis, is present in the early therocephalian, then any corresponding structure may have been formed by cartilage. Mature early therocephalian specimens, such as *Glanosuchus macrops* GS M796, and *Ptomalestes avidus* SAM 11942, do not give any indication of a fenestra rotunda in any form, not even by a notch in the fenestra ovalis as Olson (1938a fig.1 p143) noted in gorgonopsians.

4.3.9 The Openings of the Inner Ear

The following openings penetrate the inner ear and the lateral surface of the braincase, namely:

The fenestra ovalis.

The foramen for nerve VII.

The internal auditory foramen for nerve VIII.

4.3.9.1 The Fenestra Ovalis

The fenestra ovalis opens laterally and slightly ventrally. In most therocephalians, its outer border is an out-turned lip. Four bones contribute to the rim of this structure, namely the prootic antero-dorsally, the opisthotic postero-dorsally, the parabasisphenoid antero-ventrally and the basioccipital postero-ventrally (Fig. 5). In *Ictidosuchus* (Crompton 1955), the fenestra ovalis is formed only by the periotic. In *Thrinaxodon* (Fourie 1974 p384) it is formed by the prootic, opisthotic and the basioccipital. In lateral view, the parabasisphenoid and basioccipital form the basal tubera, which are situated ventro-medial to the fenestra ovalis. The suture of the parabasisphenoid and basioccipital runs down the centre of the basal tubera.

In *Glanosuchus macrops* SAM K238a, the stapes is present on the left side and will be described briefly in in Sub-section 4.4.1.1. (Fig. 3B)

4.3.9.2 The Foramen for Nerve VII

The foramen for nerve VII lies at the base of the antero-ventral process of the prootic. The lateral opening of this foramen has a small depression for the position of the gasserian ganglion. On the medial surface, the opening is situated anterior to the fossa for the external ampulla (*pf*2) and forms its anterior edge (Fig. 5). In all the sectioned therapsids compared in this study, the foramen for nerve VII is present and is situated in a similar position similar to that found in *Glanosuchus macrops* SAM K238a.

4.3.9.3 The Foramen for Nerve VIII

This study refers to the foramen for nerve VIII as the internal auditory foramen, because it appears to correspond with this foramen in mammals. It is situated between the cochlear recess and the cranial cavity, and apparently conducted the auditory nerve from the inner ear to the brain. The foramen leads into the cerebellar region of the braincase cavity. The presence of this foramen in other sectioned therapsids compared in this study has not been noted (Fig. 5).

In *Glanosuchus macrops* SAM K238a, the foramen is situated at the anterior rim of the cochlear recess, and is formed dorso-medially by the postero-dorsal process of the prootic and ventro-medially by a part of the ventral process of the supraoccipital (Figs 6, 7, 8).

Apart from the auditory nerve VIII, the internal auditory foramen possibly also conducted blood vessels from the ear. The veins from the cochlea and vestibule unite with the semicircular canal veins at the base of the internal meatus to form the internal auditory vein in mammals (Cunningham 1937 p1123).

4.4 The Middle Ear

The mammalian external ear consists of an external auditory meatus which terminates in a tympanic membrane. The middle ear consists of a cavity called the tympanic cavity, which contains the three hearing bones. These are the malleus, incus and stapes. The tympanic cavity is connected to the pharynx via the Eustachian tube.

The three hearing bones are connected to each other with ligaments, and to the tympanic membrane by the malleus and the fenestra ovalis by the stapes.

The footplate of the stapes is situated in the fenestra ovalis in the vestibule. The fenestra rotunda opens below the fenestra ovalis. Above the vestibule of the bony labyrinth is the semicircular canals, and antero-ventrally to the vestibule is the cochlea.

Inside the bony labyrinth is the membranous labyrinth, which is smaller but corresponds in shape to the bony labyrinth. The vestibule contains the utriculus, the sacculus and the endolymphatic canal which exits the vestibule and gives rise to the endolymphatic sac.

In therapsids, the inner ear is the only part of the ear inside the skull, unlike mammals where the external auditory meatus is situated in the temporal bones. The middle ear of therapsids is situated outside the fenestra ovalis.

4.4.1 The Early Therocephalian Middle Ear

It is not necessary to discuss the middle ear of the early therocephalian in detail, because this region has been described by Van den Heever (1987). The left middle ear is damaged in *Glanosuchus macrops* SAM K238a, and the stapes and a small portion of the quadrate is present on the left side of the braincase. The right side of the skull has broken off completely. These few sections in the braincase of the sectioned therocephalian are briefly described here.

4.4.1.1 Stapes

The stapes present on the left side of the braincase of *Glanosuchus macrops* SAM K238a is almost complete (sections 461-480). It is not situated in its original position but has moved slightly laterally (Fig. 3B). The stapes is dumbbell-shaped. The stapes of *Glanosuchus macrops* GS M796 is described by Van den Heever (1987 p134).

4.4.1.2 Quadrate

In cross-section, a remnant of the left quadrate of *Glanosuchus macrops* SAM K238a is present in sections 498-528). The quadrate of early therocephalians is a triangular bone with a wide basal part and a broad dorsal flange. The basal region has a roller on the ventral surface that articulates with the glenoid fossa of the articular. The dorsal flange of the quadrate is situated in a pocket in the squamosal. The quadrate is discussed by Van den Heever (1987 p120).

4.5. Summary

The bony and membranous labyrinths of mammals and reptiles appear very similar in structure. The main differences between the mammalian and reptilian inner ears, are the size of the utriculus and sacculus, the length of the hearing organ, the cochlea or lagena, and the position of this hearing organ in relation to the vestibule. The inner ear of mammals and reptiles are compared in the Summary Table at the end of this section.

In mammals, the utriculus is large and the sacculus is small. In reptiles, the utriculus is small and the sacculus is enlarged. These structures are situated at the base of the cochlea or lagena.

The elongation and coiling of the cochlea is a significant occurrence in the development of the mammalian inner ear. Romer (1986 fig.388 p534) postulates the evolution of the mammalian cochlea from a primitive reptile through to mammals and birds with crocodiles as a middle development stage. This process involves the lengthening of the short perilymphatic duct into a lagena or cochlear duct and then into a very long coiled cochlea. The cochlea delivers a nervous impulse which is directed to the brain by nerve

VIII. The brain interprets these impulses as sound. It faces anteriorly in mammals. In reptiles, the lagena is a sac-like structure which varies greatly in size. In archosaurians (crocodiles) the lagena enlarges in size to form a large blunt sac with an enlarged lobe at its end. In lizards and snakes, the lagena is a very elongated tube which is postero-laterally directed.

Discussion of the early therocephalian inner ear indicates a few certain facts. The first important fact is the lack of ossification in the otic region of the braincase. This appears to be a permanent characteristic in therapsids, and not a feature restricted to juvenile specimens such as *Glanosuchus macrops* SAM K238a. An unossified otic capsule is present in all the other sectioned therapsids compared in this study.

The inner ear of early therocephalians consists of three definite fossae that housed the sacculus, the utriculus and the cochlea. The utriculus was a broad tube, the sacculus was a small sac-like structure situated posterior to the utriculus but anterior to the cochlea. The cochlear recess of *Glanosuchus macrops* SAM K238a displays slight coiling, but it is not certain whether this is artificial or not. No other sectioned therapsid indicates grooves in the cochlear recess.

There is a definite foramen between the cochlear recess and the braincase cavity. It is assumed, due to its position, that it conducted the vestibulo-cochlear nerve, VIII.

The middle ear of early therocephalians consists of a quadrate that articulates with the articular and the stapes. The footplate of the dumbbell-shaped stapes rested in the fenestra ovalis. The shape and size of the stapes in *Glanosuchus macrops* SAM K238a and *Glanosuchus macrops* GS M796 indicates that the early therocephalians were possibly suited to low frequency terrestrial sound. This is the case in modern living reptiles (McGowan 1992 p80).

There is no indication that the fenestra rotunda is positioned below the fenestra ovalis in early therocephalians. A postulate by Olson (1944 p32), namely that the perilymphatic duct is represented by a groove situated between the fenestra ovalis and the jugular foramen, appears feasible in *Glanosuchus macrops* SAM K238a. A groove, similar to the one described by Olson (1944, 1938a, 1938b) in therocephalians and gorgonopsians is present in the early therocephalian braincase.

Summary Table of the Functions of the Membranous Inner Ear Structures In Mammals and Reptiles (Tortora and Anagnostakos 1987 Table.17.2 p393).

Semicircular Ducts: Contain cristae, receptors for dynamic equilibrium.

Ampullae: Contain cristae, receptors for dynamic equilibrium.

Utriculus: Contains macula, receptor for static equilibrium.

Sacculus: Contains macula, receptor for static equilibrium.

Cochlea: Contains fluids, channels and membranes that transmit sound waves to the organ of hearing in the cochlea. These waves generate nerve impulses and transmit them to the auditory nerve VIII.

Lagena: In reptiles the function is the same as the cochlea in mammals and performs the same functions. In mammals a region at the base of the sacculus persists, called the lagena by some authors, and contains maculae receptors for static equilibrium.

Endolymphatic Sac: Controls the production of endolymph and regulates its pressure in the cochlea or lagena.

Perilymphatic Sac: Controls the production of perilymph regulates its pressure in the cochlea or lagena.

CHAPTER 5

THE DISCUSSION OF THE BRAIN

This chapter deals with the proposal of a possible early therocephalian brain shape, reconstructed from structures, fossae and foramina in the medial braincase wall. To aid the reconstruction of the brain, certain parts of reptilian and mammalian brains are discussed, and compared to corresponding structures in the endocast. Furthermore, the relation between the brain shape and the activity rate of the living early therocephlian is postulated.

5.1 The Reptilian and Mammalian Brain

The brain of vertebrates includes three main regions, namely the forebrain, the midbrain and the hindbrain (Romer 1986 p570, Kardong 1994 p647). The brains of reptiles and mammals are very different from each other, but the components remain the same.

Only certain portions of the brain is discussed in the early therocephalian because of the lack of certain detail on the medial wall of the braincase. The components of the brain evident from the sectioned early therocephalian braincase, are the medulla oblongata and the cerebellum of the hindbrain, the pituitary gland and the epiphysis of the midbrain, and the cerebrum and olfactory lobes of the forebrain.

Phylogenetically, there is a tendency for the cerebellum and the cerebrum to enlarge (Kardong 1994 fig.16.33 p647). This accompanies development of complex behaviour, sensory awareness and improved muscle control (Kardong 1994 p647).

5.1.1 The Olfactory Lobes

The paired olfactory lobes are associated with smell. The size of the lobes varies with the acuteness of the sense of smell (Romer 1986 p587). The olfactory lobes are connected to the forebrain by the olfactory tracts (Kardong 1994 fig.17.6 p668). In reptiles, these olfactory tracts vary in length, but a reduction in length of the tracts occur in mammals (Romer 1986 fig.418 p577, Kardong 1994 fig.16.35 p650). The olfactory lobes of recent reptiles may extend to the anterior end of the nasals as in *Varanus* (Starck 1979 fig.10 p21), or to the olfactory capsules in the premaxillary as in chelonians (Starck 1979 fig.11 p22).

In recent reptiles, such as *Sphenodon punctatus* and *Varanus salvator* (Starck 1979 fig.10 p21), a very high broad cartilaginous septum, the septum internasalis, is present in the anterior portion of the brain cavity. This septum extends dorso-ventrally between the base of the olfactory tracts and the olfactory lobes to the parabasisphenoid, pterygoid and vomer. The cartilage of this septum forms the floor of the anterior portion of the braincase and divides the nasal cavity into left and right chambers.

The olfactory lobes of mammals are well developed, as the sense of smell is acute. In some mammals, for example *Gymnura*, the tree shrew, the length of the olfactory tracts has decreased greatly (Romer 1986 fig.418 p577, Kardong 1994 fig.16.35 p651). In other mammals, such as the horse *Equus*, the olfactory lobes have moved to a ventral position below the anterior edge of the cerebral lobes and is greatly reduced in size.

5.1.2 The Cerebrum

The cerebrum is positioned posterior to the olfactory lobes and tracts, and consists of two hemispheres. The cerebral hemispheres are the hind lobes of the brain. The original function of the cerebral hemispheres was probably solely for reception of olfactory stimuli. In tetrapods, the cerebral lobes became enlarged and began to function as centres for sensory correlation. The development of the original olfactory centre indicates how important the sense of smell is to animals, to gain information about the surrounding environment.

In mammals, the cerebral hemispheres are greatly enlarged and the surface is convoluted (Romer 1986 p587, Kardong 1994 p654). This phylogenetic enlargement also occurs partly because the cerebrum processes more sensory information from the forebrain (Kardong 1994 fig.16.35 p650).

In reptiles, the cerebral hemispheres are advanced over those of amphibians in both complexity of organization and relative size compared to other brain parts (Romer 1986 p590). This is evident in comparisons between *Rana* and *Alligator* (Romer 1986 fig.418 p577, Kardong 1994 fig.16.35 p650). The lobes of the cerebrum are much smaller than those of mammals and their surface is not convoluted.

5.1.3 The Optic Lobes

The optic lobes form part of the midbrain in tetrapods. These lobes are involved in processing visual information. Their size varies with the importance of sight. The eyes appear to have been responsible for the development of important association centres in the anterior region of the brainstem (Romer 1986 p585).

In reptiles, the optic lobes are quite large, but not as large as those in birds and teleosts. The lobes are situated postero-dorsally to the cerebral lobes and the epiphysis of the midbrain (Starck 1979 fig.18A p31). Starck (1979) illustrates the size of these lobes in dorsal view in various living lizards, such as *Sphenodon Punctatus* (1979 fig.15 p28) and *Varanus salvator* (1979 fig.17A p30).

In mammals, the optic lobes are replaced by four small swellings in the roof of the midbrain, called the corpora quadrigemina. Of these, the anterior pair (superior colliculi) is concerned with visual reflexes and represent the optic lobes of reptiles. The function of the posterior pair (inferior colliculi) is associated with the relay of auditory stimuli to the cerebral hemispheres (Romer 1986 fig.418 p577, p586, Kardong 1994 fig.16.35F p651).

5.1.4 The Pituitary Gland

The pituitary gland or hypophysis lies on the ventral surface of the midbrain, directly below the cerebrum. It is a bilobed structure situated in the sella turcica of the braincase. This is the most important of the endocrine structures (Romer 1986 p584) and secretes various hormones regulating growth, water retention, blood pressure and the reproductive systems.

The reptilian hypophysis conforms to the typical tetrapod structure but is remarkably varied in shape and size. The mammalian structure is similar to the reptilian hypophysis, but also varies greatly in size, although the shape remains constant. Both parts of the hypophysis in mammals and reptiles are supplied with blood vessels from the internal carotid arteries.

5.1.5 The Cerebellum

The cerebellum is a single, dome-shaped lobe situated anteriorly on the hindbrain. It is often large but varies in size from group to group. The surface is often highly convoluted and folded. On either side of the cerebellum is a finger-like protrusion. These are called the lateral lobes or auricles.

The cerebellum has two functions. The first one is to maintain equilibrium. The auricles are especially concerned with this function and are closely associated with the inner ear (Romer 1986 p581). The incoming information results in the maintenance of balance and muscle tone. The second function is to modify and refine muscular action (Kardong 1994 p649).

The degree of development of the cerebellum roughly correlates with the intricacy of bodily movement, and this structure is therefore large in mammals but smaller in reptiles (Romer 1986 p581). This implies that in higher vertebrates, improved muscular control facilitates improved locomotion.

The pons forms the base of the midbrain below the cerebellum and undergoes a distinct enlargement only in mammals. It contains nerve fibres passing to and from other parts of the brain stem. Three nerves, namely V, VI and VII, take root in the pons.

5.1.6 The Epiphysis or Parietal Eye-Pineal Complex

This structure is present in reptiles as the parietal eye-pineal complex and in mammals as the epiphysis. It is an evagination of the roof of the midbrain posterior to the cerebral hemispheres.

In *Sphenodon* and many lizards the parietal eye-pineal complex is dominated by two structures, namely the parietal eye and the pineal organ (Romer 1986 fig.374 p519). Some lizards, snakes and tortoises possess only a pineal organ and the parietal eye is absent. In those reptilian groups possessing a parietal eye, the parietal eye affects the perception of photoradiation, and is situated just under the skin in a foramen in the parietal called the pineal or parietal foramen. This may allow the parietal eye to respond to changes in the photoperiod and detect seasonal or daily light changes (Kardong 1994 p604).

In mammals, the parietal eye-pineal complex has become very reduced to form the epiphysis. Its function is completely different and it has become an endocrine organ. The pineal organ has also been known to regulate reproductive cycles in a variety of vertebrates (Kardong 1994 p685).

5.1.7 The Medulla Oblongata

This part of the brain is situated posterior to the cerebellum. It is simpler in structure to the other regions of the brain and appears to be a thick tube. The posterior portion of the medulla oblongata is very similar in structure to the spinal cord. The cranial nerves VIII, IX, X and XII arise from the medulla oblongata.

This part of the brain has three major functions. Firstly, it houses the nuclei of the cranial nerves. Secondly, the medulla serves as a pathway to and from higher centres of the brain. Thirdly, it contains centres for auditory, visceral and proprioceptive reflexes, including reflex centres for heartbeat, respiration and intestinal motility (Kardong 1994 p649).

There is very little difference in the structure of the mammalian and reptilian medulla oblongata (Kardong 1994 fig.16.35E,F p650-651).

5.2 The Early Therocephalian Brain

A factor that may severely hamper the accuracy with which the therocephalian brain is reconstructed, is the extent to which the brain filled the brain cavity. In mammals, the brain fills the cranial cavity (McGowan 1991 p172), but in reptiles, there are large spaces between certain parts of the brain and the braincase (Starck 1979 fig.10 p21). It has been noted in the previous chapter (Section 4.4) that parts of the antero-medial walls of the braincase lack any structures or fossae representing the contact between the brain and braincase. The postero-ventral portion of the braincase contains deep, definite fossae (Fig. 5). This indicates that the brain of the early therocephalians (and other therapsids) represents an intermediate stage between mammals and their reptilian ancestors (Olson 1944 p106) (Fig. 25).

5.2.1 The Olfactory Lobes

The olfactory lobes were in close contact with the ventral surface of the frontals. This is evident from the single fossa on the ventral surface of these bones. The length of the olfactory lobes cannot be established, because the frontal trough is continuous with the parietal trough, and the olfactory and cerebellar lobes cannot be differentiated from each other (Fig. 24).

As stated above in Sub-section 5.1.1, the olfactory lobes of reptiles were supported ventrally by a cartilaginous internasal septum. There is no evidence of this septum in the sectioned *Glanosuchus macrops* SAM K238a, presuming that it must have been cartilage if it was present. The only evidence of such a septum, would be the groove created by the palate and the pterygoid, which would clasp the ventral edge of the septum.

In the gorgonopsian *Arctognathus* (Kemp 1969 p54, fig.18A p55), the nasal cavity is divided into two parts by a bony septum. There appears to be a portion of cartilage in the region of the pterygoid, indicating that the interseptum was only partly ossified (Kemp 1969 fig.18A p55). This is based on its position and the crystalline texture of the matrix, which Kemp (1969 p55) presumed was cartilage. In the cynodont *Procynosuchus* (Kemp 1979 fig.10 p96), a dorsal process is present on the vomer. It is presumed that a cartilaginous septum was also present in *Procynosuchus*, but it is

uncertain how far back it recedes, or how close to the roof of the braincase it is situated. In *Glanosuchus macrops* SAM K238a there is indication of a septum.

5.2.2 The Cerebrum

The cerebrum in *Glanosuchus macrops* SAM K238a appears to have been situated anterior to the pineal foramen, within the trough on the ventral surface of the frontal and parietal (Fig. 4B). The cerebrum is enlarged and convoluted in mammals, but in reptiles it is a reasonably large, apparently smooth structure. In both mammals and reptiles, the cerebrum is paired. It is assumed that the cerebrum of the early Therocephalia may have been paired, even though the parietal trough is single. The parietal trough housing the olfactory lobes is paired in *Procynosuchus* (Kemp 1979 fig.14 p106) as it is in other cynodont endocasts (Hopson 1979 fig.29 p134). It is therefore assumed that since the olfactory lobes of the cynodonts are paired, the cerebral hemispheres are also paired.

The separation of the cerebral and olfactory lobes is not indicated by the single parietal trough in *Glanosuchus macrops* SAM K238a. The lateral sides of the cerebral hemispheres contacted the anterior processes of the supraoccipital which bear elongated fossae on its medial surface. It appears that the cerebral lobes of the early therocephalian resembled those of reptiles, in that the length was much greater than the width.

5.2.3 The Optic Lobes

The shape of the optic lobes of *Glanosuchus macrops* SAM K238a are not readily evident. In reptiles, these lobes are enlarged and rounded. They are situated lateral and ventral to the epiphysis. In mammals, these lobes have decreased in size. It is possible that the optic lobes, assuming that they resembled those of reptiles in position and shape, were situated below the pineal foramen (Fig. 24). Therefore, the fossae which these lobes would form on the medial wall of the dorsal lamina of the epipterygoids are not evident. This implies that the optic lobes were separated from the medial walls of the braincase.

5.2.4 The Pineal Organ

It is assumed that the shape, function and position of the epiphysis in therocephalians were similar to those of living lizards, as both taxa possess a pineal foramen. It is further assumed that the epiphysis was an evagination of the dorsal surface of the brain between the cerebrum and the cerebellum (Figs 24, 25).

The pineal foramen is well-developed in *Glanosuchus macrops* SAM K238a, and possibly housed a well-developed epiphyseal structure. A fact that cannot be established from the pineal foramen, is whether the pineal foramen housed a parietal eye-pineal complex or just a pineal organ as in some lizards, snakes and tortoises.

It is assumed that the function of the epiphysis in therocephalians was similar to that of extant reptiles, which is to monitor photoperiods and seasonal changes, rather than a glandular function as in mammals.

5.2.5 Cerebellum

The ventral surface of the supraoccipital, posterior to the interparietal bears a deep cone-shaped fossa. It is highly probable that this fossa housed the cerebellum. In reptiles and mammals, the cerebellum is a single lobe posteriorly situated to the cerebrum. The size of the supraoccipital fossa indicates that this lobe was large and well-defined in the early Therocephalia (Fig. 24). The fossa is very closely situated to the otic capsule. In mammals and reptiles, the cerebellum is closely associated with the function of the inner ear.

In vertebrates, the development of the cerebellum is correlated with the intricacy of the body movement. It is larger in mammals than in reptiles. In the early therocephalian, it appears as if the cerebellum was similar to that of reptiles in shape, but larger. This suggests that muscular control and locomotion of the early therocephalians had improved beyond the reptilian level.

The most significant feature of the cerebellum, is the development of the auricles or the floccular lobes. These floccular lobes were situated in the floccular fossae located in the

medial wall of the prootic. In *Glanosuchus macrops* SAM K238a, the floccular fossae are situated anterior to the cerebellar fossa in the supraoccipital. This position is more anteriorly situated than in the therapsids reconstructed by Olson (1944 fig24.p107) or in reptiles.

Watson (1913 p224) suggests that in *Diademodon*, the presence of a floccular fossa indicate that the brain filled the cranial cavity at that level. He (Watson 1913 p228) also stated that the remarkable size of the cerebellum in *Diademodon* may be correlated with the advanced locomotion of cynodonts. The first part of the brain that appears to have developed is the cerebellum, and it may have done so very early in the therocephalians. The reason being that in early therocephalians, the lobe is well-developed.

5.2.6 Hypophysis or Pituitary Gland

The pituitary gland in early therocephalians is situated in the sella turcica in a similar position to the reptiles and mammals. In *Glanosuchus macrops* SAM K238a, the pituitary fossa in the parabasisphenoid is very well-developed (Fig. 5). This suggests that the pituitary gland was well-developed (Fig. 24). As in mammals and reptiles, this gland is supplied by the internal carotid arteries and the foramina for these arteries open on the anterior lip of the pituitary fossa (Fig. 5).

5.2.7 Medulla Oblongata

The medulla oblongata of the early Therocephalia appears very similar to that of mammals and reptiles, as well as the therapsid reconstructed by Olson (1944 fig.24 p107) (Fig. 24). The presence of two lateral swellings on either side of the medulla oblongata in the early Therocephalia, represented by two diagonal fossae on the medial wall of the exoccipital (Fig. 5) has an unknown function. It may have been that the fossae accommodated thickened brain membranes or blood sinuses.

5.3 Deductions from the Brain of the Early Therocephalia

Study and comparison of the reptilian and mammalian brains allow certain deductions to be made concerning the relation between the therocephalian brain shape and its activity rate in a living state. The internal structure of the braincase of *Glanosuchus macrops* SAM K238a indicates that the brain had underdeveloped olfactory lobes (because of the feeble troughs present on the ventral surface of the frontal), a moderately developed cerebrum, a well-developed cerebellum and a medulla oblongata similar to reptiles and mammals.

The size of the olfactory lobes indicate that the therocephalian probably depended on its olfactory senses, to the same extent as reptiles but not as much as mammals. This is possibly an indication that the therocephalians possessed a vomero-nasal organ, to supplement its relatively poor sense of smell.

The development of the cerebrum suggests that there was not much difference in the lobes of therocephalians and modern reptiles, except that in early therocephalians these lobes were larger. The development of the cerebral lobes implies that these lobes processed an increasing amount of sensory information from the forebrain. This may have been due to the increase in the effectivity of locomotion, as well as an increase in predatory skills. This would require an improved sensory system, which is indicated by the olfactory lobes and the cerebrum.

Modifications of the position of the limbs and girdles of therapsids allowed increased agility of the limbs. Furthermore, the posture in which the limbs are held close to the body contrasts to the sprawling posture seen in amphibians and reptiles. This modification in limb posture, combined with an increase in agility and locomotory speed, appears to be indicated by the enlarged size of the cerebellum of the early Therocephalia.

A second function of the cerebellum, is to maintain equilibrium. This is indicated by the large size of the floccular lobes which are closely associated with the function of the inner ear. A further indication of an increase in awareness of the environment by the therocephalian, is evident in the intricacy of the inner ear structure. An increase in the sensory ability of the inner ear is indicated by an increase in size of the floccular lobes. If the grooves present in the cochlear recess are genuine structures, the presence of

coils in the cochlea would be indicative of the transition of the inner ear from a reptilian to a more mammalian-like level. The development of a cochlea implies that the theriocephalian was capable of detecting higher frequency sound than reptiles, but not as competent as mammals. However the coiling of the cochlea in early Theriocephalia has yet to be established.

An increase in the efficiency of the locomotory system requires an increase in metabolism. Shifts in metabolic strategy reflect an increased ability for sustained activity. A remodelling of the inner and middle ear permits an extension of the range of audible sounds. The development of heterodont teeth, and changes in the musculo-skeletal system of jaws reflected changes in feeding mechanics. Each of these changes require significant parallel changes in the central nervous system.

An understanding of anatomical changes is important to obtain an overall concept of the evolution of the mammal-like reptiles to mammals. However, it is clearly more difficult to study evolutionary changes in the nervous system than in skeletal systems, as no soft tissue remains after fossilization. The only clue to determine the form of the brain, is to study the endocast.

CHAPTER 6

CONCLUSIONS

The braincase is primitive because of the lack of contact between the epipterygoid and the prootic. In later therocephalians, these two bones contact each other. Another primitive characteristic is the presence of open ended incisura prootica in the prootic for the trigeminal nerve V. In later therocephalians, the notch is closed off by the development of surrounding bones to form nerve foramina. These foramina are further developed in cynodonts.

The braincase of the early therocephalian contains bone and cartilage. The cartilaginous areas are the unossified zone situated on the suture between the parabasisphenoid and the basioccipital, and the medial wall of the otic capsule. These two zones appear in all sectioned therapsids and the permanent presence of cartilage is characteristic of therapsid braincases.

Other unossified zones appear to be the anterior processes of the supraoccipital in dicynodonts and gorgonopsians, and the postero-medial surface of the supraoccipital in early cynodonts.

The internal structure of the braincase in the early therocephalian is similar to that of other sectioned therapsids, from later therocephalians to later cynodonts. The medial wall of the otic capsule is incomplete and it is assumed that it was cartilaginous. The semicircular canals of the inner ear are positioned over the floccular fossa, which supported the floccular lobes of the brain. This is an indication that the medial wall of the otic capsule was formed completely by cartilage to protect the membranous inner ear structures.

The inner ear structure is particularly well-preserved in the early therocephalian and very fine detail was obtained. The three bones which form the otic capsule, are the prootic, the opisthotic and the supraoccipital. The three semicircular canals are present and are only partially embedded in the lateral walls of the prootic and the opisthotic.

The vestibule is divided into two recesses, a larger utricular recess and a smaller saccular recess. Together these two recesses are referred to as the sacculo-utricular recess. The utriculus was an elongated finger-like structure that connected the semicircular canals. The sacculus was small and sac-like, and was positioned on the ventral edge of the utriculus. A third recess is present deep within the opisthotic. This is the cochlear recess which bears two grooves and four pits. The arrangement of these grooves and pits have not been established as a genuine feature in this study.

Impressions of the endolymphatic system are not present in the otic capsule, possibly because it was situated in the cartilaginous medial wall which did not preserve. The impressions of the perilymphatic system is also incomplete in the early therocephalian. A possible position for this system is indicated by a groove in the opisthotic, located between the fenestra ovalis and the jugular foramen. This structure has also been described in other therocephalians and gorgonopsians.

The fenestra rotunda is completely absent from the early therocephalians and most other sectioned therapsids. A possible position for this foramen is within the jugular foramen. The only structure possibly indicating that the perilymphatic system terminated in the jugular foramen as the fenestra rotunda, is the groove traversing the length of the opisthotic.

The reconstruction of the brain is based on the shape of the braincase cavity. Only certain components of the brain are evident. In mammals, the brain fills the cranial cavity, whereas in reptiles there are large spaces between the brain and the braincase wall. The presence of distinct fossae on the medial wall of the postero-ventral surface of the braincase and very poorly developed fossae antero-dorsally, indicate that the brain only partially contacted the braincase. This has especially hampered the reconstruction of the anterior parts of the brain.

Conclusions drawn from the possible brain shape, indicate that the olfactory lobes appear to have been poorly-developed. The cerebrum is larger than that of reptiles, but smaller than in mammals. This implies that the sensory perception of the early therocephalian was above the reptilian level, but below the mammalian level. The greatest development of the brain is found in the cerebellum. This lobe is well-developed and large. This implies that the muscular control and the locomotor ability of

the therocephalian was improving towards the mammalian condition. The second function of the cerebellum is to maintain balance. This is indicated by the large floccular lobes which are closely associated with the inner ear in mammals and reptiles. These large lobes indicate that the therocephalian hearing was similar to reptiles, but not as competent as mammals.

APPENDIX A

The Equation Used to Determine the Distance Between the Sections in the Pusey Reconstructions.

Pusey's methods are devised to give accurate reconstructions of sectioned material with the minimum of effort, without resorting to the manufacture of wax-plate models.

The equation applied to determine the distance between the sections in the reconstructions in this study is the following:

$$D = T/(C) \times N \times S$$

where

D = the distance plotted between sections

T = thickness between sections

C = conversion of millimetres to microns

N = increment of the sections

S = scale of the drawings

and

$$T = 1/5\text{mm} = 200 \text{ microns}$$

$$C = 1\text{mm} = 1000 \text{ microns}$$

$$N = 1$$

$$S = 1:5 = 5.$$

Therefore

$$D = 200/1000 \times 1 \times 5$$

$$= 1\text{mm}.$$

The answer is one millimeter between each section.

APPENDIX B

PC3D - Computer Reconstruction Package

PC3D is a computer reconstruction package which has been devised to create complete images from transversely or longitudinally sectioned objects, eliminating the manufacture of wax-plate models. The package produces a contour image by stacking the sections, each time showing only the parts of the structures projecting behind the outlines from the previous sections. These images are multicolour, three-dimensional displays on the monitor, which may be plotted out by a plotter.

Several images may be produced from the information, and can be rotated so that they are viewed from all angles. This reduces the need to enter information into the computer more than once. The images created resemble drawings done by Pusey's contour method.

This appendix is not a complete guide for the use of PC3D, but it is only a brief description of the parts of the program used for the skull reconstruction in this thesis.

The main objective of this program, is to insert individual sections and then to reconstruct the detailed object from the sections. Sections can come from any source, including electron microscopy, macroscopic sectioning and many others. The advantage of reconstructing in this manner, is the retention of detail found in some delicate structures (like kidney tubules) may be lost in wax model reconstructions.

Information regarding the sections is loaded into the computer by tracing the outlines of the separate structures in each serial, by means of a digital pen (stilette) and tablet. Each serial structure is called a polygon, a multi-sided, two-dimensional shape. That is, the outline of every component contained in the section forms the polygon. For example, the polygons in a section through the abdomen of a vertebrate will consist of cross-sections through bone, organs etcetera. After sections have been entered into the computer, the three-dimensional object can be reconstructed and viewed. Rotation of the image around three axes (X,Y,Z) allows the object to be viewed from all sides and angles.

Besides being viewed on-screen, multicolour PC3D images can also be produced on a compatible plotter.

PC3D Stages

There are seven stages in using the programme, and they are as follows:

- 1.1 Trace
- 1.2 Describe
- 1.3 Edit
- 1.4 Display
- 1.5 Volume
- 1.6 Movie
- 1.7 Plot

Prior to invoking the computer, the sections have to be prepared in a specific manner. This entails that all serial sections must be drawn to a constant magnification.

A reference point is then chosen, and is placed onto each drawing or slide. This point must have a constant position on every section, and is of utmost importance in the display stage when the computer reconstructs the images. Each section is piled according to the reference points, and if moved, the reconstruction is incorrect and out of line.

For this thesis, the skull peels were redrawn to a 1:5 scale, and two reference points were allocated onto each drawing for easier piling.

1.1. 3D-Trace

3D-Trace involves entering serial data into the computer by means of the tablet and stilette. The section to be traced is placed onto the tablet, corresponding the reference points of the drawing and the tablet.

The connection between the computer monitor and tablet is such that any contact between the stilette on the tablet, results in a corresponding line appearing on the monitor. Before drawing can commence, a reference frame has to be created on the monitor by means of two points entered onto the tablet, namely a lower left corner and an upper right corner. These borders set the trace scale on the monitor and register only lines from the tablet within the reference frame. All lines outside the borders are not registered on the monitor.

Once into the 3D-TRACE heading, choose the GENERATE subheading and enter the reference points, the lower left corner and the upper right corner. Drawing can commence. Trace the outline of one polygon at a time, and once the begin and end points have met, the computer gives a beep sound. If the points do not connect, press the C-key to CLOSE.

After the polygon has closed, it has to be named. All similar polygons are allocated to the same class (for example, polygons of bone = 1, kidney = 2, liver = 3 etc.). Each class of polygon is then allocated a number from one to nine, or alphabet letters A to F. Name each polygon according to its identification. Giving the same name to each polygon in a class is important, because each class of polygon is allocated a colour in the reconstruction stage. This colour remains constant throughout the image. Colour assists immediate identification on the screen.

When the section is complete, press ESCAPE and name the section (for example, skull.1, skull.2, skull.3). This is called a trace file. The order in which the trace files are entered is unimportant, because the computer arranges them numerically.

When all sections are entered into the computer, the series has to be defined by the 3D-DESCRIBE SECTION.

1.2. 3D-Describe

This defines the series for reconstruction. The computer requires a generic name for the trace file (that is, a trace file name has to be provided after each section is completed), and usually the number of the section is incorporated with the generic name. Additional information to be entered in this part include the number of trace files the computer has

to view (each section, or every tenth section etc.), whether you wish to create new file set, magnification required, true distance between the sections, object description and discription of each polygon class.

1.3. 3D-Edit

Once the series has been entered and described, each section can be viewed and modified. Possible errors made in naming the polygons in the tracing stage can be corrected. The trace file generic name, the increment and file format (ASCII or BINARY) and image number is provided.

The command F4 pages forward through the images, and F3 pages to the previous image. Any mistakes found can be corrected by moving the cursor (using the right arrow key) onto the incorrect polygon, and pressing the number of the correct polygon name required. The polygon is now corrected. The image has to be saved using the F5 command. One can move through the polygon classes (indicated at the right side of the screen) using the down arrow keys.

Any required image can be called up using the F2 command. To quit out of 3D-EDIT, press F10, and ESCAPE will exit to DOS.

1.4. 3D-Display

This stage creates the three-dimensional images from the traced serial sections. Change the display mode by pressing M, and then I to produce the interactive window on the monitor. This window allows one to select the desired colour for each polygon class, enter the files for saving screen images and plotting, and for choosing the rotation of the image on the screen. Initiating the reconstruction of the image is generated with the F10 command.

Rotation occurs around the X,Y and Z axes, but the image may only be rotated only around one axis in a plane (within planes XZ, or XY, or ZY). Each axis has a rotation field of 360 degrees. The combination of any axes rotates the image in a given direction. Scale can be set within any plane, either enlarging the image or reducing it.

Care should be taken when rotating one image around a number of axes, since the order of rotations are important.

1.5. 3D-Movie

This is an optional module which displays multiple views of three-dimensional reconstructions rapidly in a fixed series. This allows all sides of the image to be viewed in quick succession. This module was not used for the reconstruction in this thesis.

1.6. 3D-Volume

This calculates the volume of every polygon class. It is used to assess how many times each section is to be incorporated into the reconstruction. It is valuable in that repetition of certain sections achieves a fuller, improved reconstruction.

1.7. 3D-Plot

This function feeds the reconstructions created with PC3D into the plotter. All images are multi-colour and three-dimensional. When creating the reconstructions in this part, a file name to be used when plotting a specific recreation has to be provided (e.g. skull.plt). The plotter reads the image information from this file and plots it onto A4 or A3 paper. The reconstruction size can be changed to fit the image onto the paper. In this section, the plotting speed and pen colours are also chosen.

Conclusion

The computer program is of value when used to reconstruct objects with not much small, delicate detail. The process of entering information onto the computer with the pen and tablet is very time consuming. One also has to be careful redrawing the sections to ensure that no detail is lost.

The reconstructions are very unrefined, and only a general impression can be obtained. I feel there are much better graphical programs available (e.g. IDL), in which the information can be scanned into the computer with a scanner. This not only reduces the time spent on entering the information, but the overall final reconstruction is much finer, and outline and detail are clearer. The individual polygon colours can be assigned to the image by means of a mouse and easy menu.

The general "user-friendliness" of the package can be improved, to make the program easier or more tolerable to use. For example, inserting a method of erasing incorrect polygons once entered would prevent one having to start the section anew.

Another function that may be introduced is a method in which to plot every individual section entered, and better menus would enhance the use of the program. PC3D switches the screen off completely before providing the required menu, but positioning the menus at the side of the screen enables one to use commands much easier without losing touch with the program itself.

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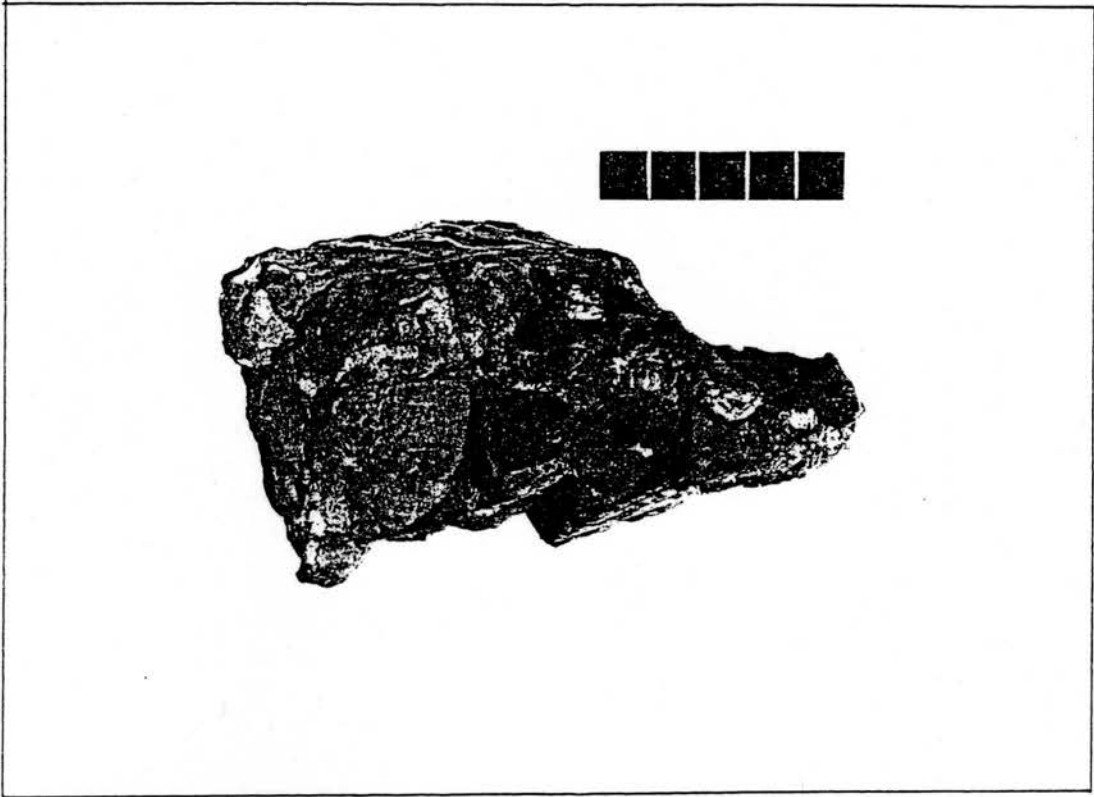
ABBREVIATIONS

aamp	anterior ampulla
aampf	anterior ampullary fossa
adpp	antero-dorsal process of the prootic
avpe	anterior ventral process of the epipterygoid
avpp	antero-ventral process of the prootic
avps	antero-ventral process of the squamosal
avsc	antero-ventral semicircular canal
bo	basioccipital
bt	basal tubera
cbl	cerebral lobes of the brain
cblc	cerebellar cavity
cbr	cerebellar lobes of the brain
cc	crus communis
coch	cochlea
cor	cochlear recess
cu	canine upper
dmgr	dorso-medial groove
dn	dorsal notch
dpo	dorsal process of the opisthotic
dpp	dorsal process of the prootic
ds	dorsum sellae
ect	ectopterygoid
eoic	external openings of the internal carotids
epi	epipterygoid
epit	exoccipital pit
exo	exoccipital
flfo	floccular fossa
fll	floccular lobe
fm	foramen magnum
fo	fenestra ovalis
fr	frontal
fso	supraoccipital fossa
GS	Geological Survey, Pretoria
hamp	horizontal ampulla
hsc	horizontal semicircular canal
iaf	internal auditory foramen
icp	incicura prootica
ioic	internal openings for the internal carotids
ipa	interparietal
ipf	interpterygoid foramen
ipo	internal process of the opisthotic
ipsq	intermediate process of the squamosal
iu	incisors upper
IX	nerve IX
juf	jugular foramen
jug	jugal
lac	lacrimal
lag	lagena
lpit	lateral pit
lre	lateral ridge of the exoccipital

lwo	lateral wall of the opisthotic
max	maxillary
med	medulla oblongata
mfo	mastoid process of the opisthotic
moc	median occipital crest
mof	median occipital fossa
mpo	mastoid process of the opisthotic
mro	medial ridge of the opisthotic
mwo	medial wall of the opisthotic
nas	nasal
nsp	nasal septum
oc	occipital condyle
olf	olfactory lobes of the brain
opi	opisthotic
opt	optic lobes of the brain
pa	parietal
pamp	posterior ampulla
pbs	parabasisphenoid
pbsk	parabasisphenoid keel
pcu	postcanine upper
pdpp	postero-dorsal process of the prootic
pg	perilymph groove
pin	pineal foramen
pit	pituitary fossa
plso	postero-lateral process of the supraoccipital
pmx	premaxillary
po	postorbital
pof	postfrontal
ppit	posterior pit
ppp	posterior process of the prootic
prf	prefrontal
pro	prootic
pt	pterygoid
ptbp	basisphenoid process of the pterygoid
pth	pterygoid teeth
ptl	pterygoid lamina
ptqp	quadrate process of the prootic
pttf	posttemporal fenestra
pttp	transverse process of the pterygoid
pvsc	postero-ventral semicircular process
q	quadrate
qptp	pterygoid process of the quadrate
ros	rostrum
sac	sacculus
sacr	saccular recess
SAM	South African Museum, Cape Town
skpl	skleral plates
smx	septomaxillary
so	supraoccipital
soap	anterior process of the supraoccipital
sof	suborbital fenestra
spit	supraoccipital pit
sq	squamosal
sta	stapes

stu	sella turcica
sur	sacculo-utricular recess
tab	tabular
tcb	trough for the cerebral lobes
tcl	trough for the cerebellar lobes
tol	trough for the olfactory lobes
ut	utricle
utr	utricular recess
uz	unossified zone
V	nerve V
vc	vidian canal
ves	vestibule
VII	nerve VII
VIII	nerve VIII
vlgr	ventro-lateral groove
vlc	ventro-lateral crest of the pterygoid
vmc	ventro-medial crest of the pterygoid
vo	vomer
vpp	ventral process of the parietal
vpp	ventral process of the prootic
vppa	ventral process of parietal
vppa	ventral process of the parietal
vpso	ventral process of the supraoccipital
X	nerve X
XI	nerve XI
XII	nerve XII

A.



B.

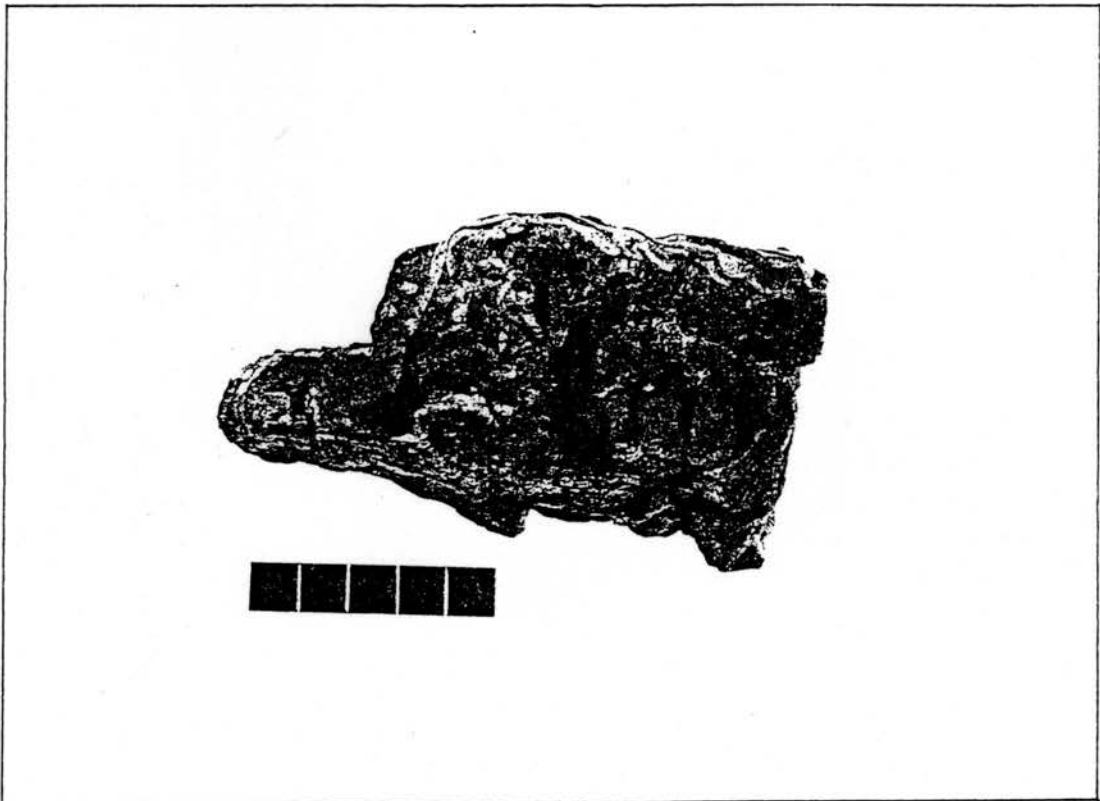
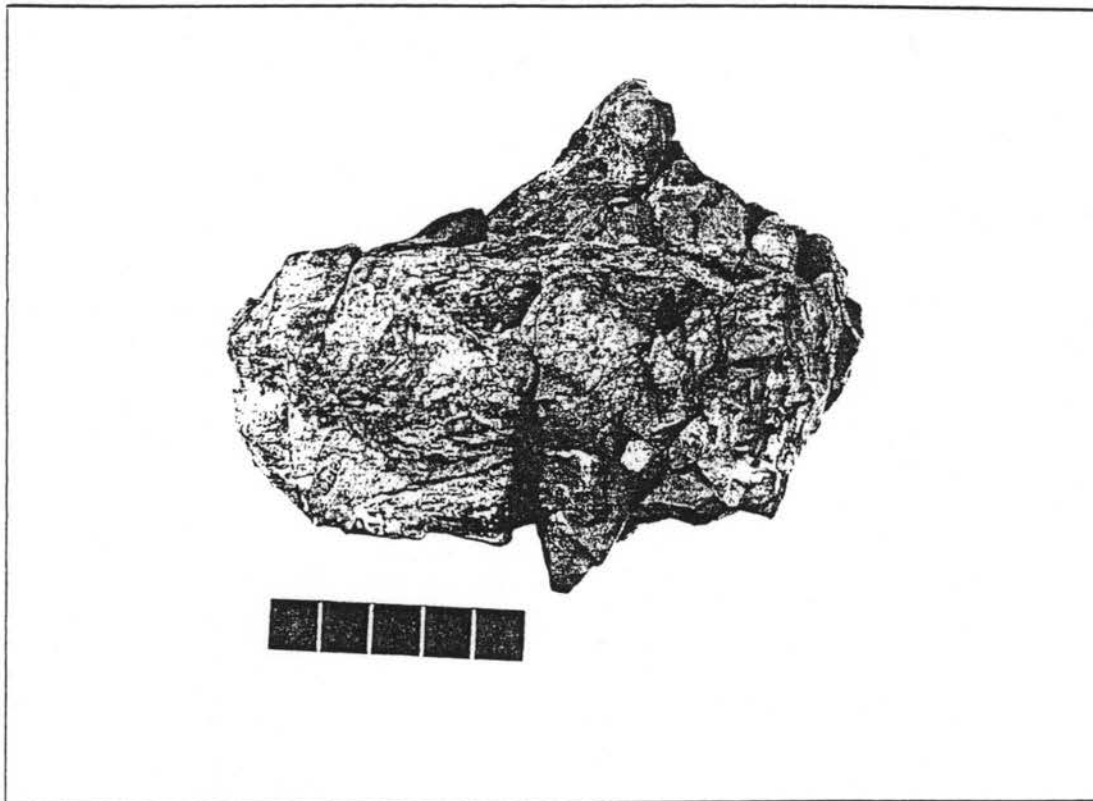


FIGURE 1. Photographs of the skull of *Glanosuchus macrops* SAM K238a prior to sectioning. A. Dorsal view. B. Ventral view.

C.



D.

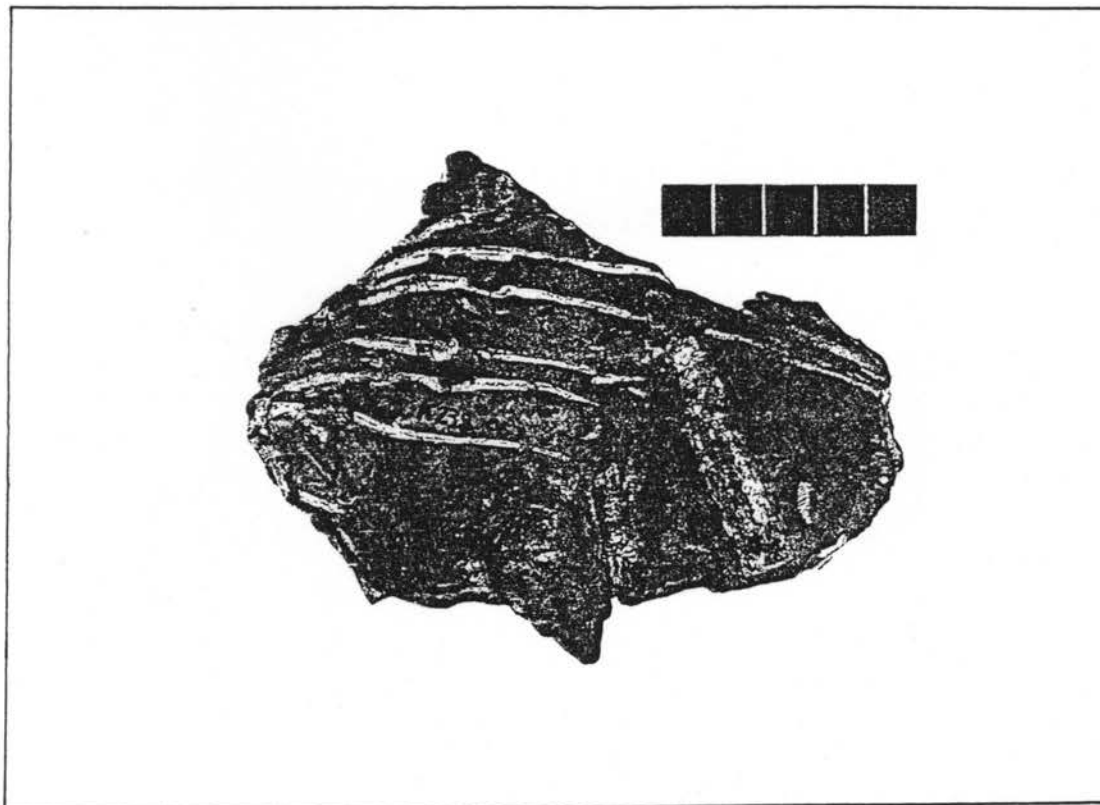
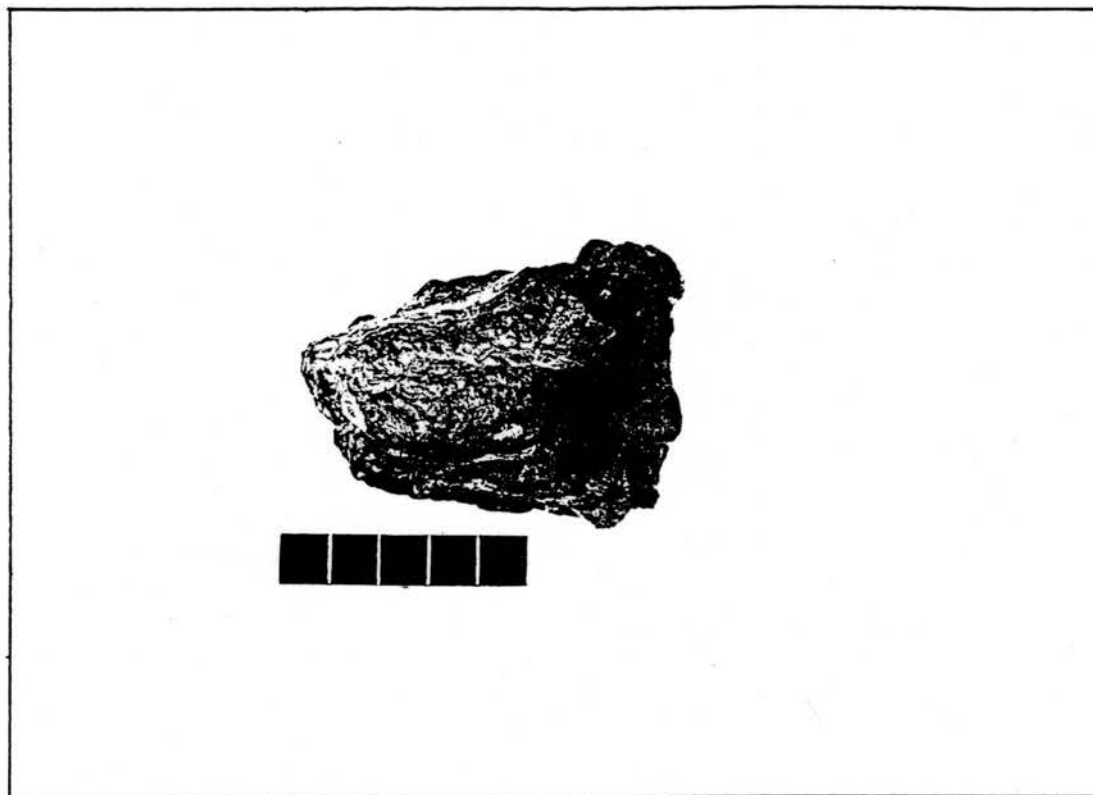


FIGURE 1. Photographs of the skull of *Glanosuchus macrops* SAM K238a prior to sectioning. C. Left lateral view. D. Right lateral view.

E.



F.

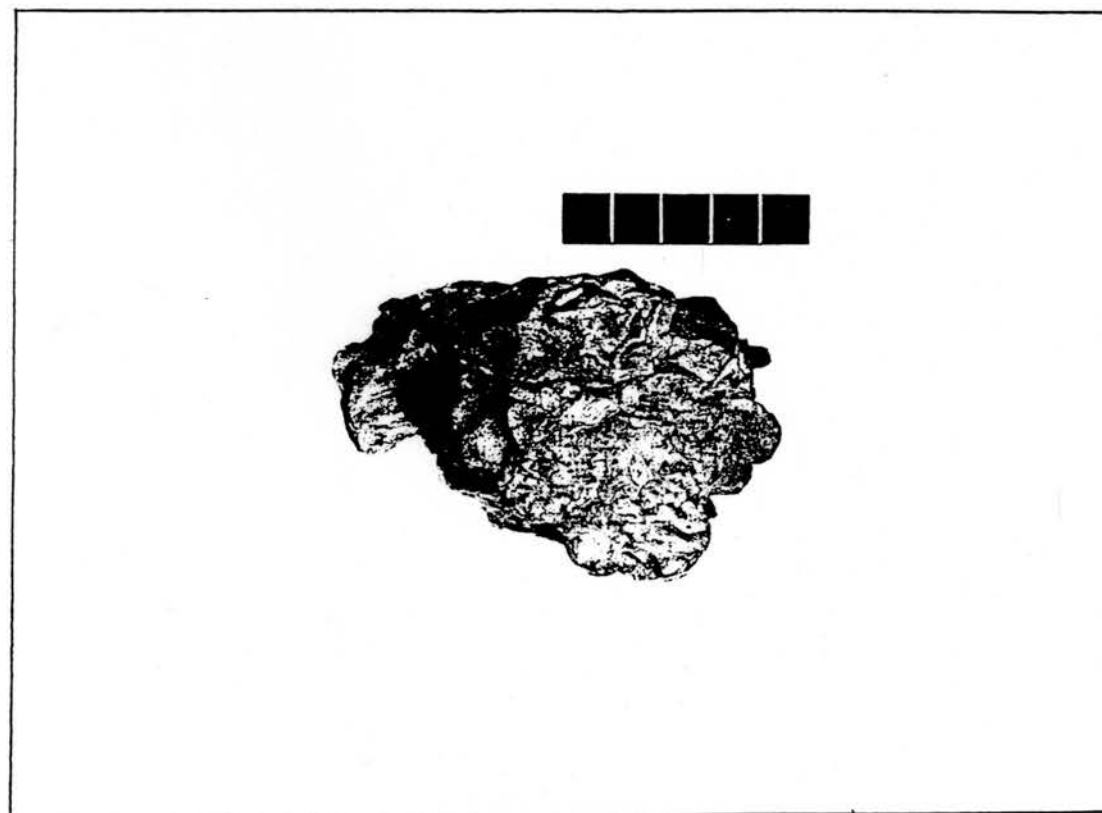


FIGURE 1. Photographs of the skull of *Glanosuchus macrops* SAM K238a prior to sectioning. E. Anterior view. F. Posterior view.

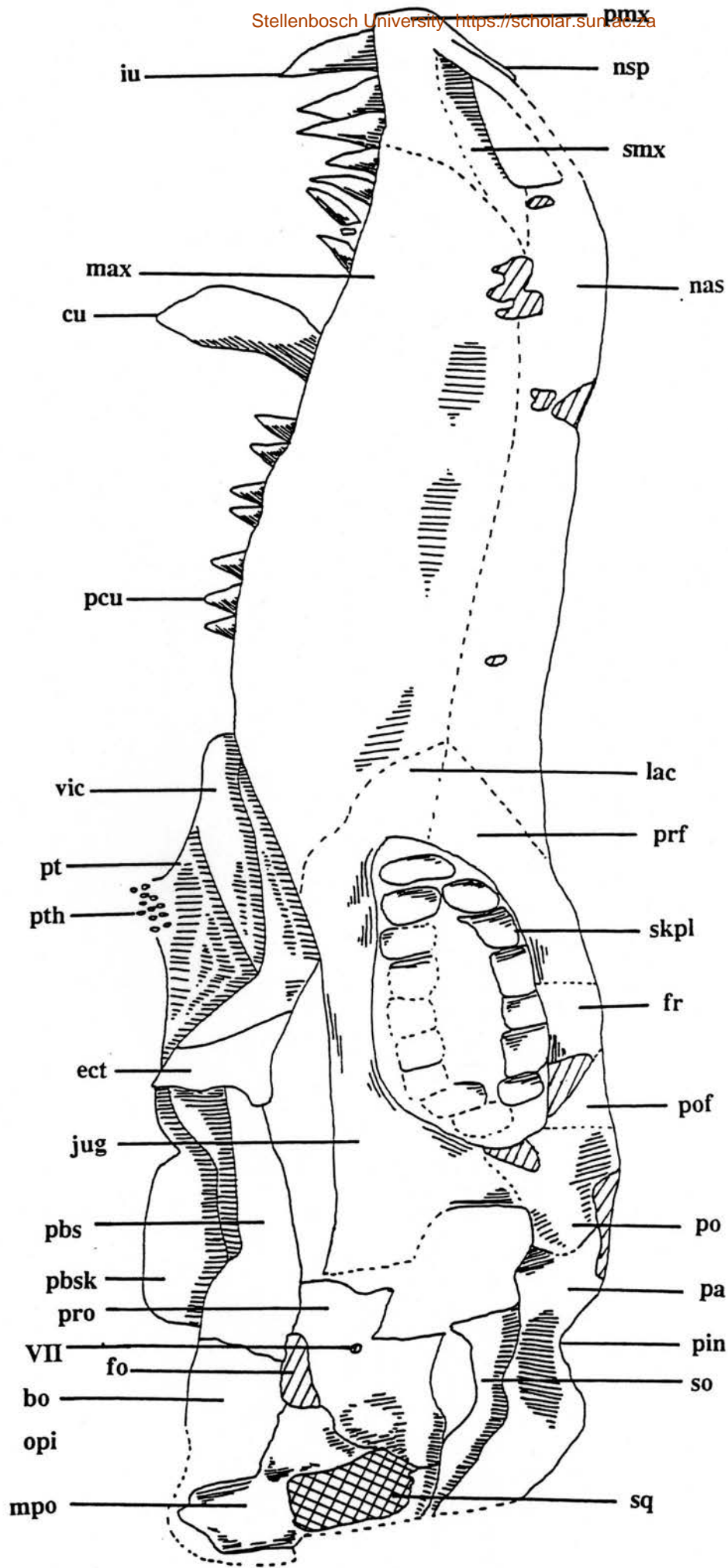


FIGURE 2. A. Left lateral view of the skull of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

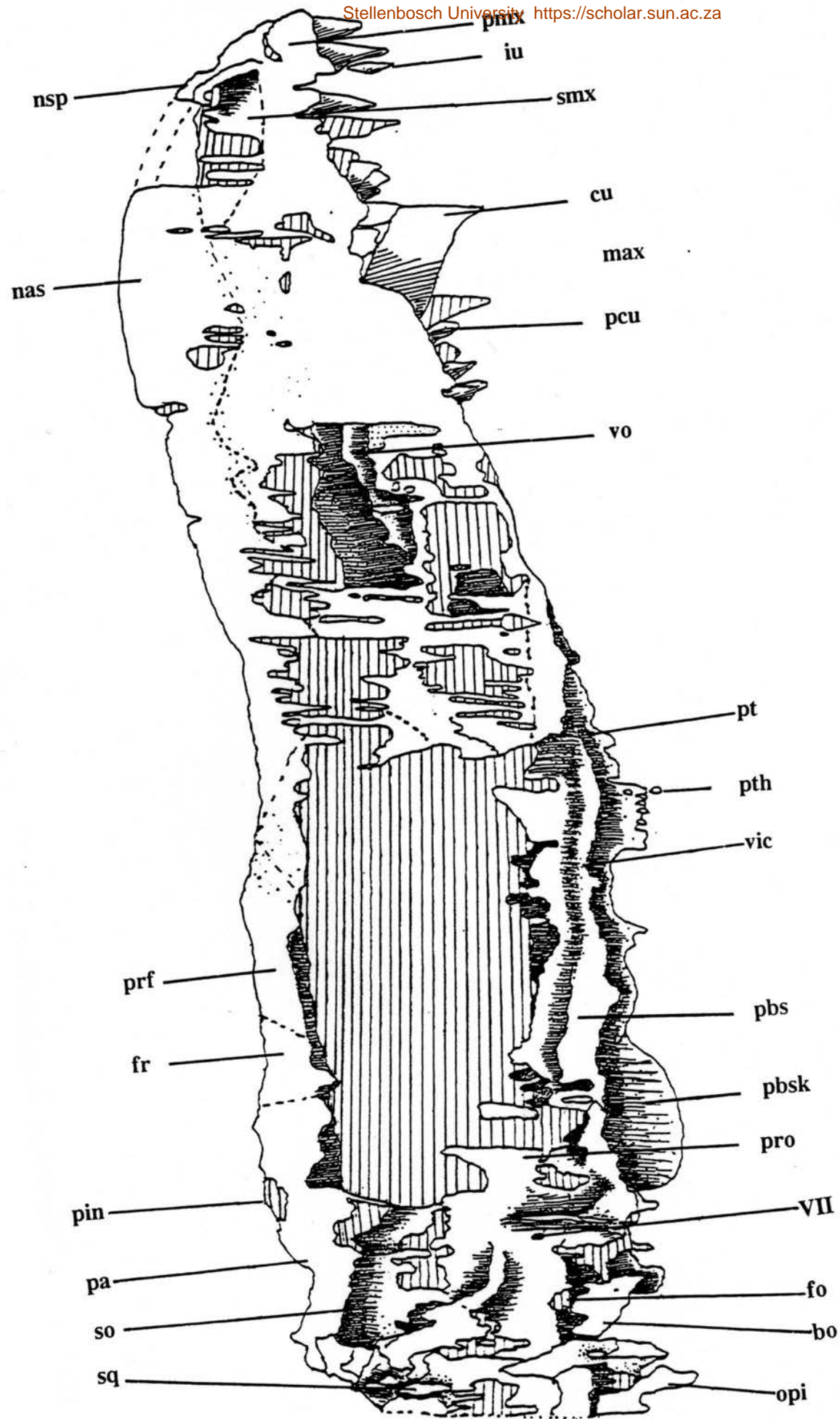


FIGURE 2. B. Right lateral view of the skull of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

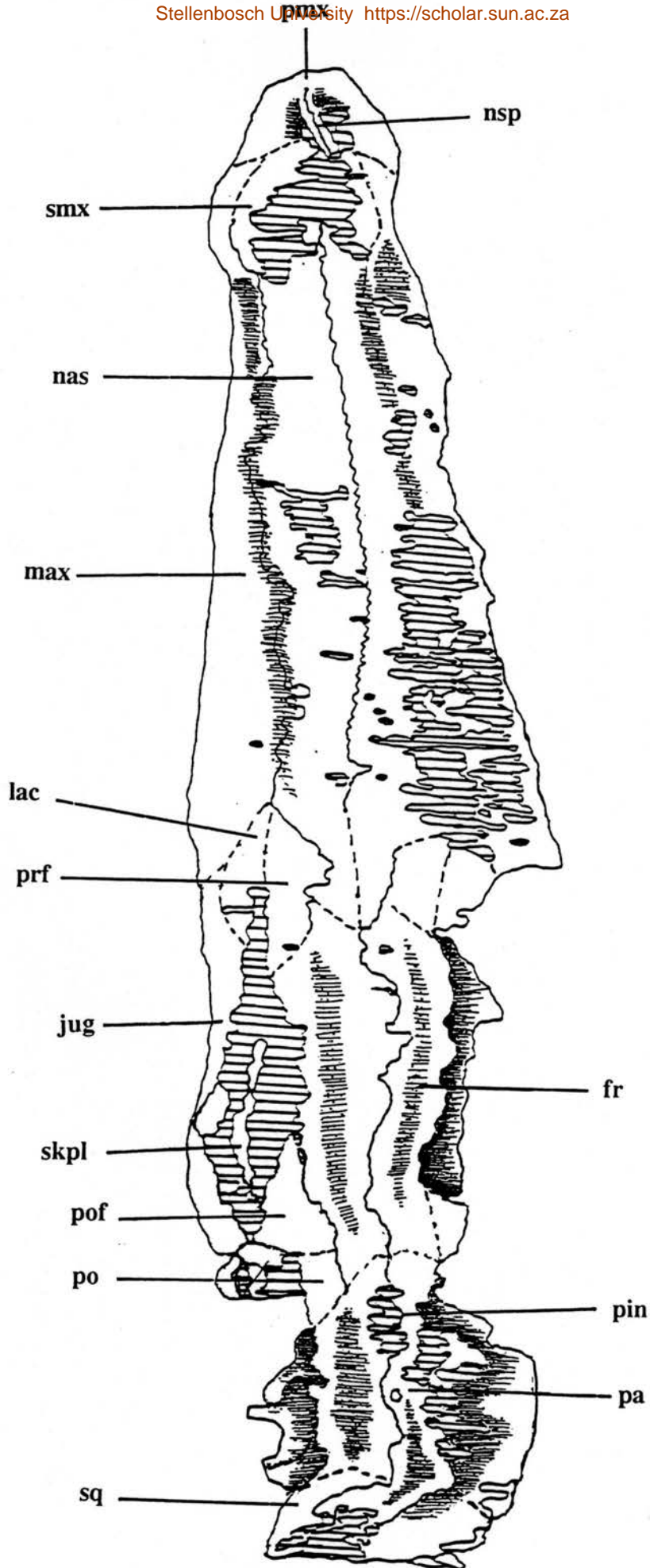


FIGURE 3. A. Dorsal view of the skull of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

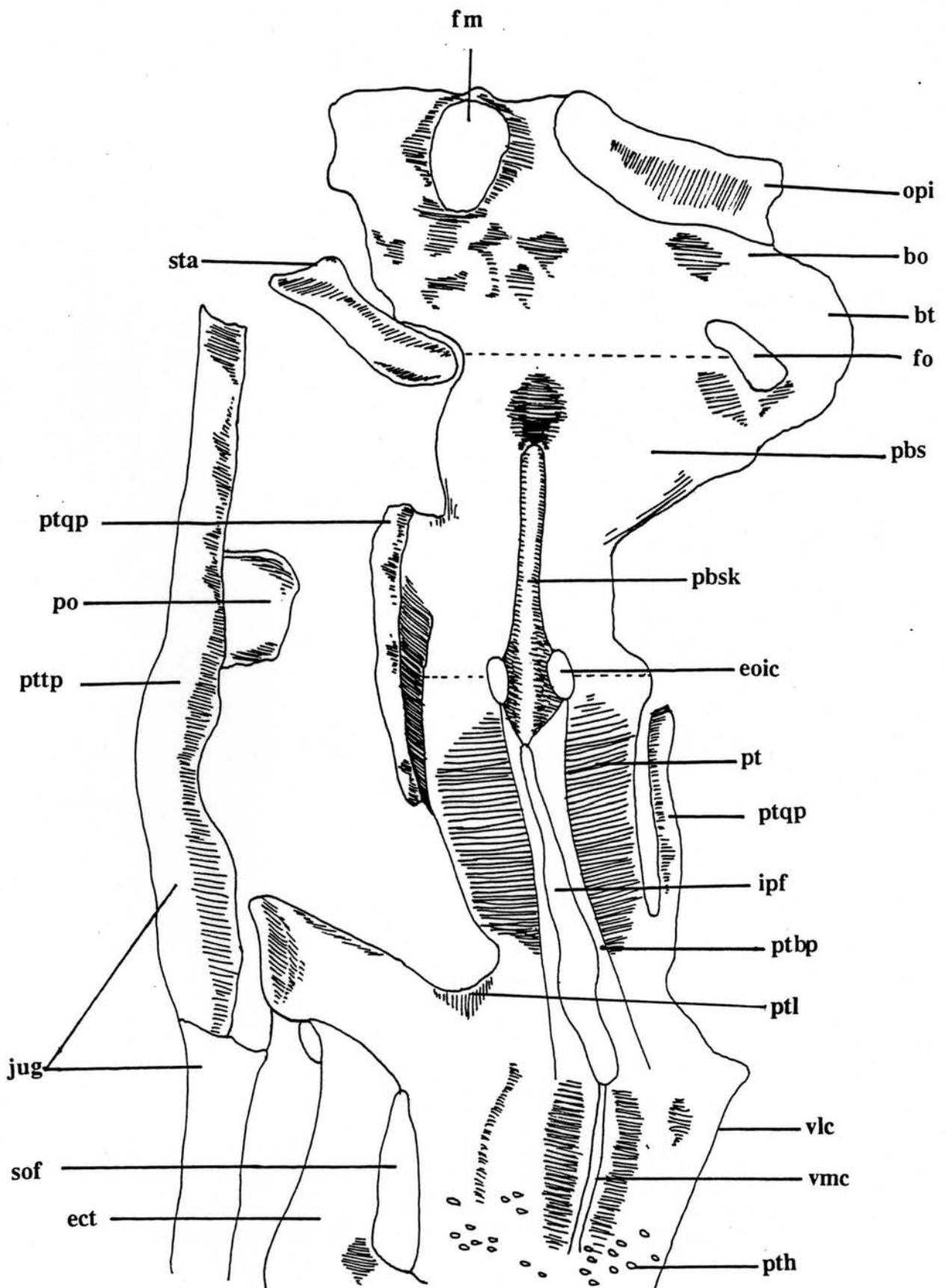


FIGURE 3. B. Ventral view of the skull of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

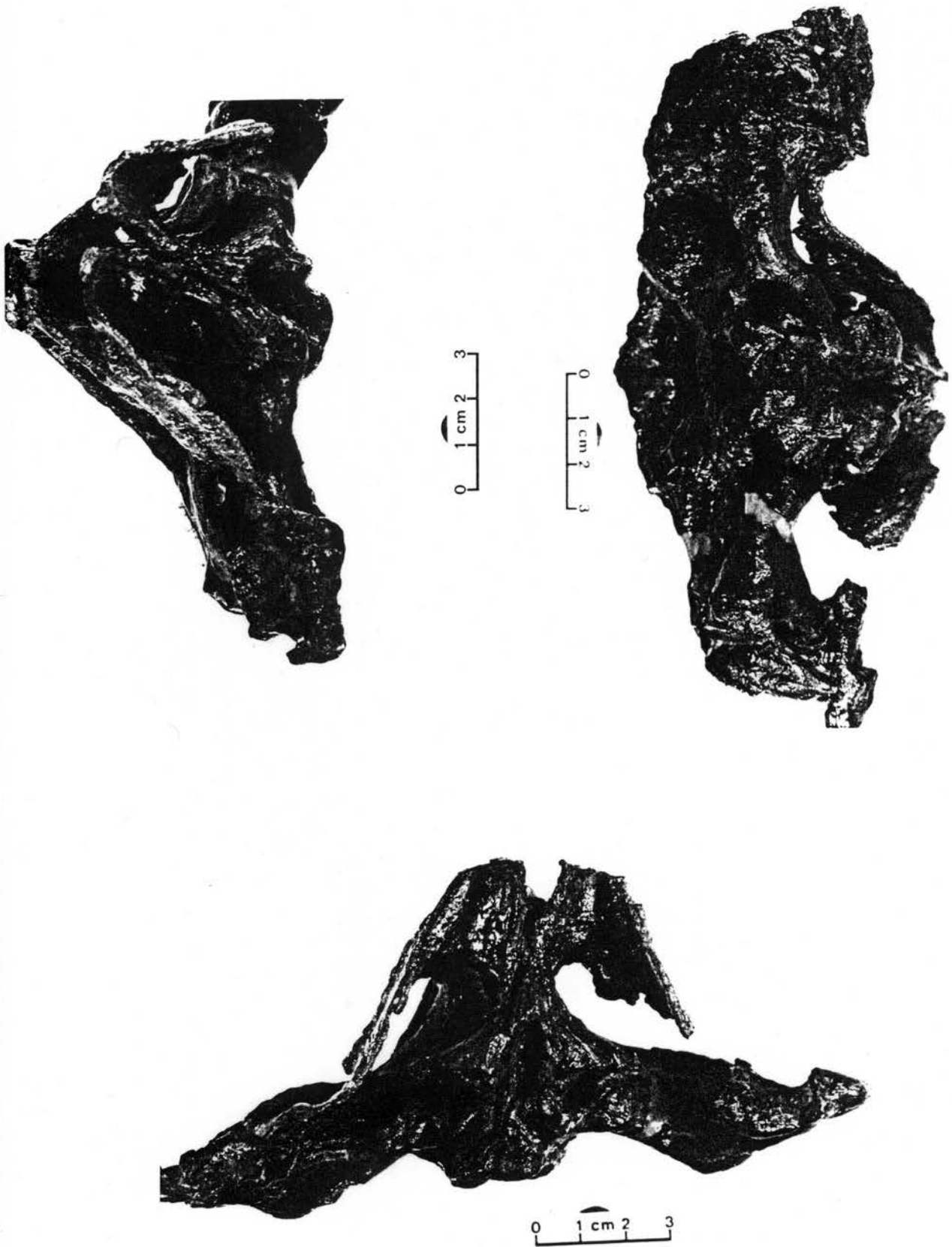


FIGURE 3. C. Ventral views of the type skull of *Ptomalestes avidus* SAM 11942.

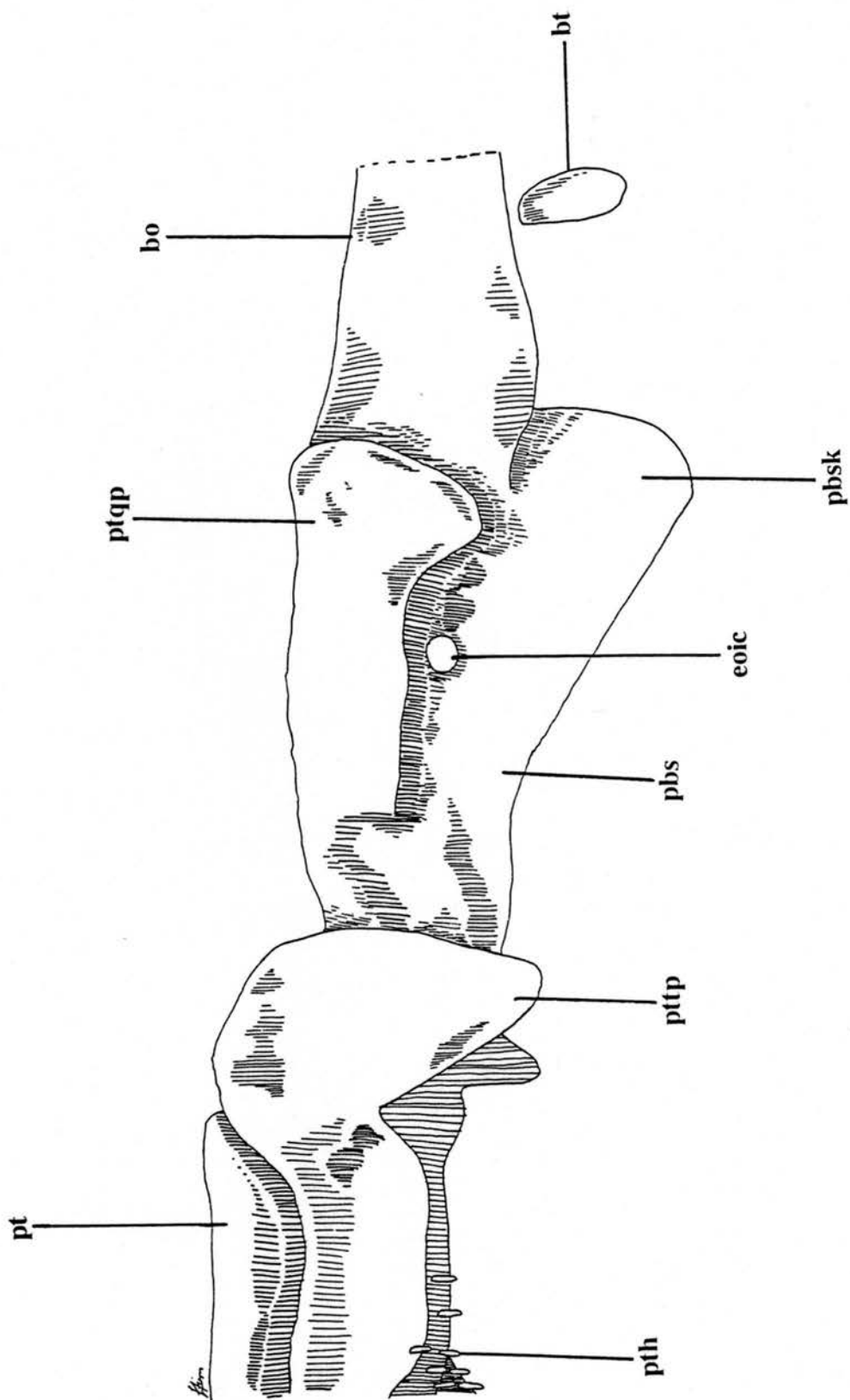


FIGURE 4. A. Left lateral view of the pterygoid of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

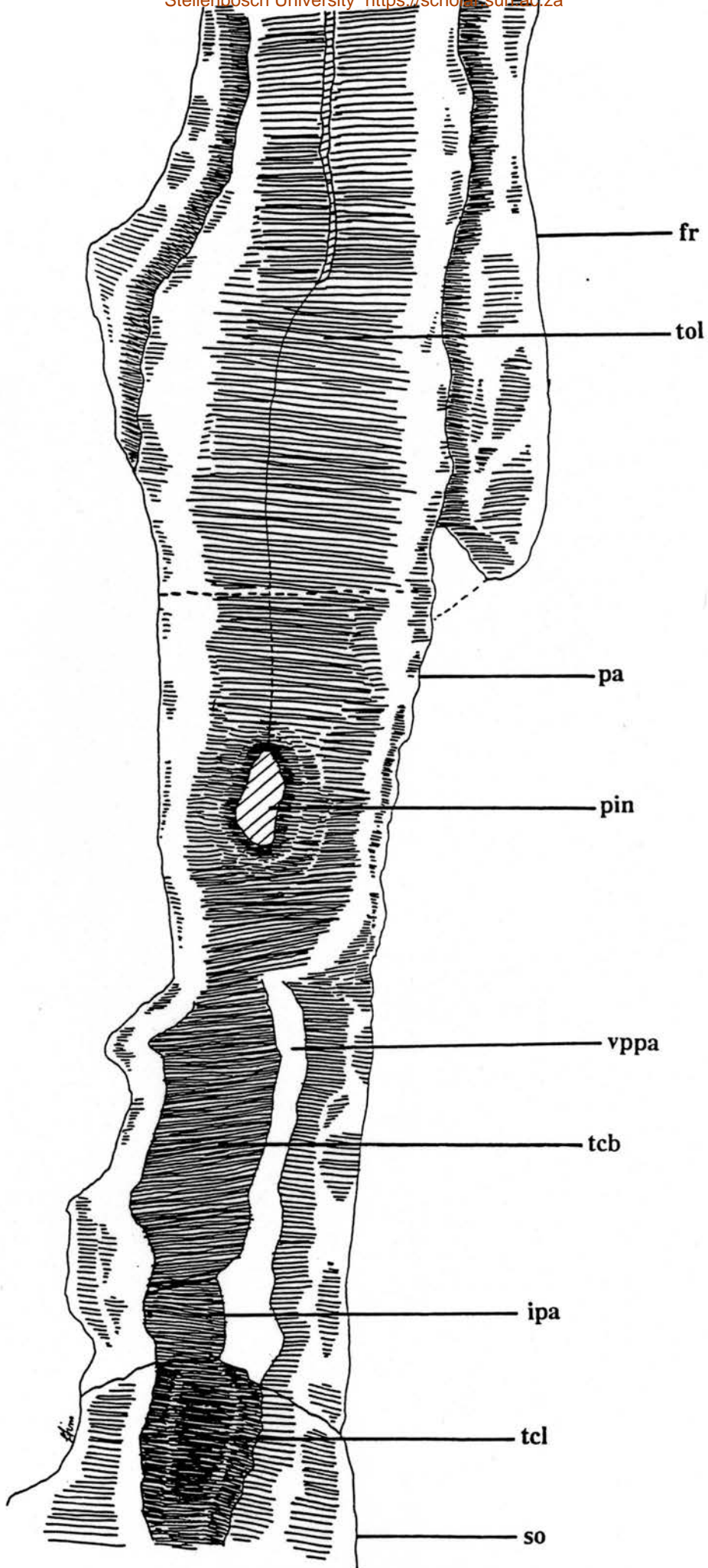


FIGURE 4. B. Ventral view of the braincase roof of *Glanosuchus macrops* SAM K238a (Pusey reconstruction method).

C.



D.



FIGURE 4. Photographs of the skull roof of *Glanosuchus macrops* GS M796 (left) and the lycosuchid GS C 60 (right). C. Dorsal view. D. Ventral view.

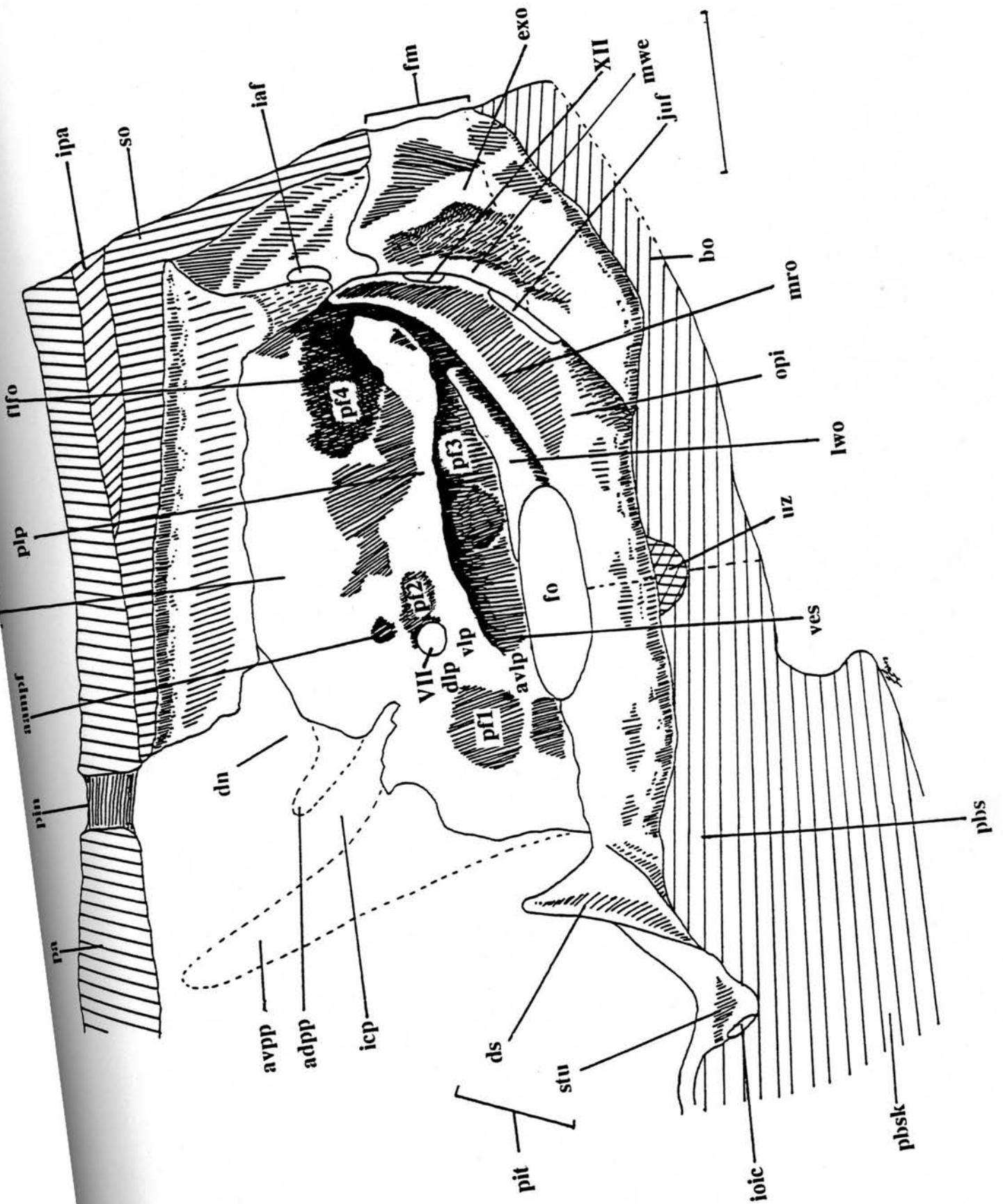


FIGURE 5. Sagittal view of the braincase of *Glanosuchus macrops* SAM K238a

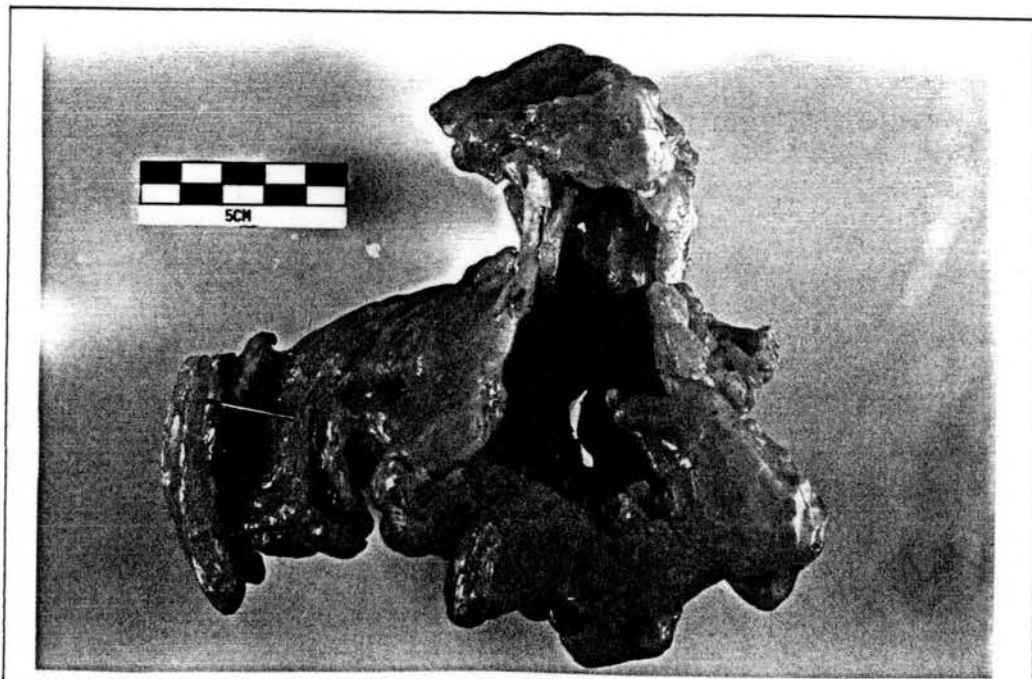
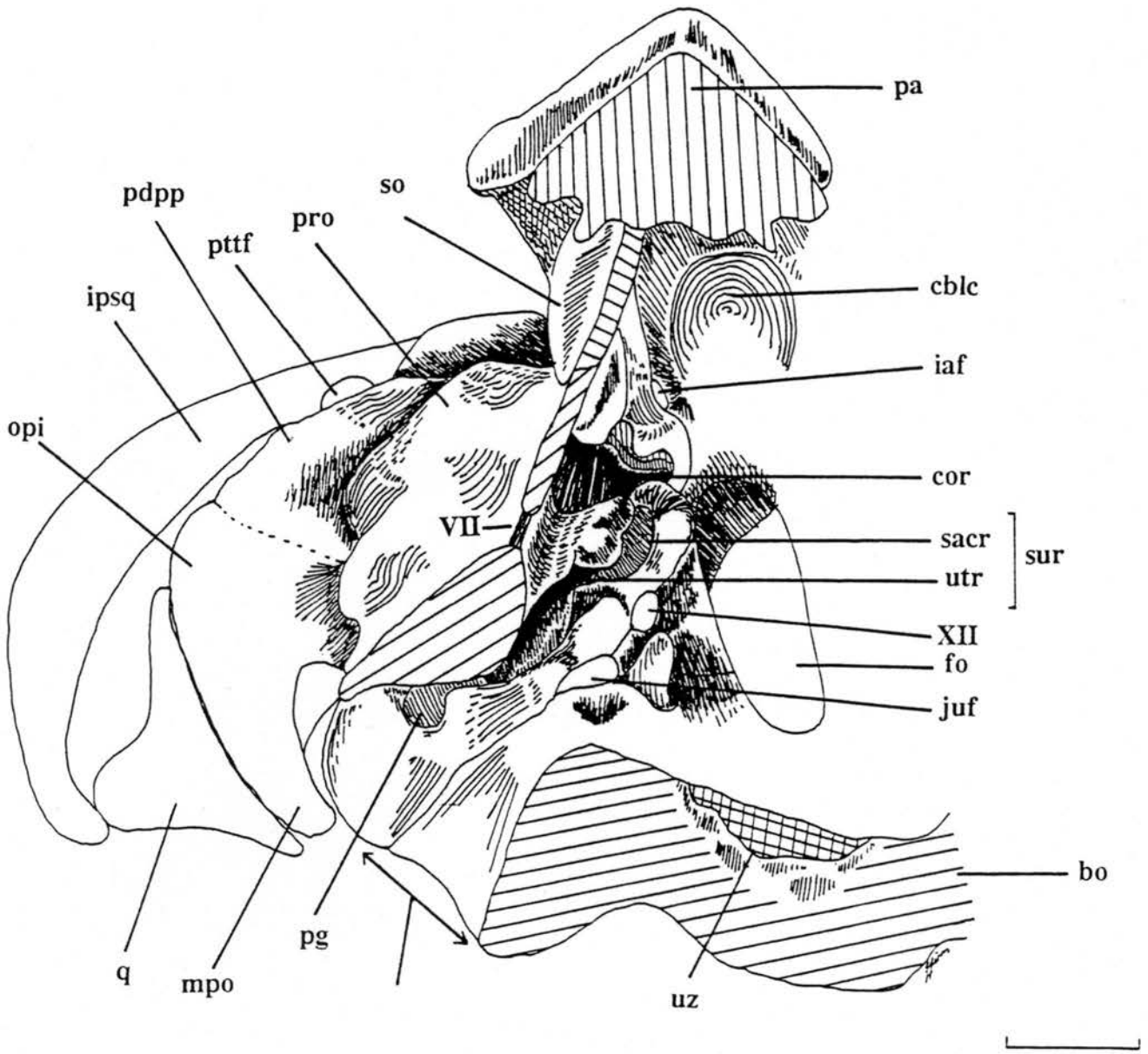


FIGURE 6. Anterior view of the braincase of *Glanosuchus macrops* SAM K238a (wax model).

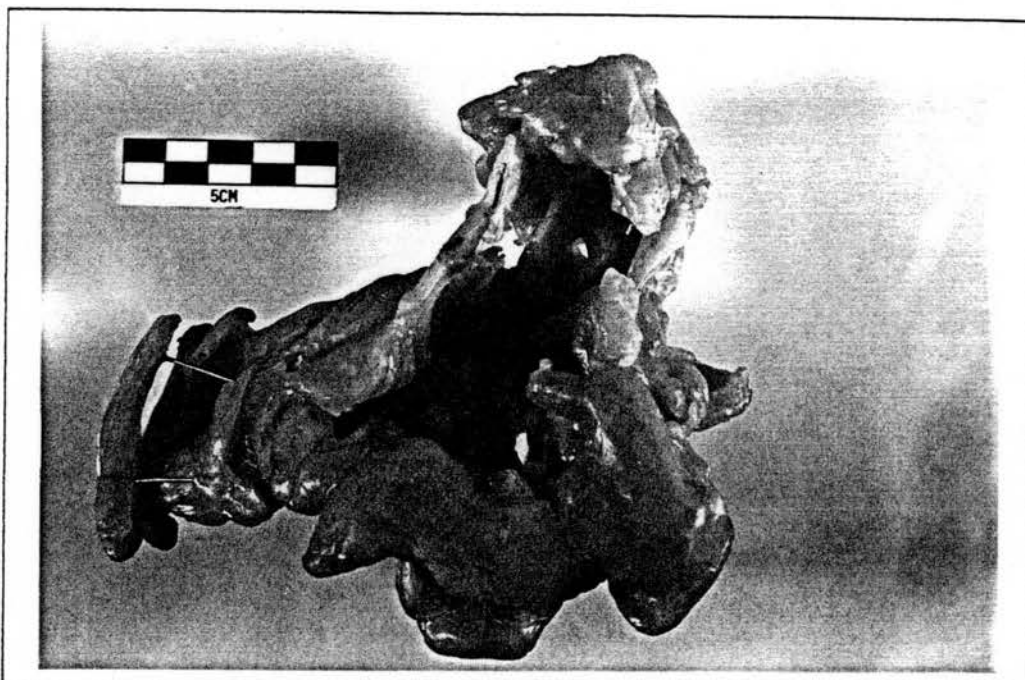
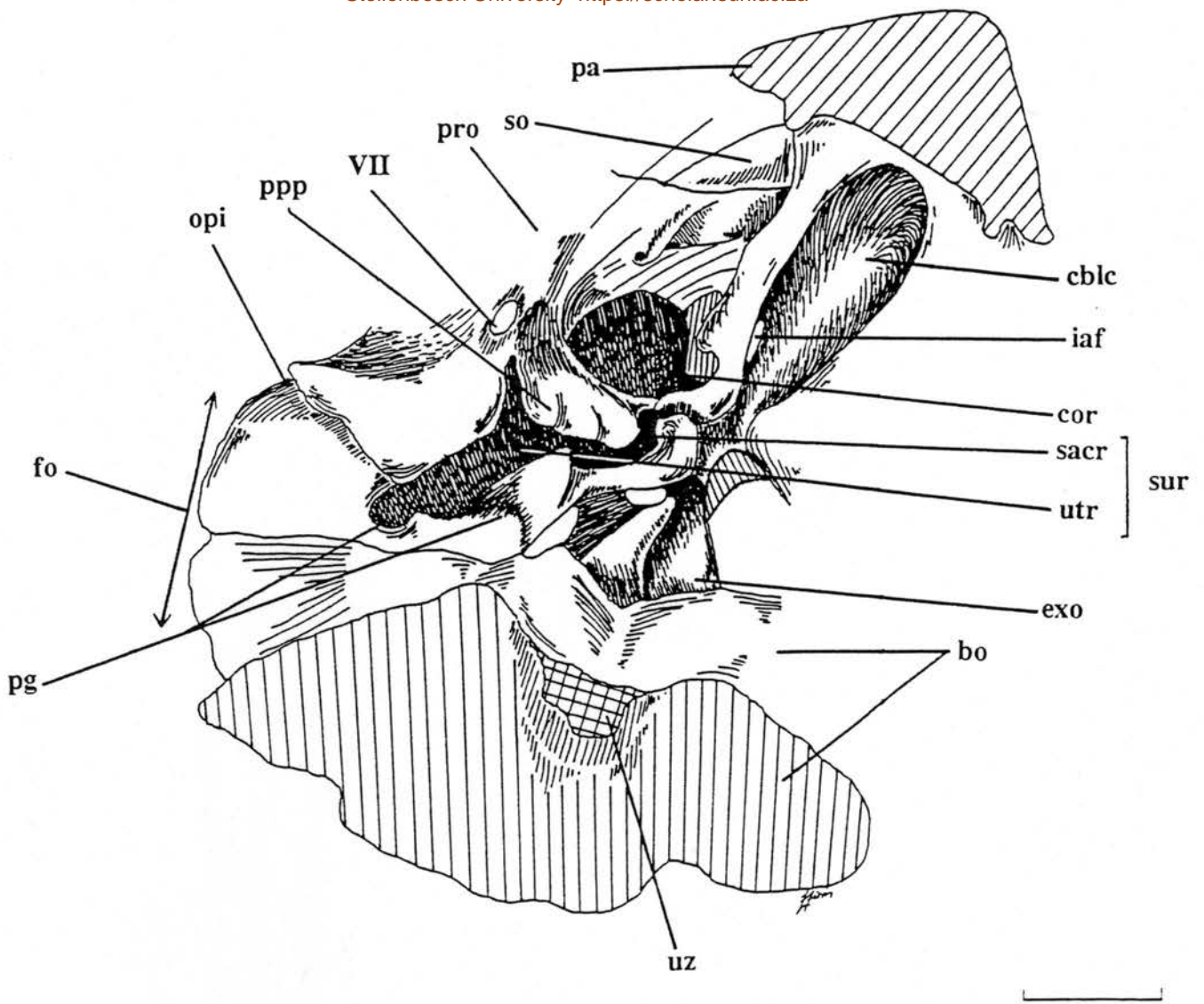


FIGURE 7. Antero-dorsal view of the braincase of *Glanosuchus macrops* SAM K238a (wax model).

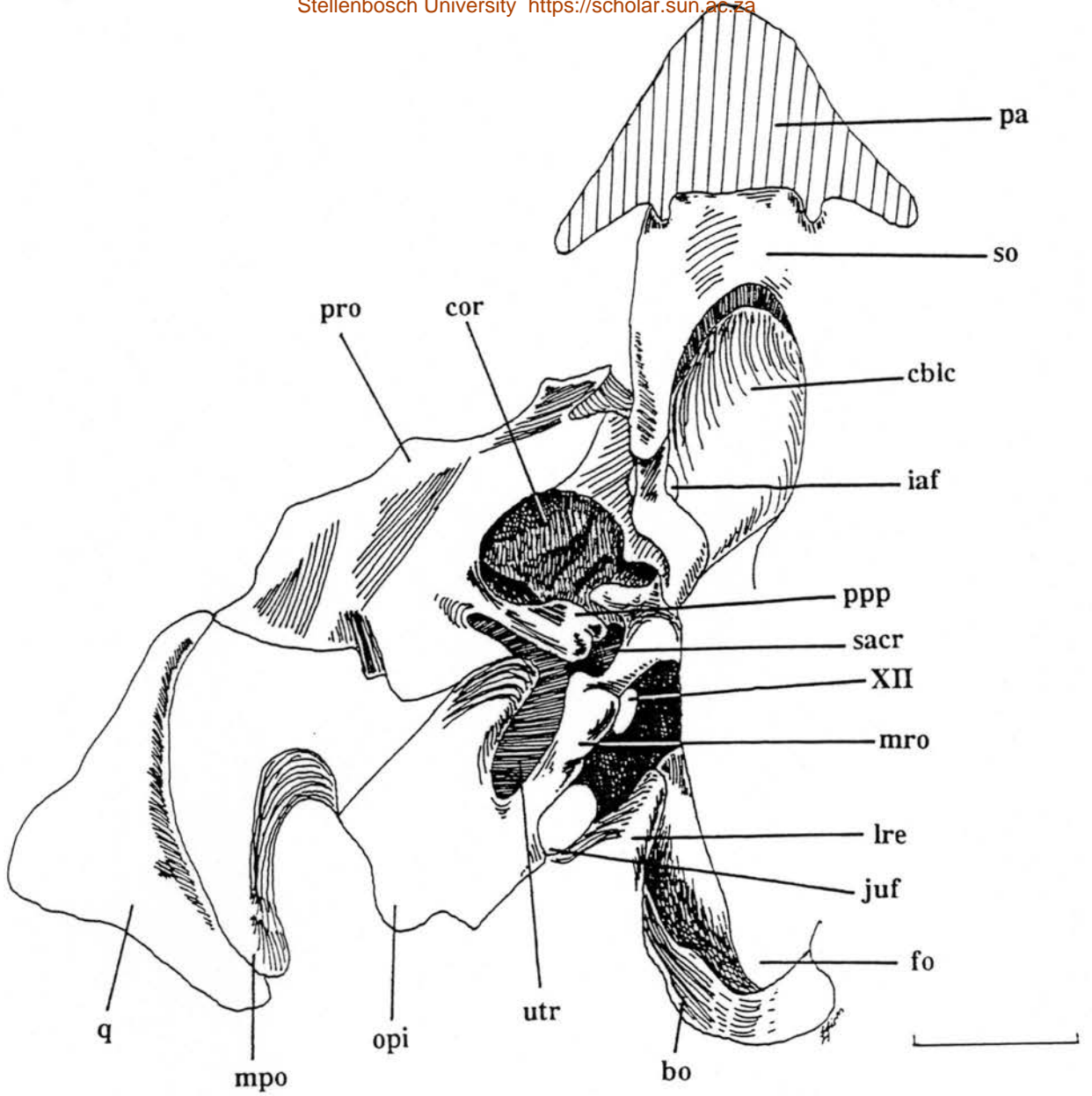


FIGURE 8. Dorso-medial view of the braincase of *Glanosuchus macrops* SAM K238a (wax model).

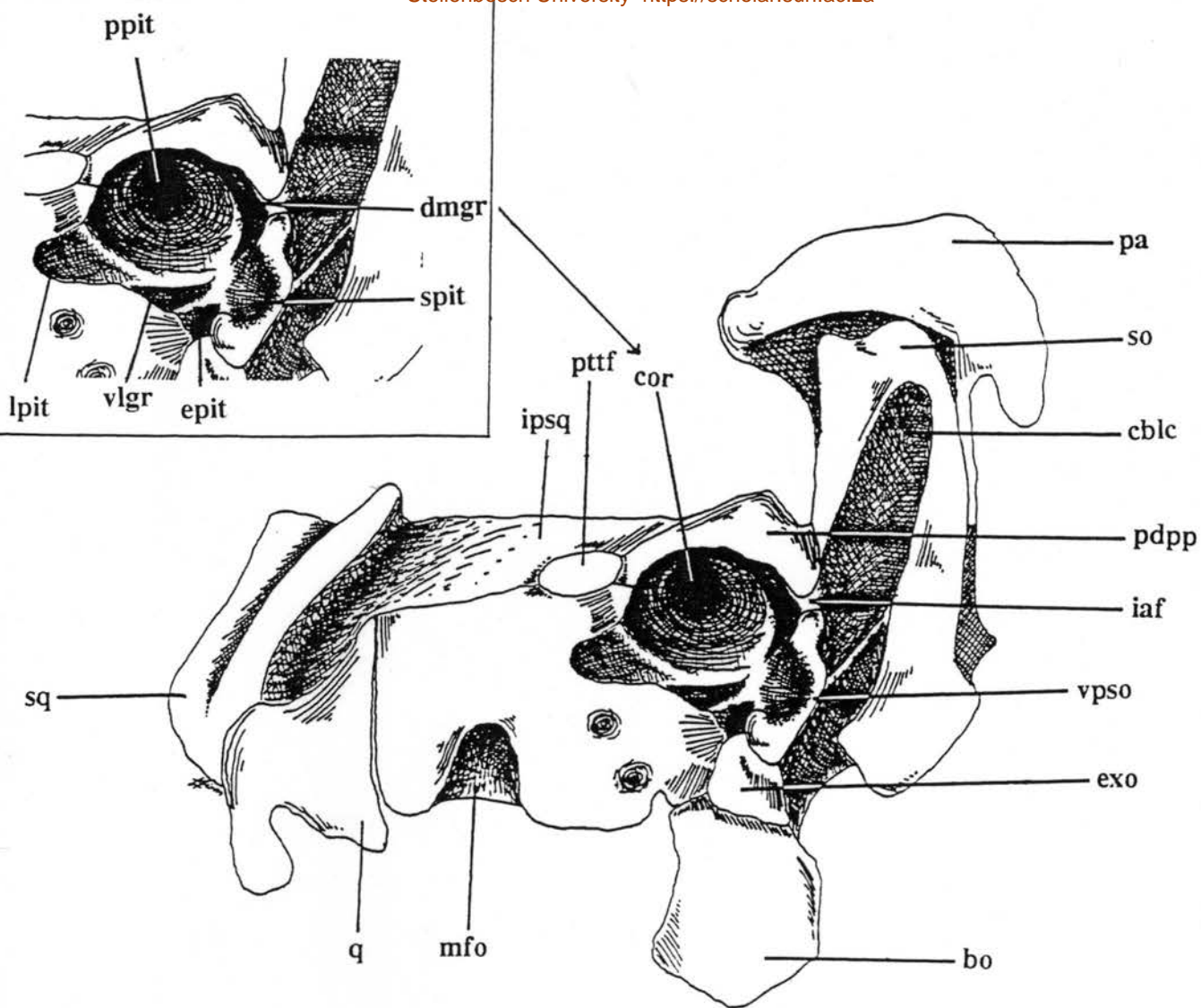
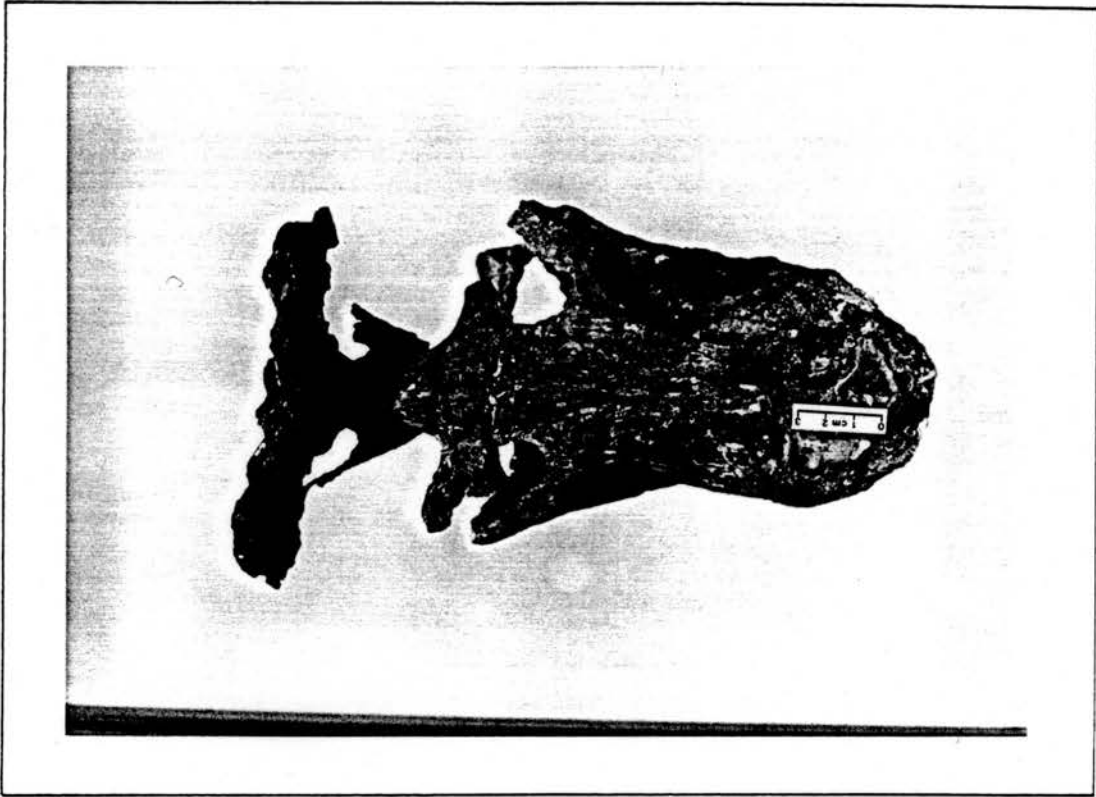


FIGURE 9. Anterior view of the cochlear recess of *Glanosuchus macrops* SAM K238a (wax model).

A.



B.

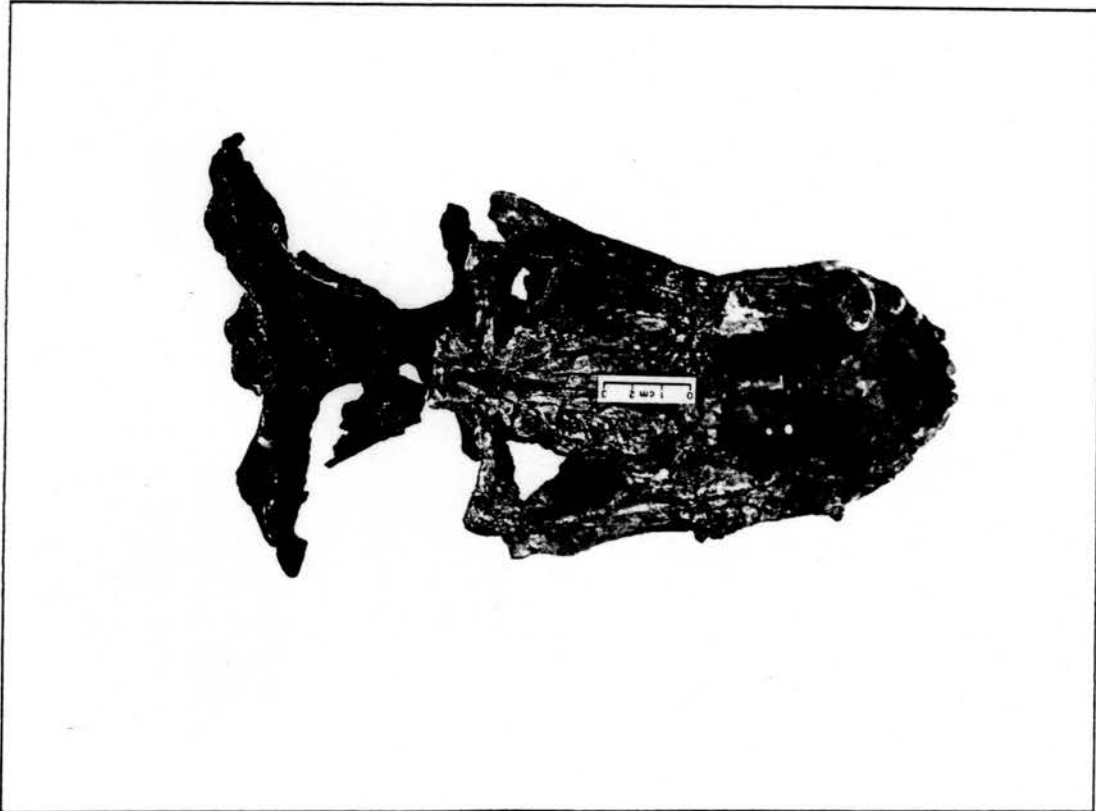


FIGURE 10. Photographs of the type skull of *Ptomalestes avidus* SAM 11942. A. Dorsal view. B. Ventral view.

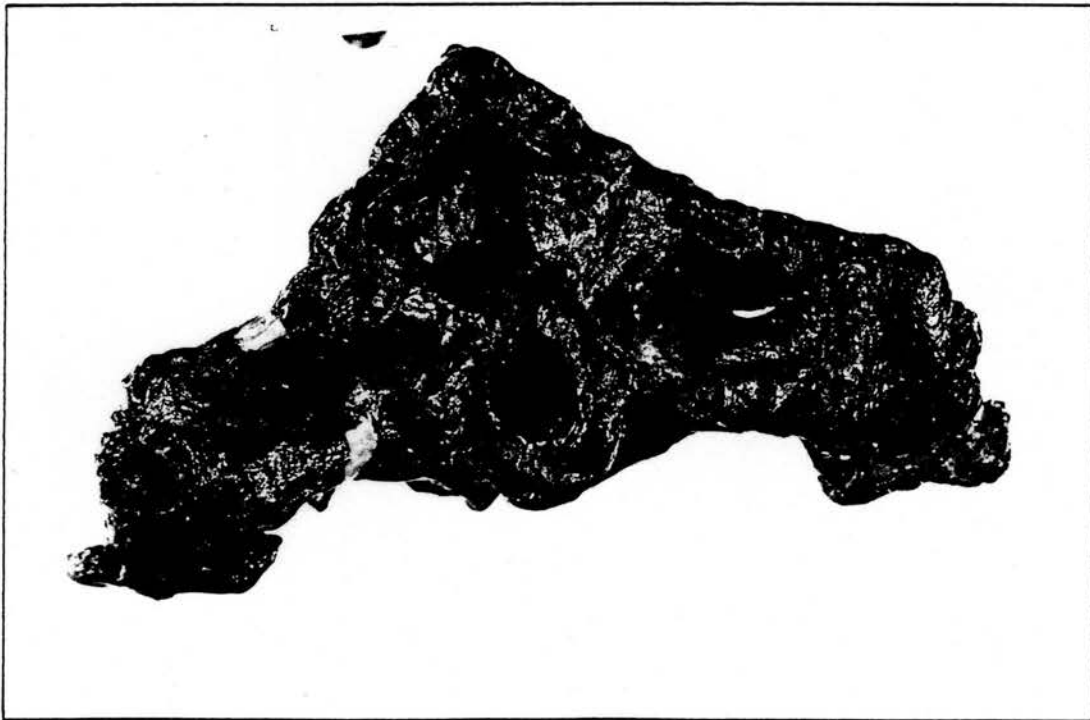
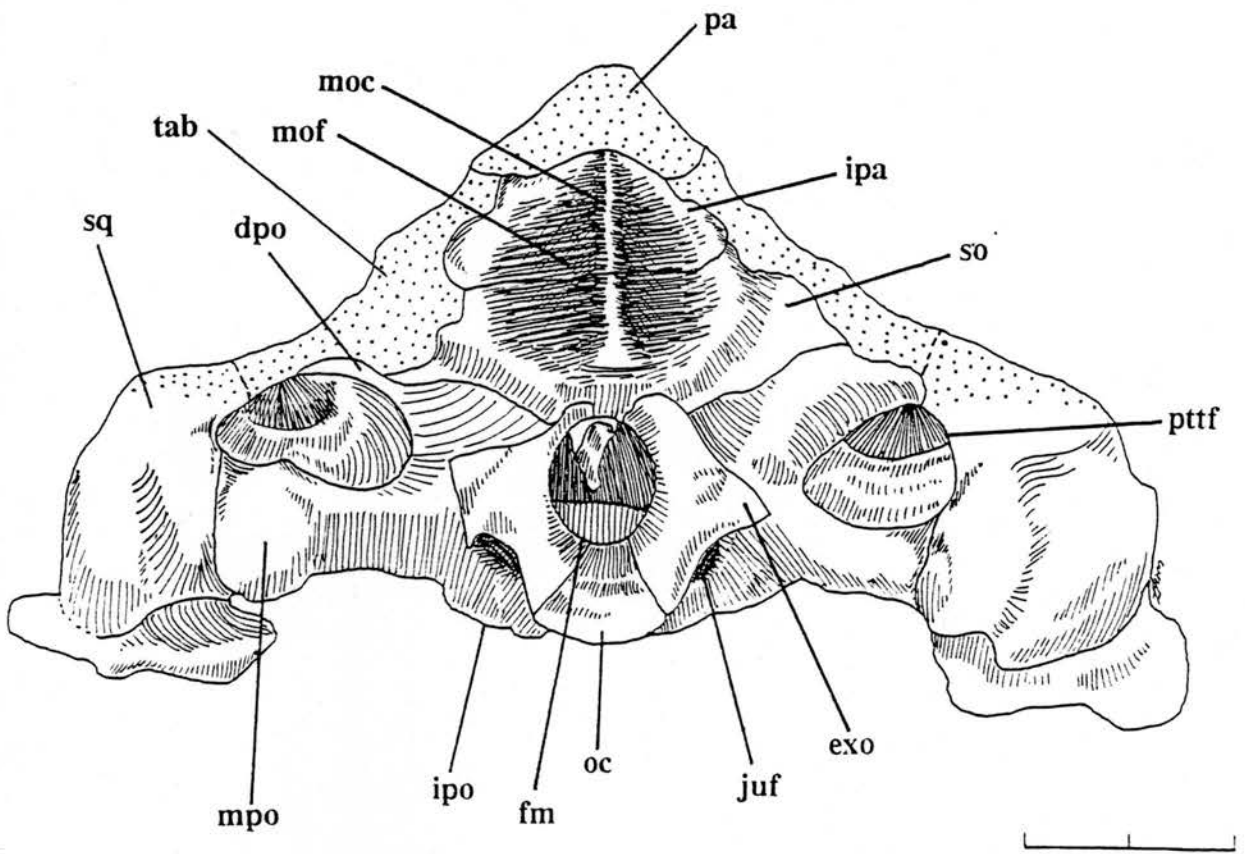


FIGURE 11. Occipital view of the type skull of *Ptomalestes avidus* SAM 11942 (after Van den Heever 1987).

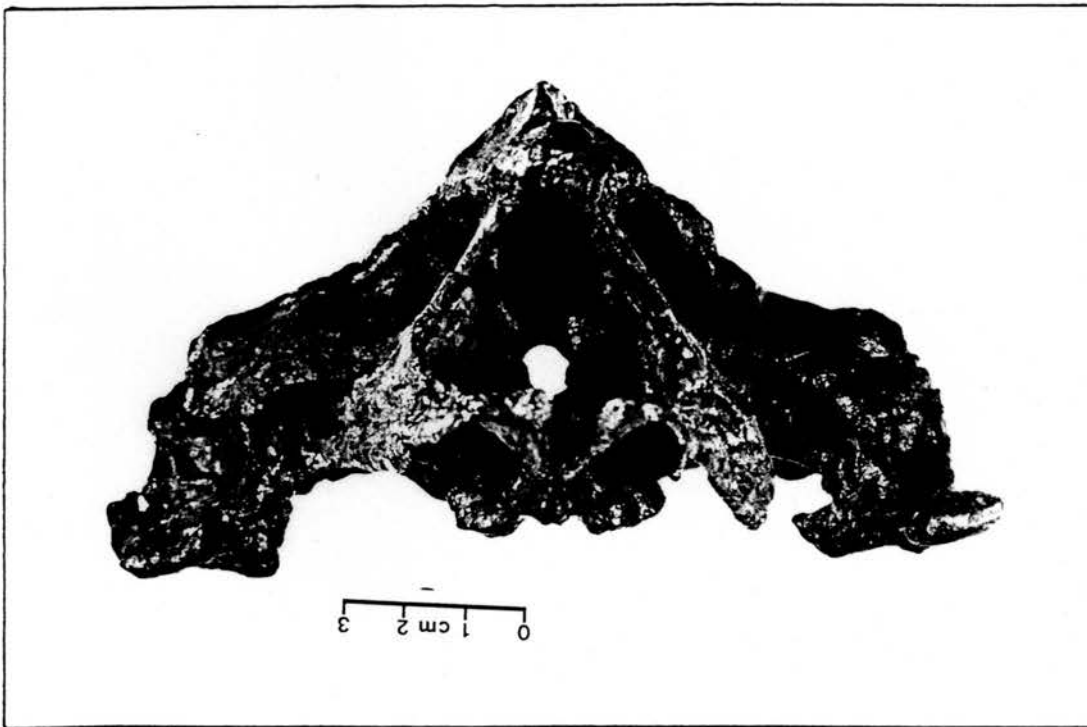
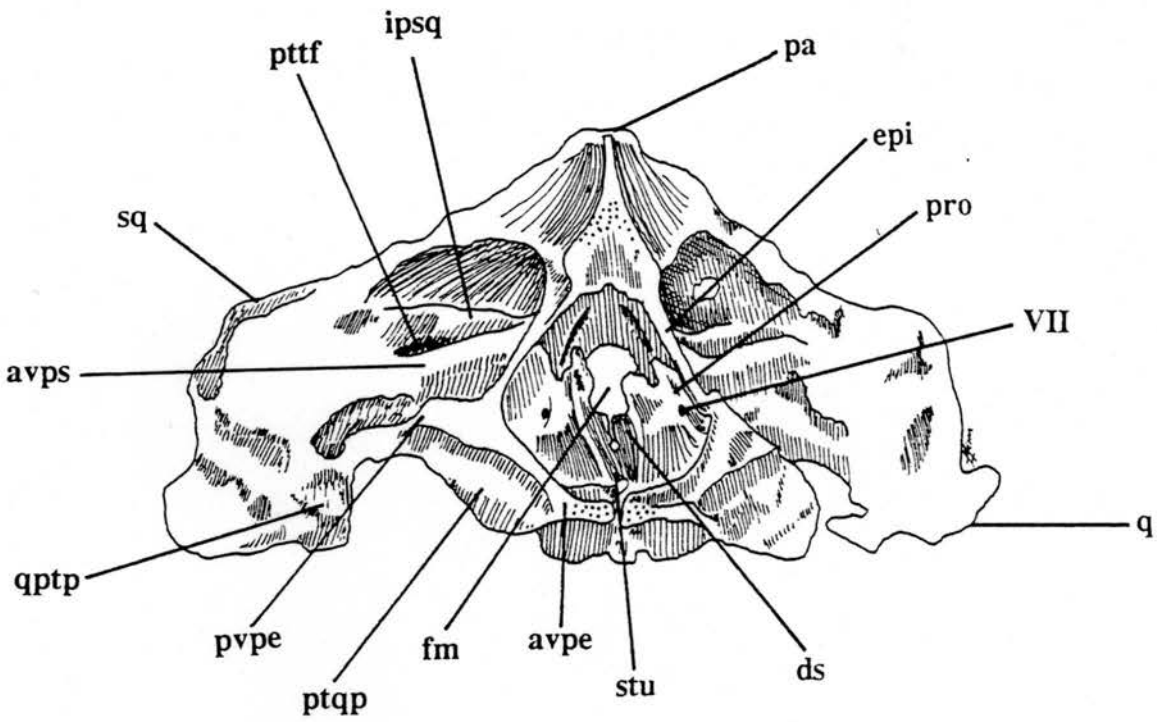
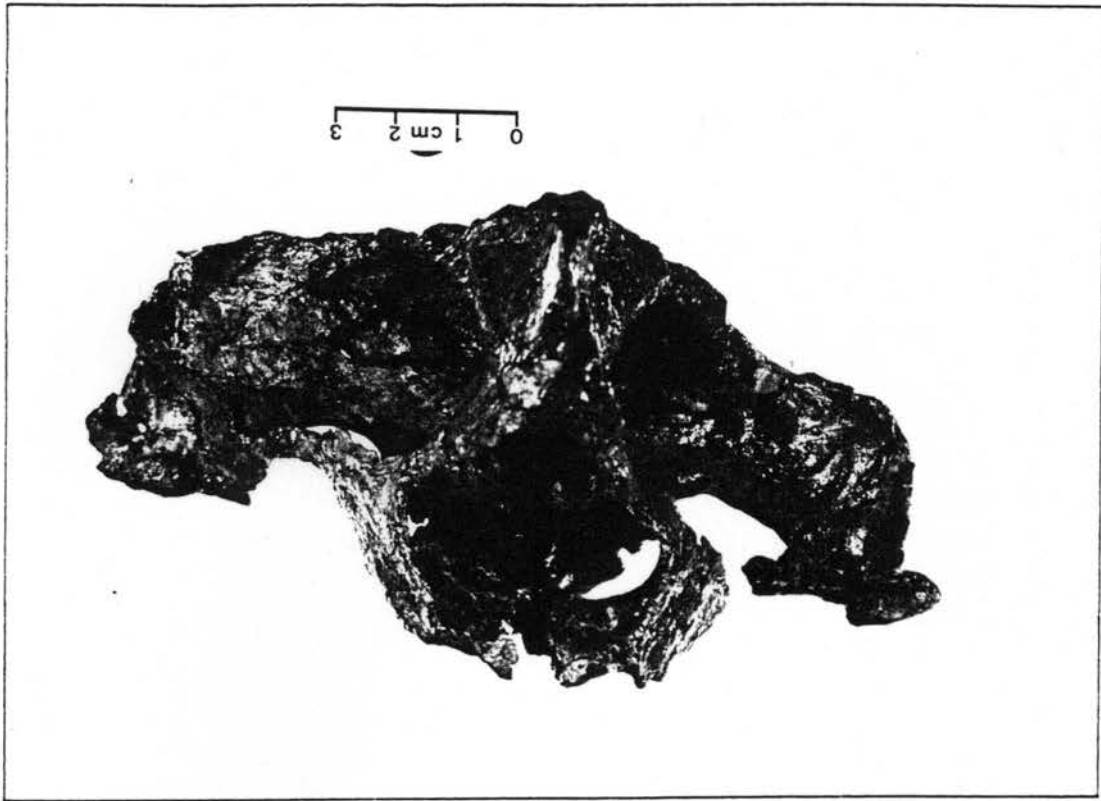


FIGURE 12. Anterior view of the braincase of the type skull of *Ptomalestes avidus* SAM 11942 (after Van den Heever 1987).

A.



B.

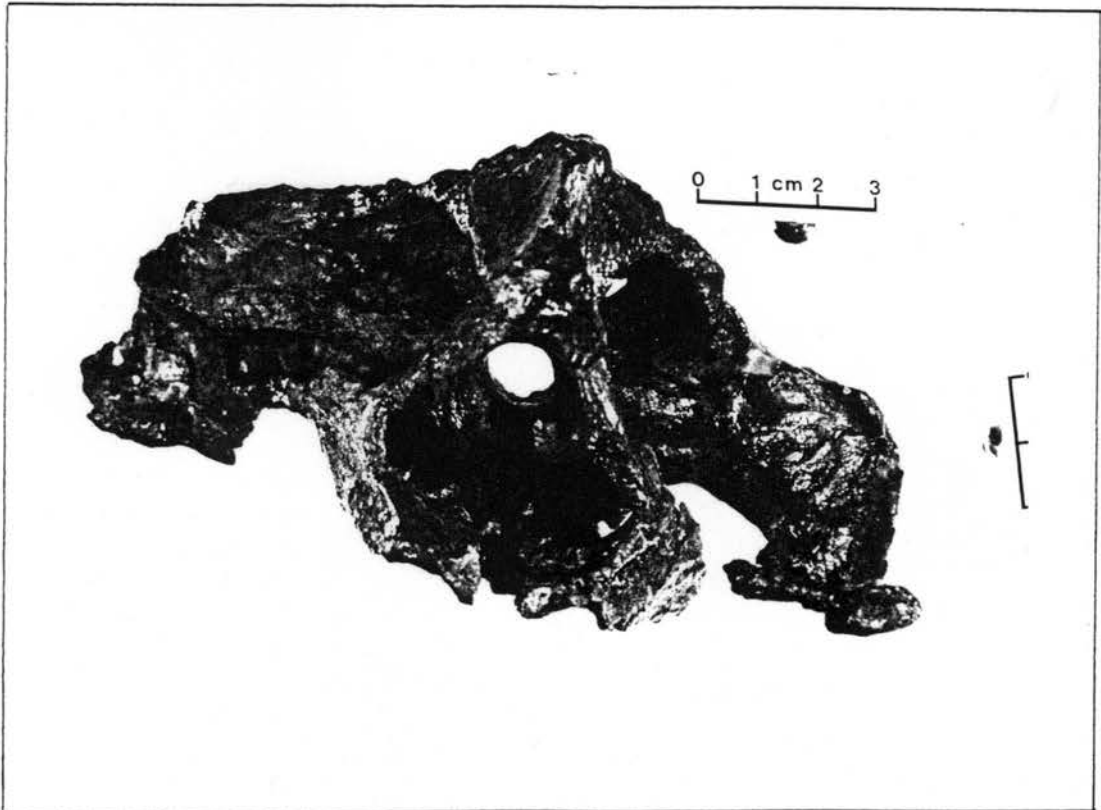
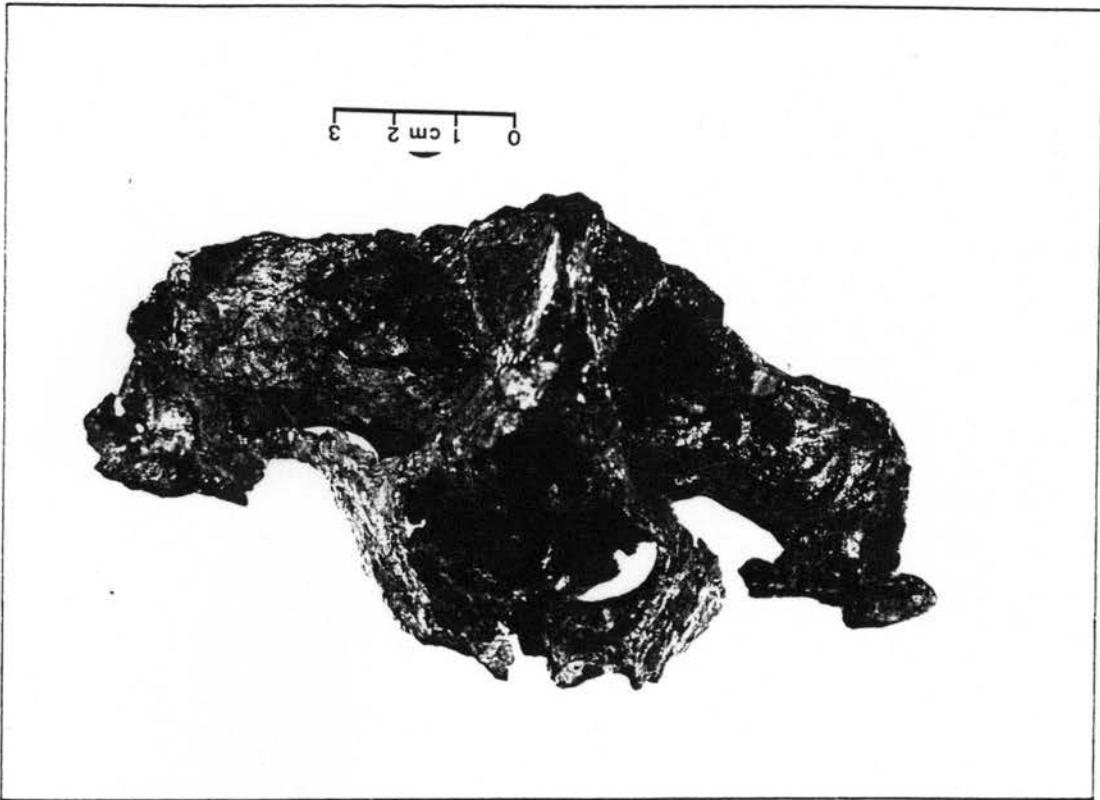


FIGURE 13. Anterior view of the braincase of the type skull of *Ptomalestes avidus* SAM 11942 indicating the pituitary fossa.

A.



B.

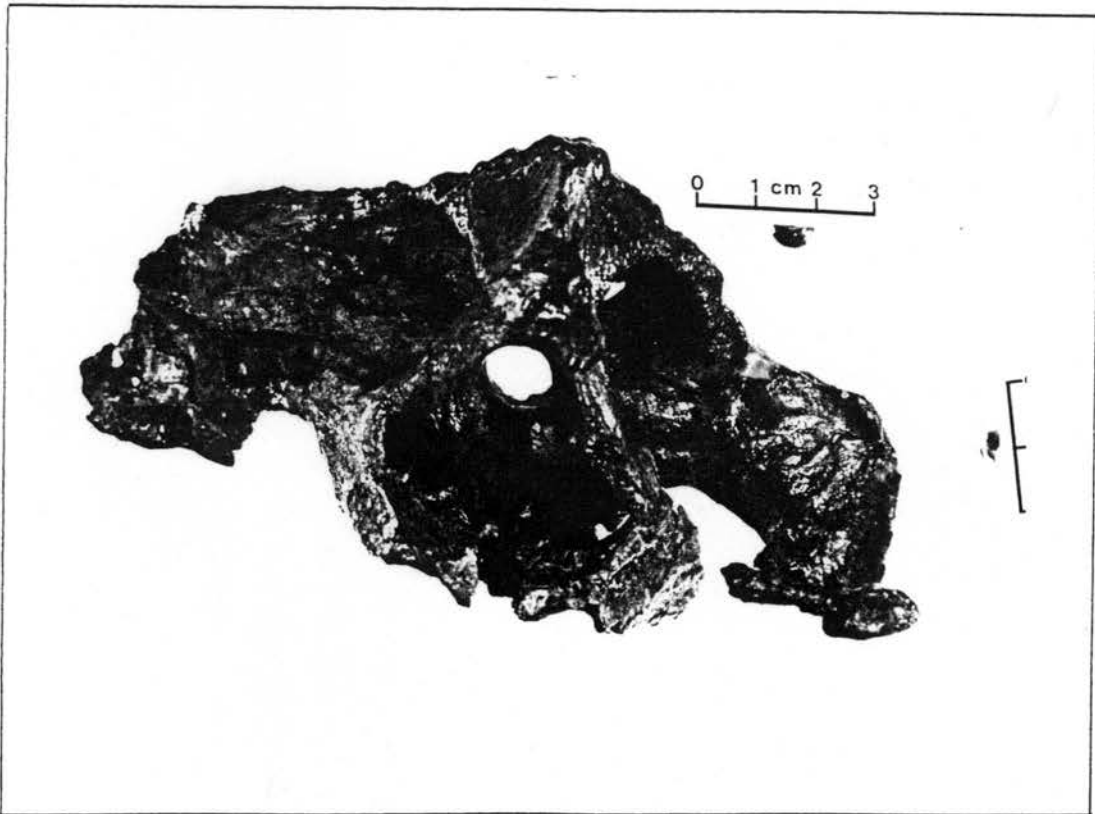


FIGURE 13. Anterior view of the braincase of the type skull of *Ptomalestes avidus* SAM 11942 indicating the pituitary fossa.

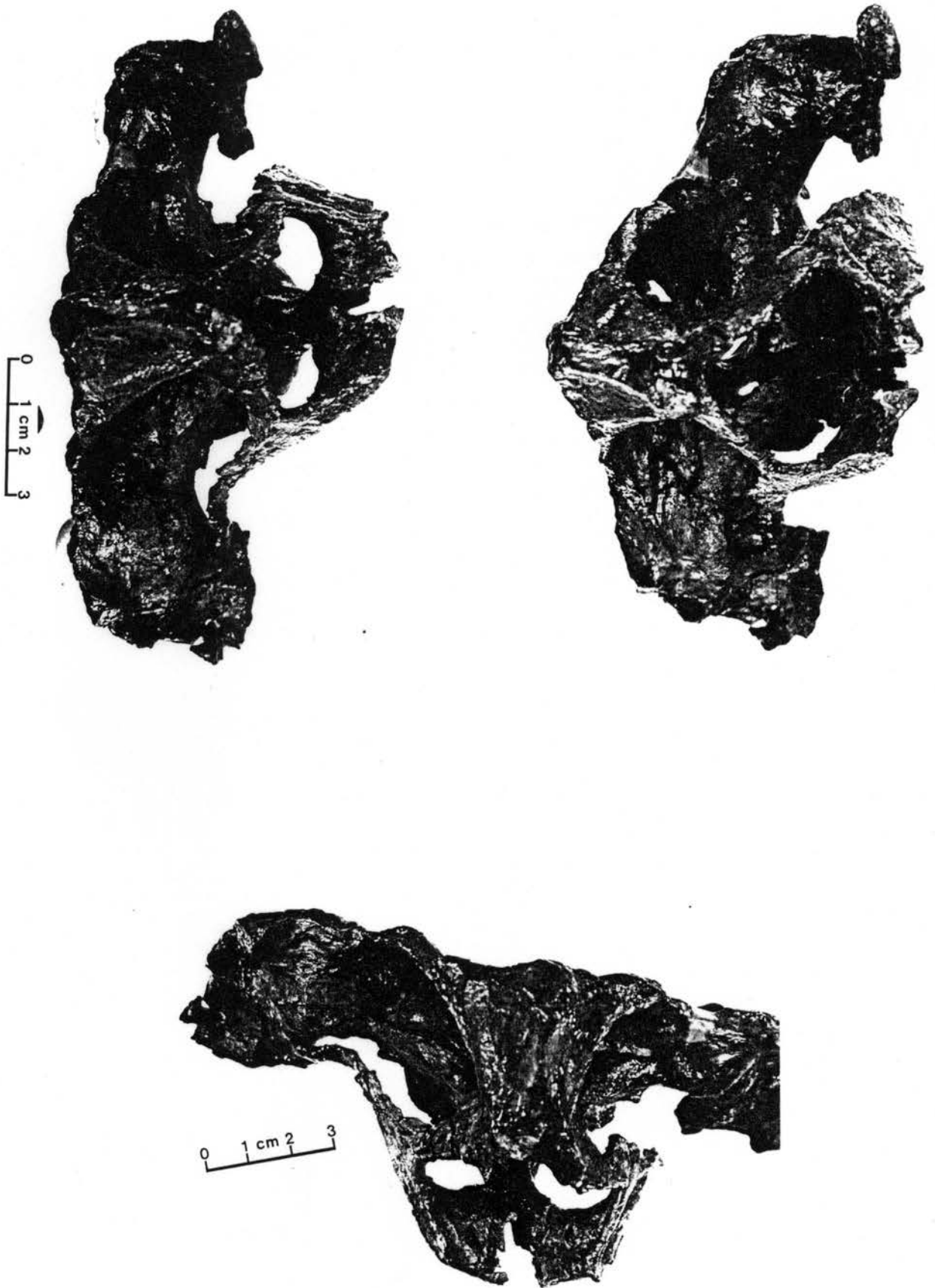


FIGURE 14. Various view of the braincase of the type skull *Ptomalestes avidus* SAM 11942.

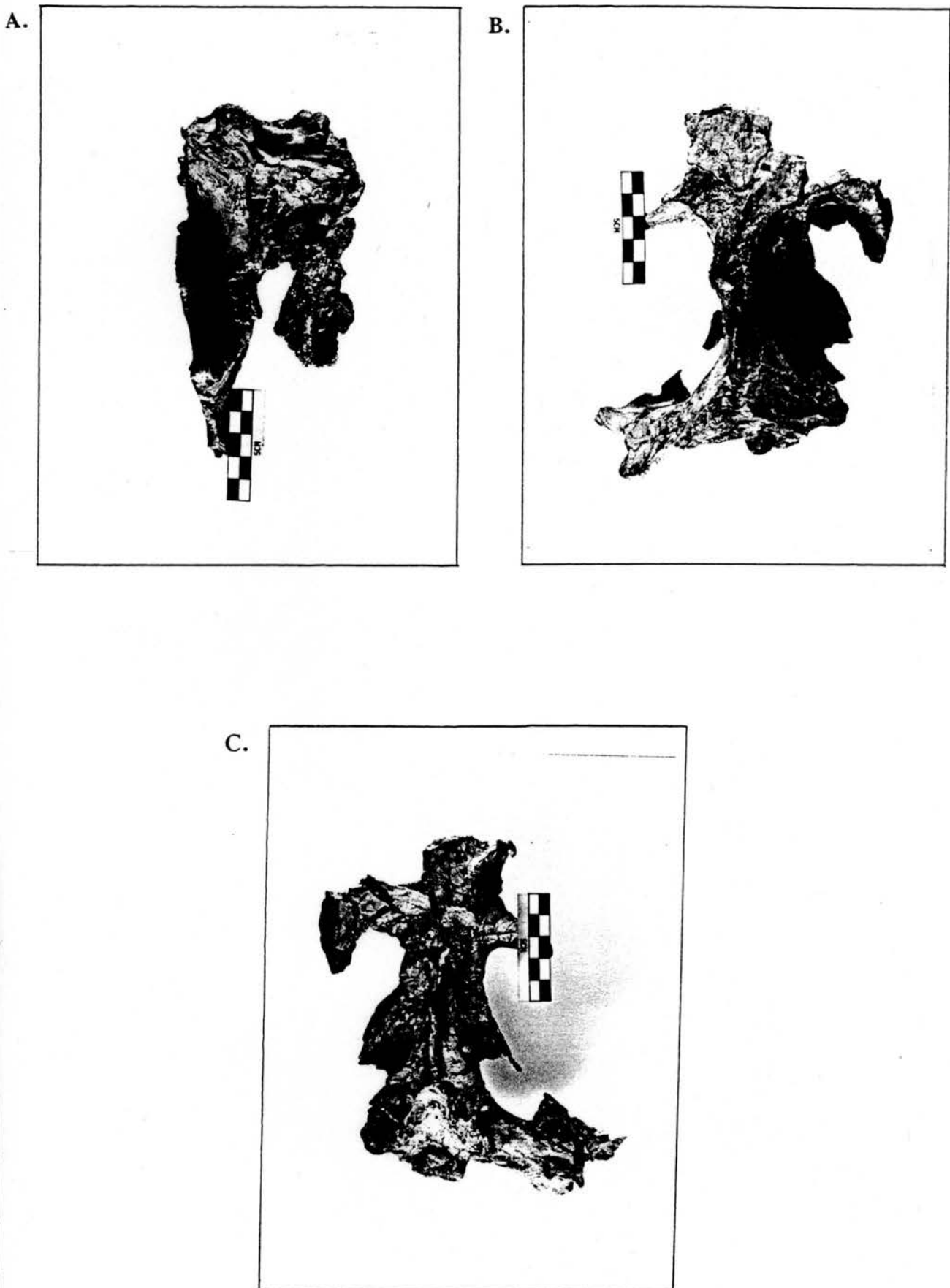


FIGURE 15. Photographs of the skull of *Lycosuchus vanderrieti* GS M793. A. Left lateral view. B. Dorsal view. C. Ventral view.

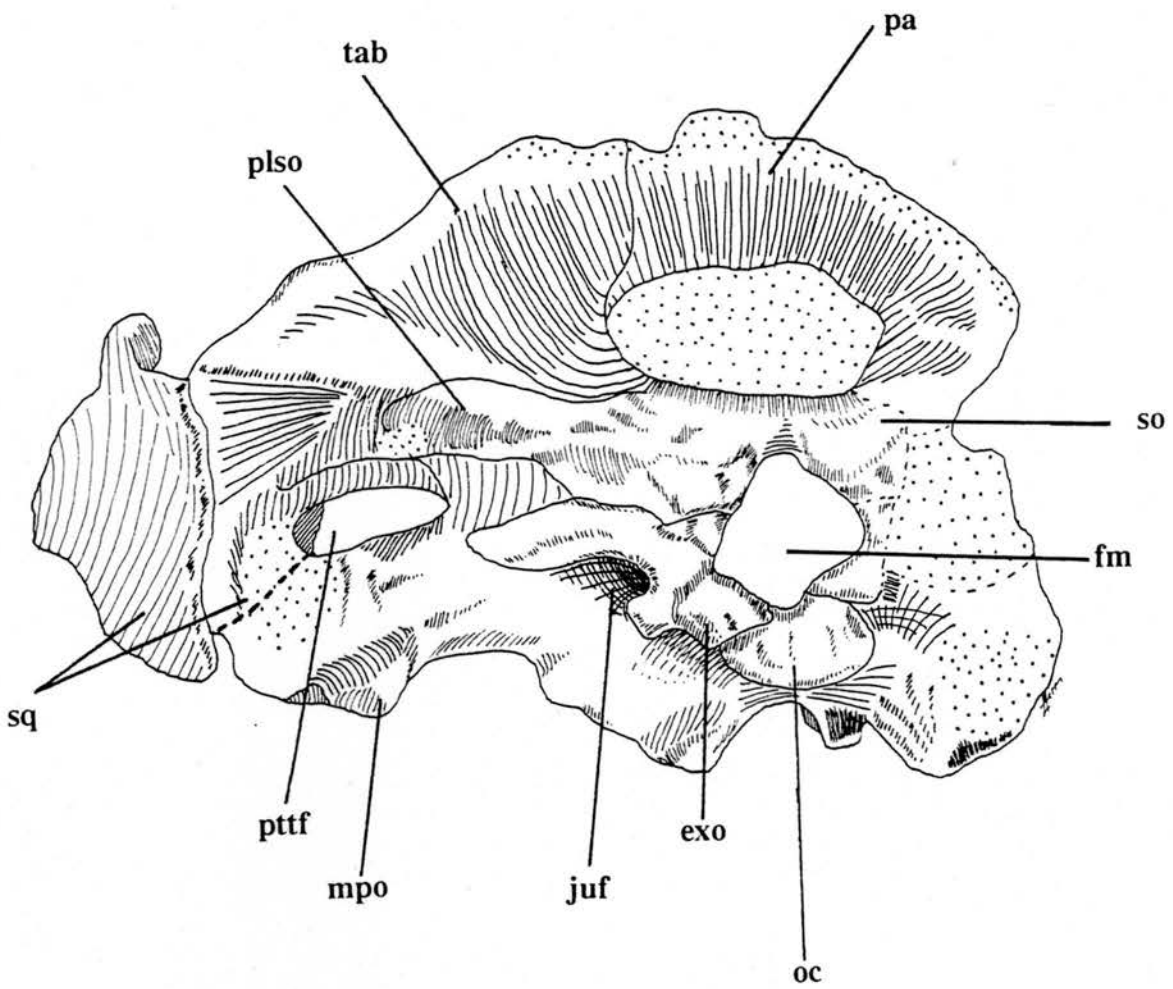


FIGURE 16. Occipital view of the skull of *Lycosuchus vanderrieti* GS M793 (after Van den Heever 1987).

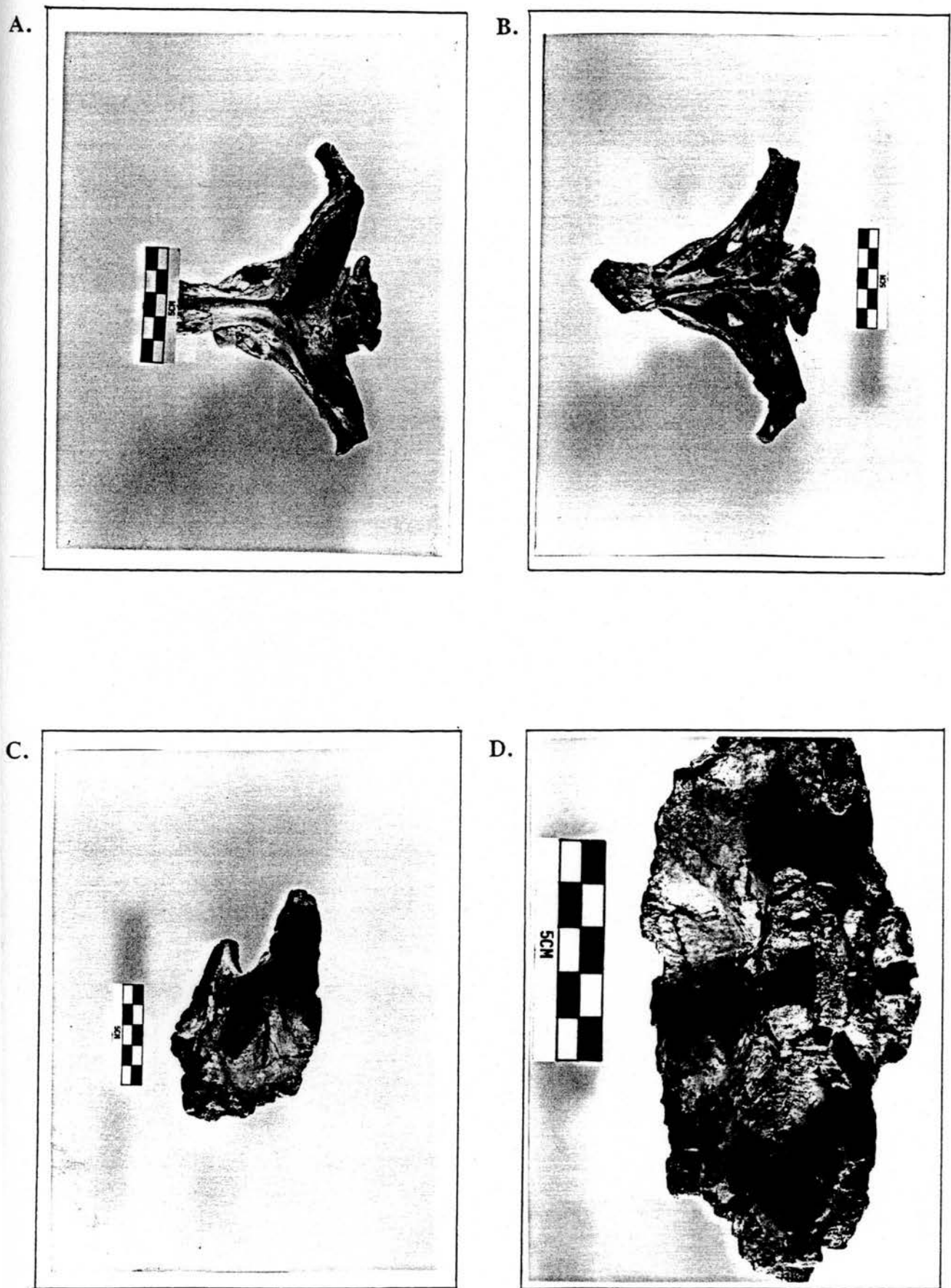
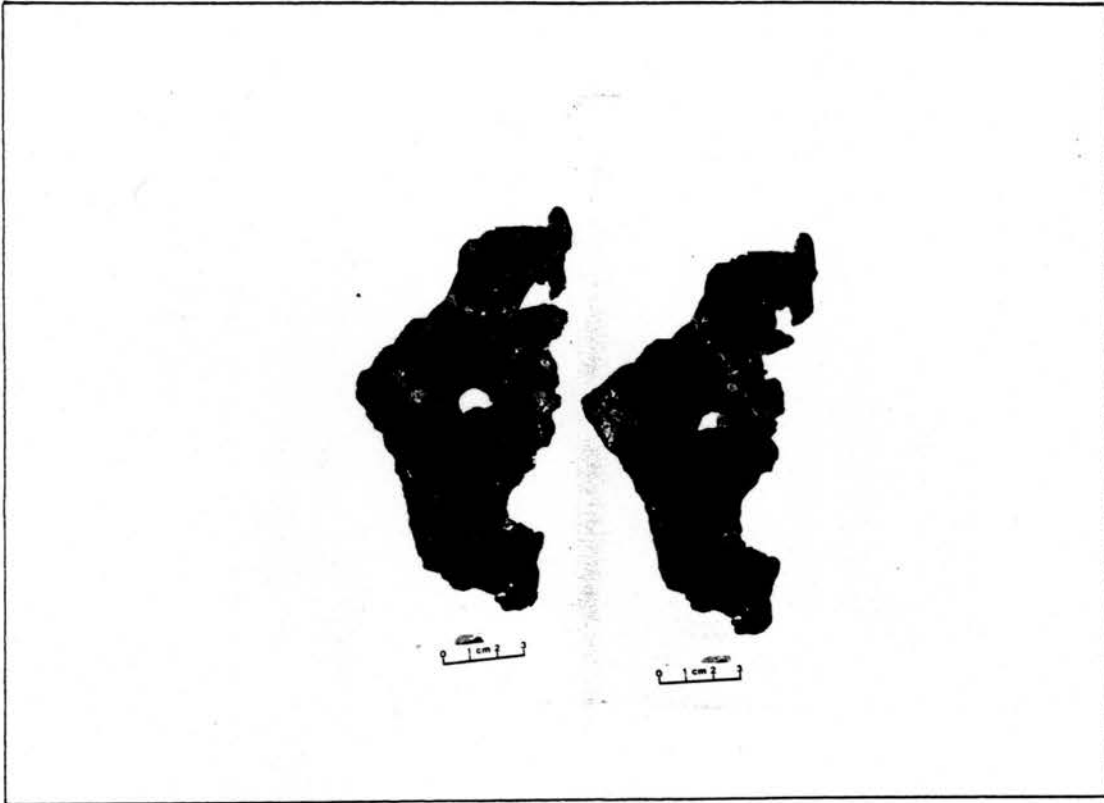


FIGURE 17. Photographs of the skull of a whaitsiid SAM K5512. A. Dorsal view. B. Ventral view. C. Lateral view. D. Occipital view.

A.

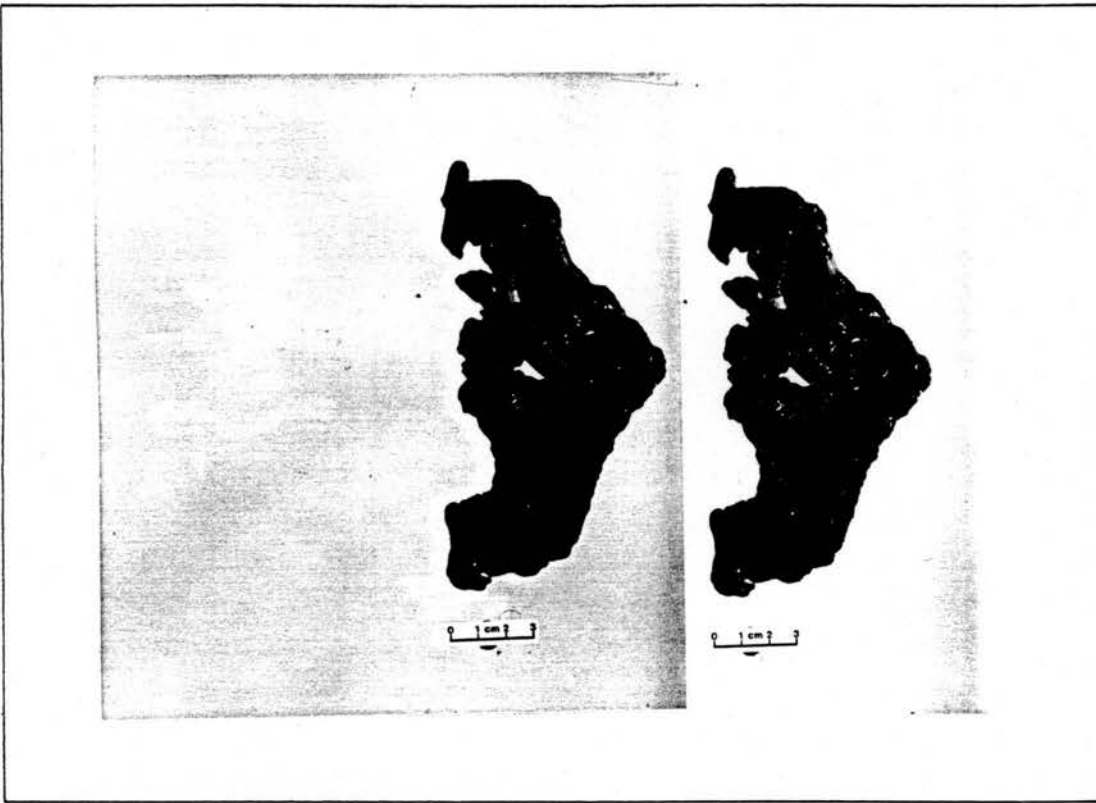


B.



FIGURE 18. Stereophotographs. A. Anterior view of the braincase of the type *Ptomalestes avidus* SAM 11942. B. Anterior view of the braincase of *Glanosuchus macrops* GS M796.

A.



B.

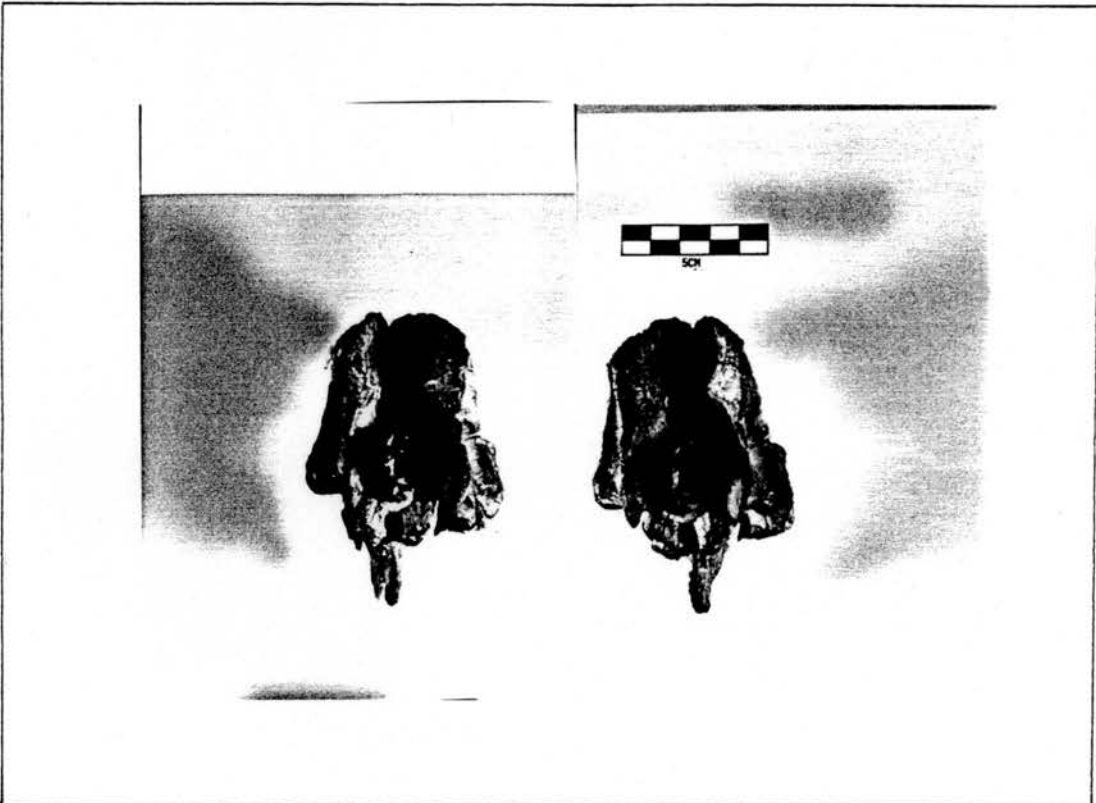
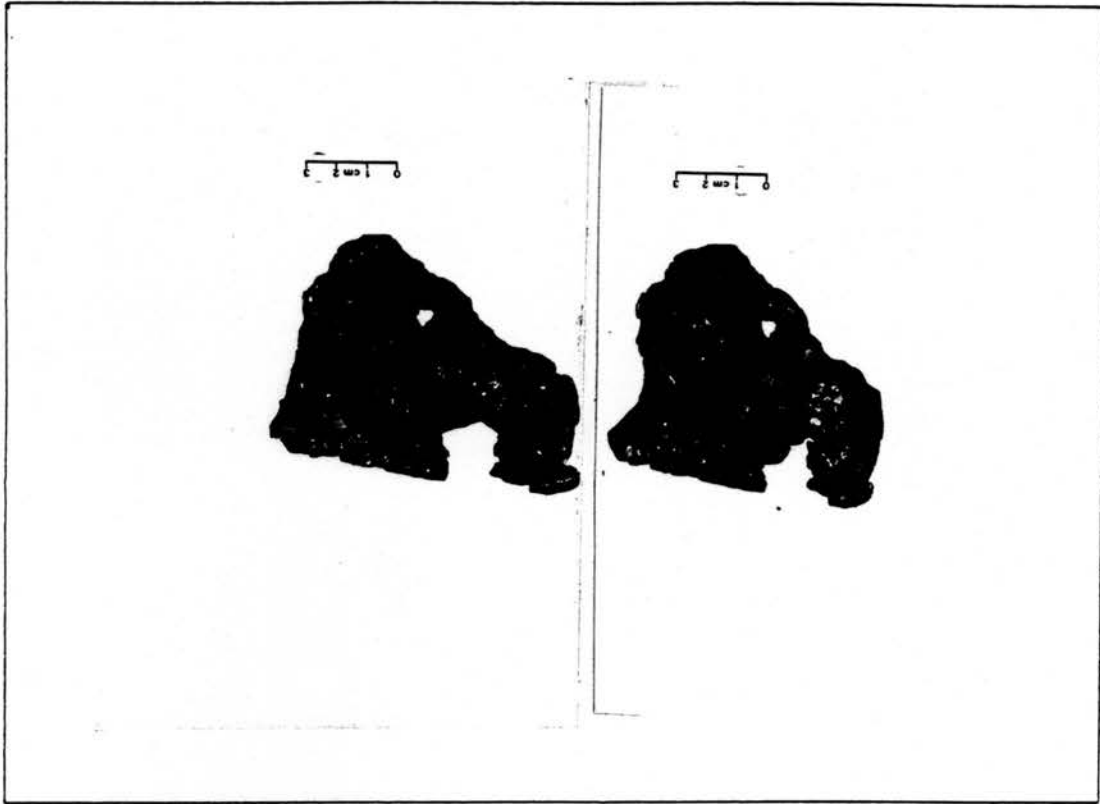


FIGURE 19. Stereophotographs. A. Posterior view of the braincase of the type *Ptomalestes avidus* SAM 11942. B. Posterior view of the braincase of *Glanosuchus macrops* GS M796.

A.



B.

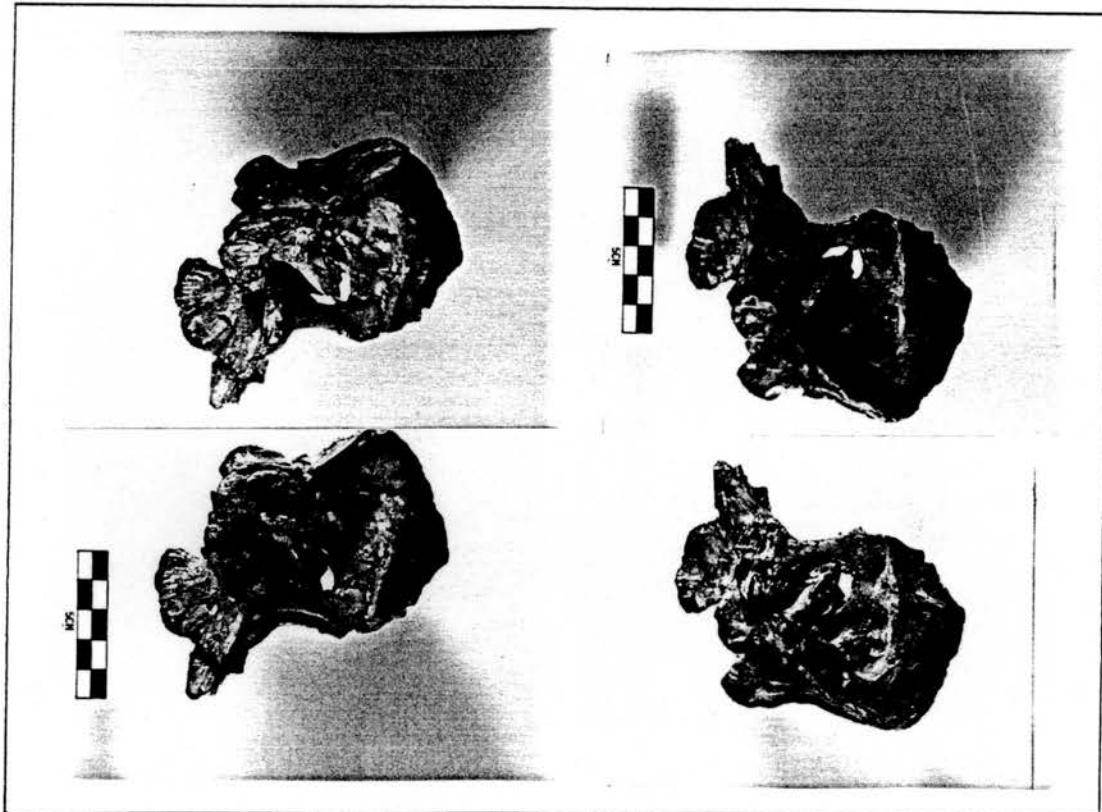
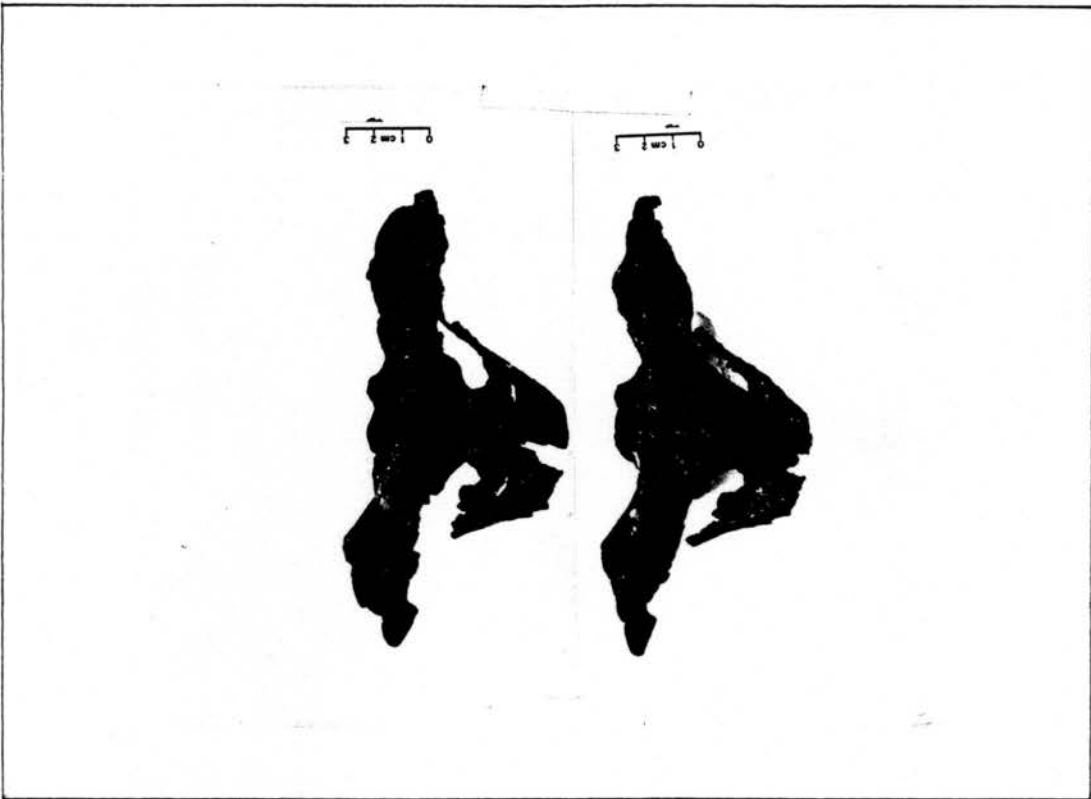


FIGURE 20. Stereophotographs. A. Lateral view of the braincase of the type *Ptomalestes avidus* SAM 11942. B. Lateral view of the braincase of *Glanosuchus macrops* GS M796.

A.



B.

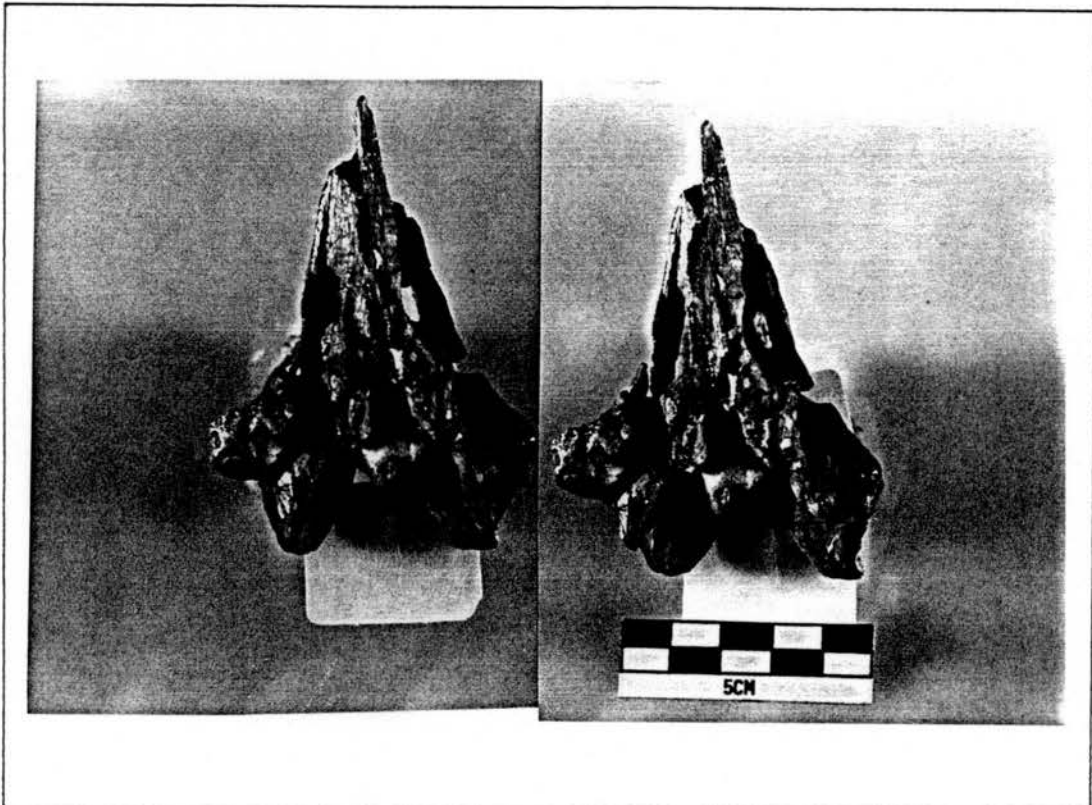
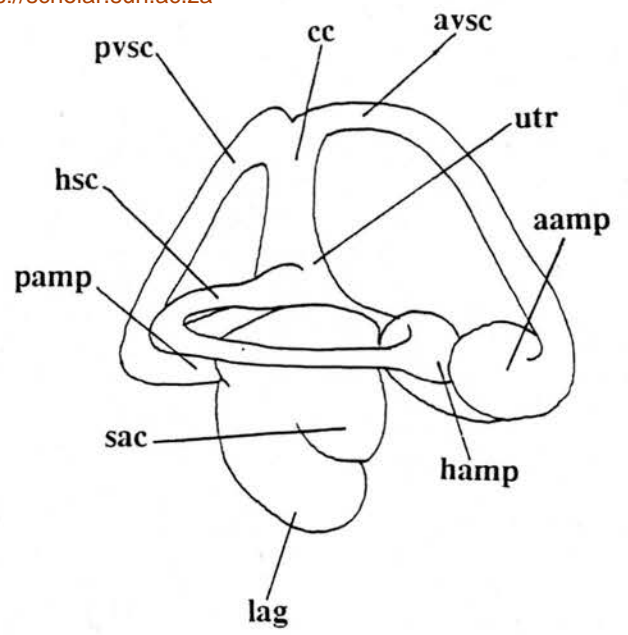
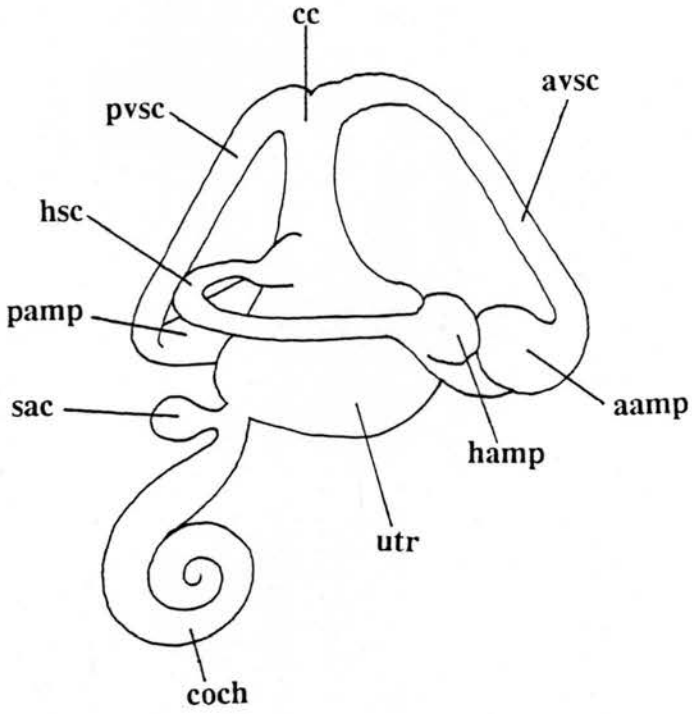


FIGURE 21. Stereophotographs. A. Ventral view of the braincase of the type *Ptomalestes avidus* SAM 11942. B. Ventral view of the braincase of *Glanosuchus macrops* GS M796.

A.



B.



C.

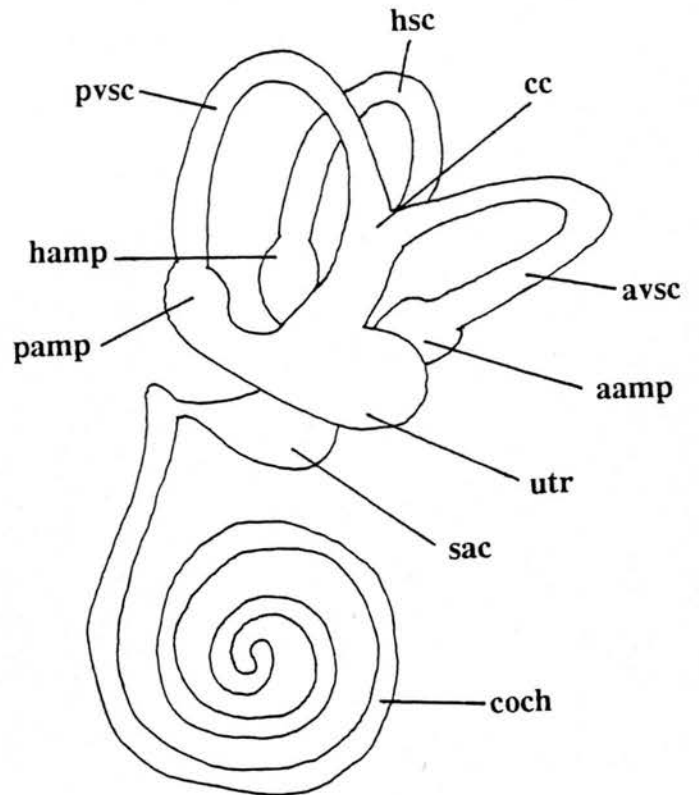
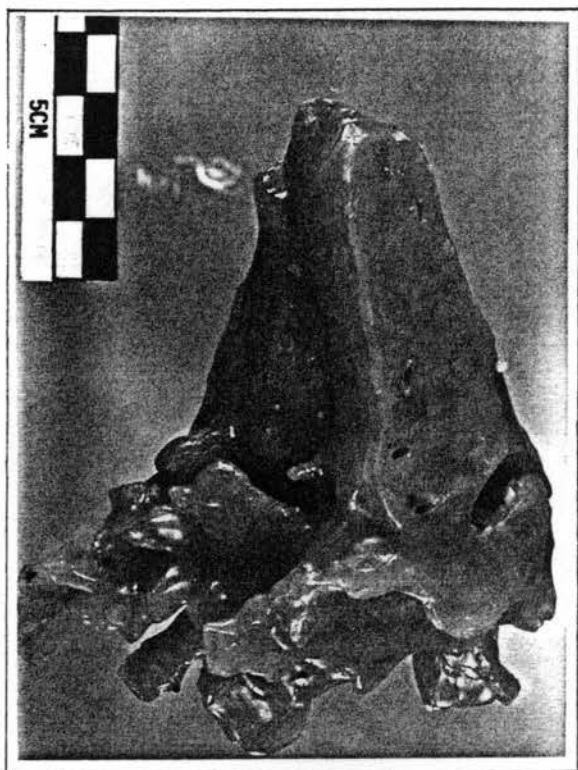


FIGURE 22. Comparison of the membranous inner ear. A. Reptiles (after Kardong 1994). B. Reconstruction of *Glanosuchus macrops* SAM K238a. C. Mammals (after Kardong 1994).

A.



B.

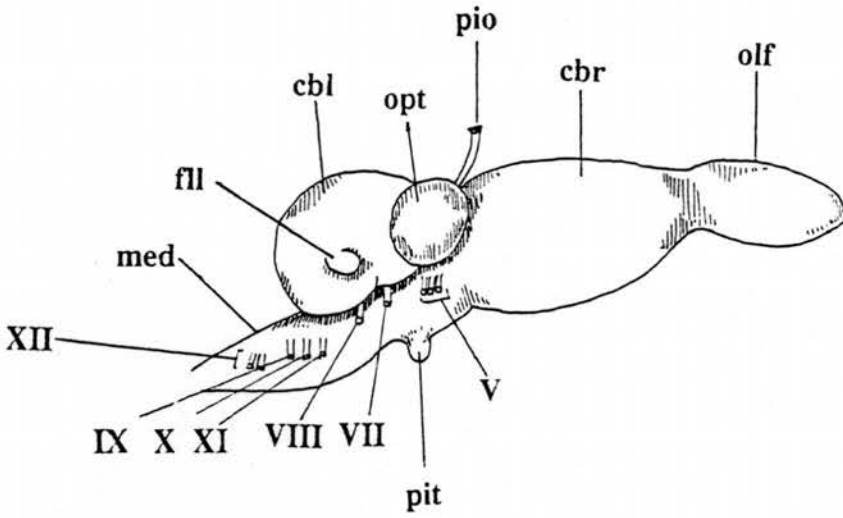


C.



FIGURE 23. Cranial endocast of *Glanosuchus macrops* SAM K238a (wax model).
A. Antero-lateral view. B. Dorsal view. C. Ventral view.

A.



B.

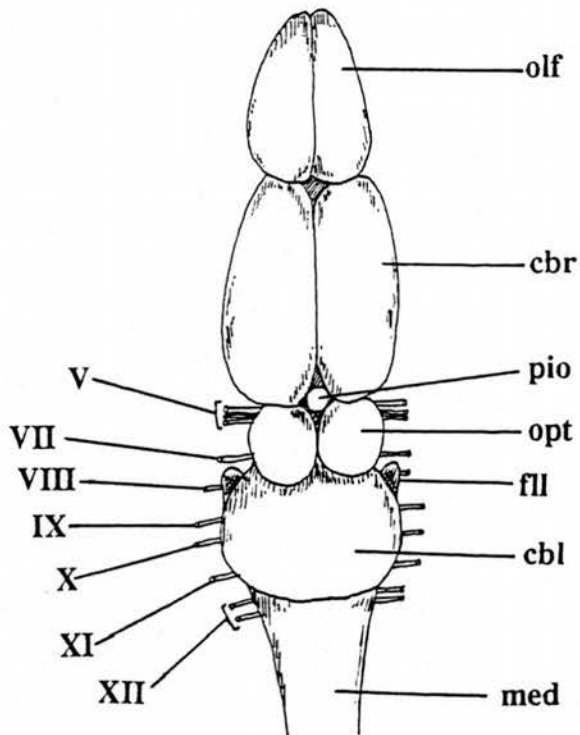


FIGURE 24. Reconstructed brain of *Glanosuchus macrops* SAM K238a. A. Lateral view. B. Dorsal view.

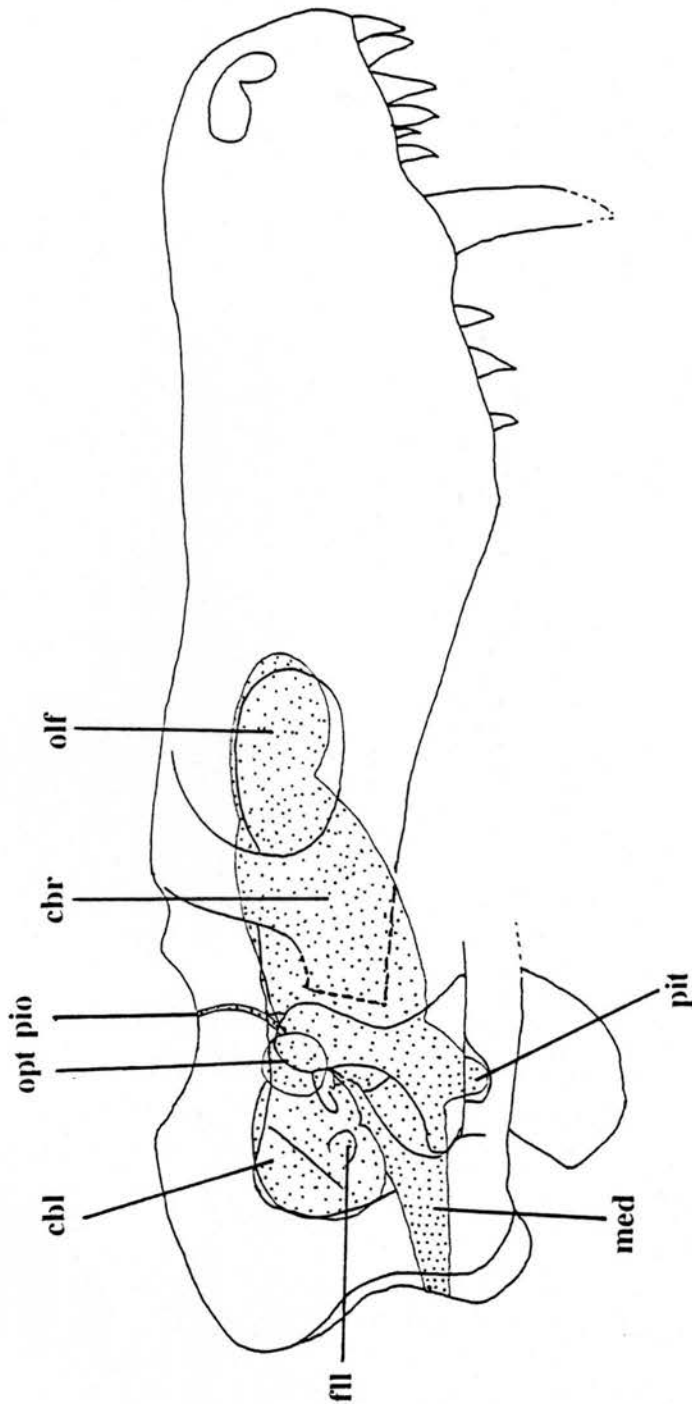


FIGURE 25. Proposed position of the brain in the skull of *Glanosuchus macrops* GS M796. A. Lateral view. B. Dorsal view.

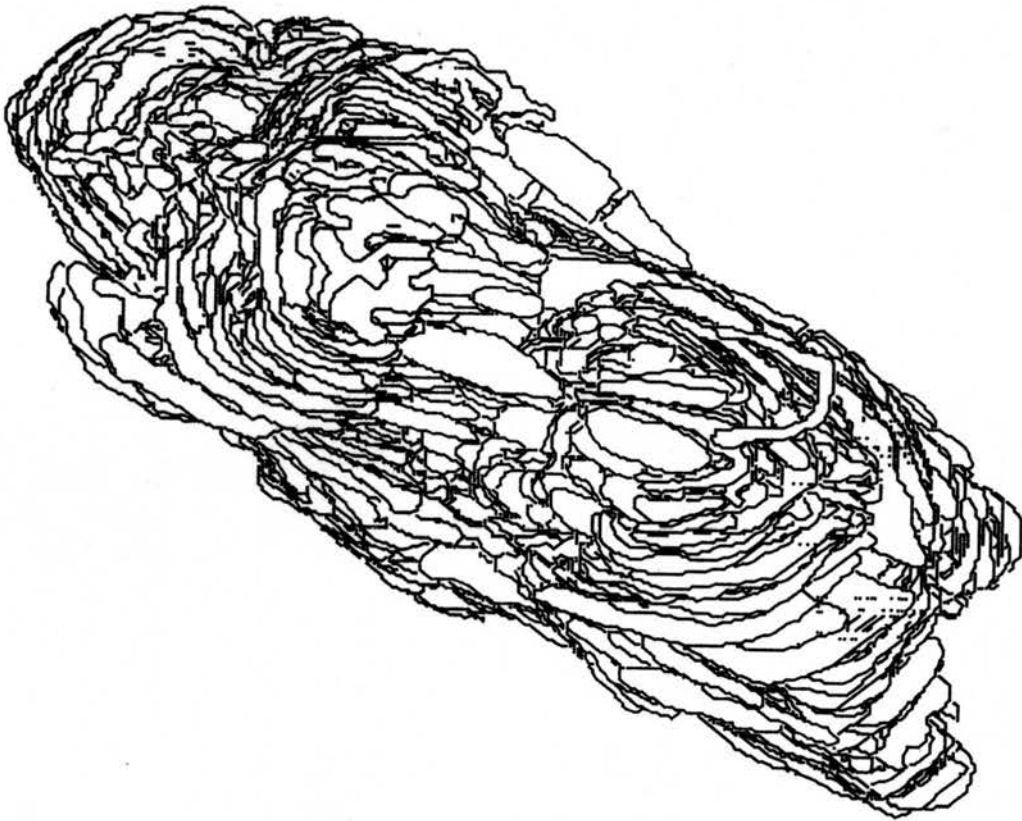


FIGURE 26. A. Reconstruction of the anterior view of the skull of *Glanosuchus macrops* SAM K238a using the computer package PC3D.

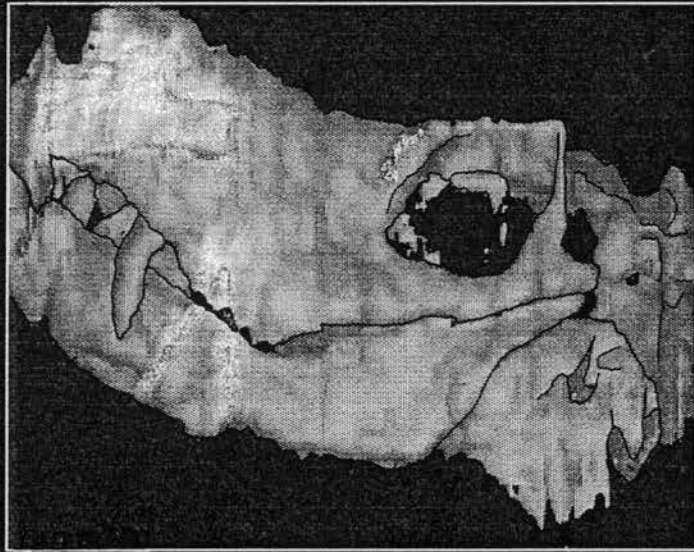
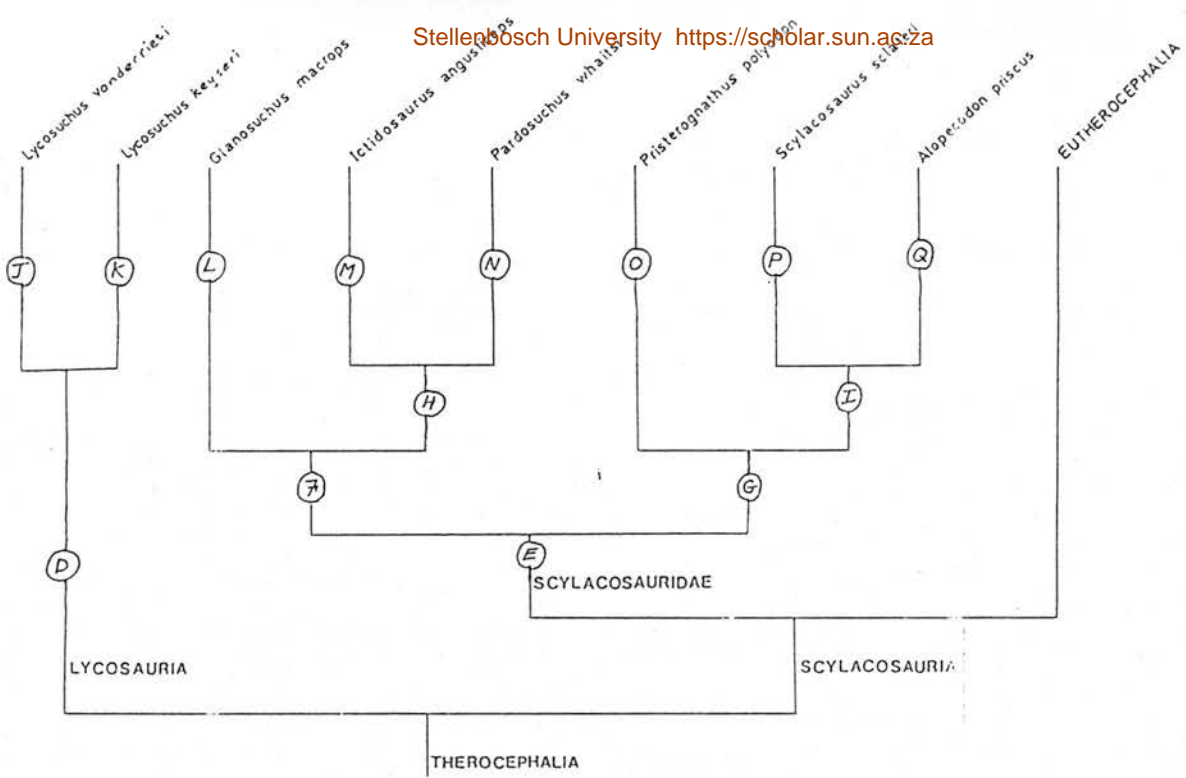


FIGURE 26. B. Reconstruction of the lateral view of the skull of *Glanosuchus macrops* K238a using the computer package IDL.



Cladogram depicting subdivision of the Lycosauria and Scylacosauria. D = 5 upper incisors, E = 6-7 upper incisors, F = 6 upper incisors, G = 7 upper incisors, H + I = precannines present, J = ventral maxillary flange present, K = ventral maxillary flange absent, L + O = precannines lacking, M + P = 1 precannine present, N + Q = 2 precannines present.

FIGURE 27. Cladogram subdividing the early Therocephalia (after Van den Heever 1987).

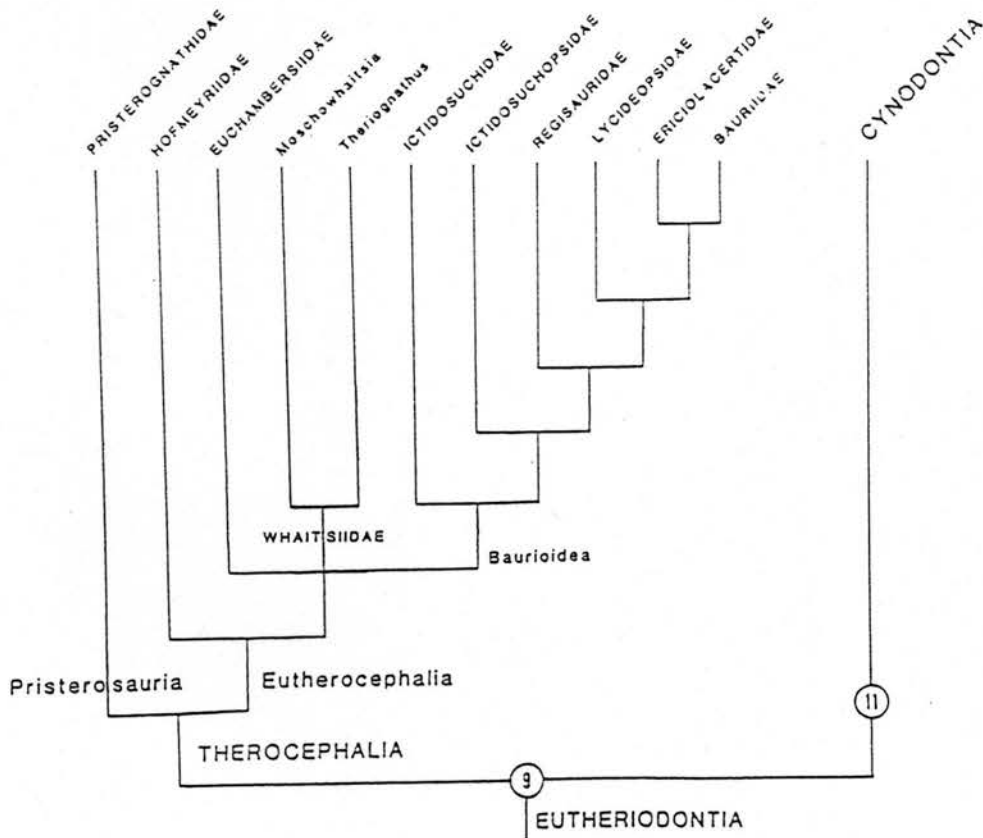
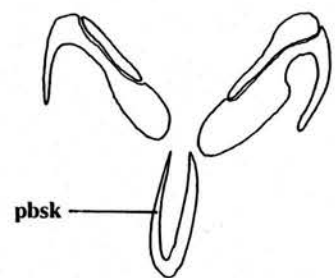
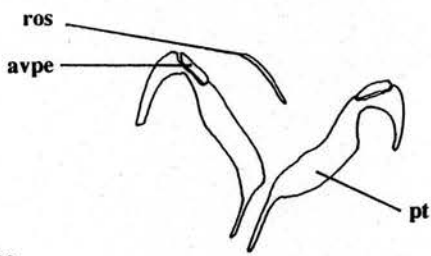
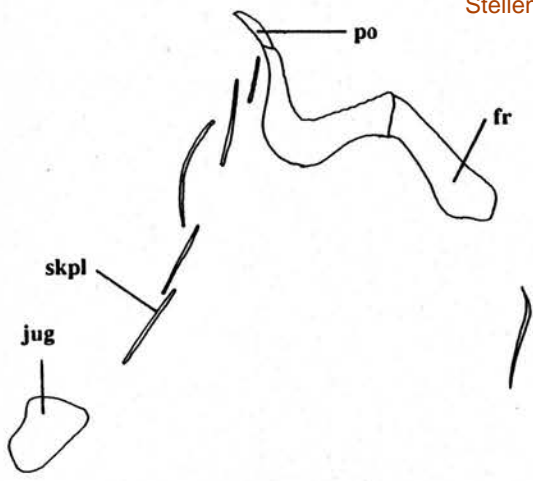


FIGURE 28. Cladogram subdividing the Therocephalia (after Hopson and Barghusen 1986).

SECTIONS OF THE BRAINCASE

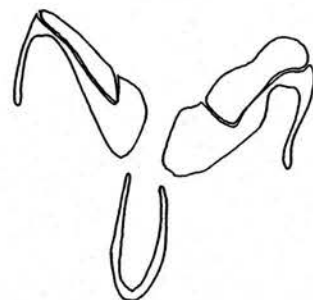
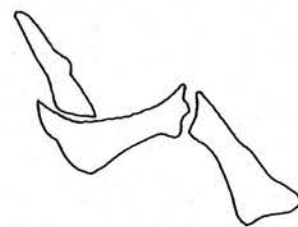
***Glanosuchus macrops* SAM K238a**

Sections 380-528



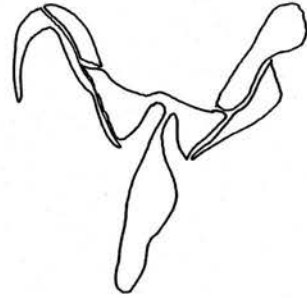
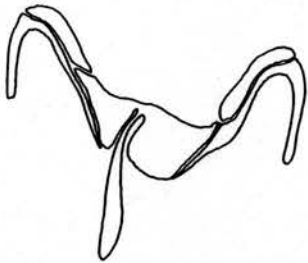
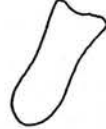
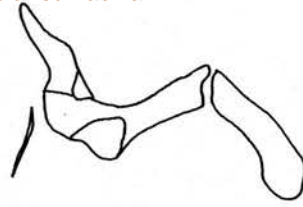
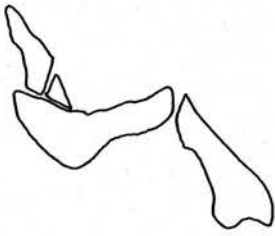
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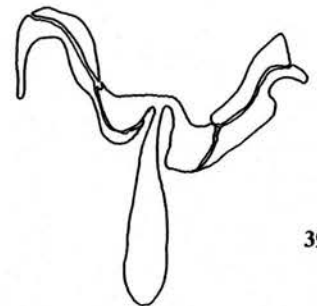
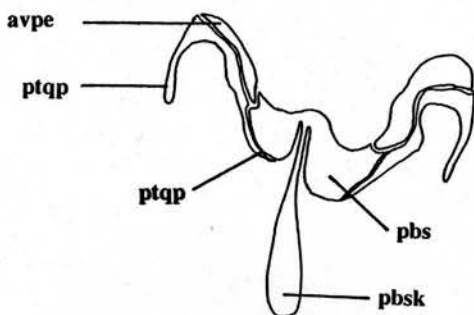
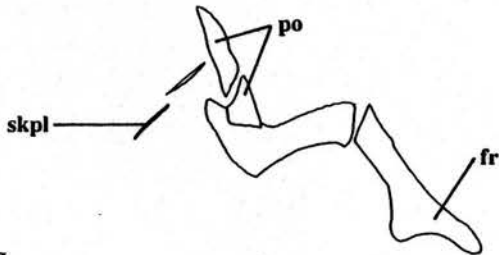
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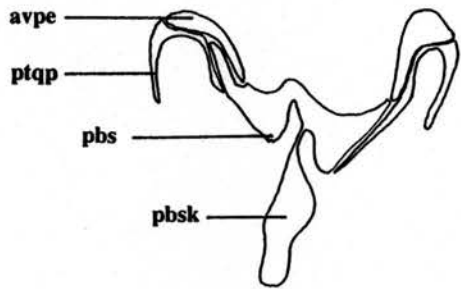
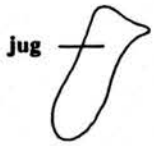
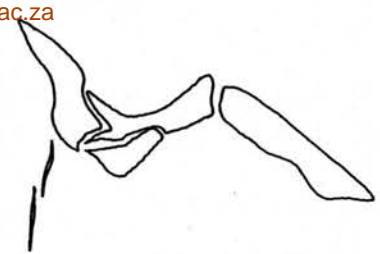
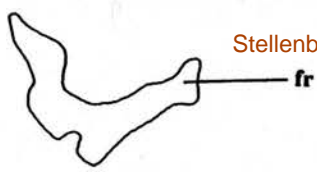
395

396



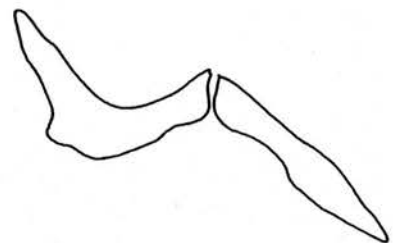
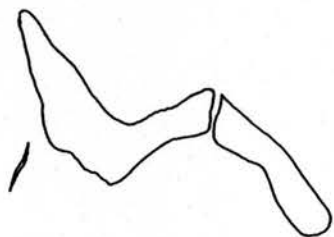
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394



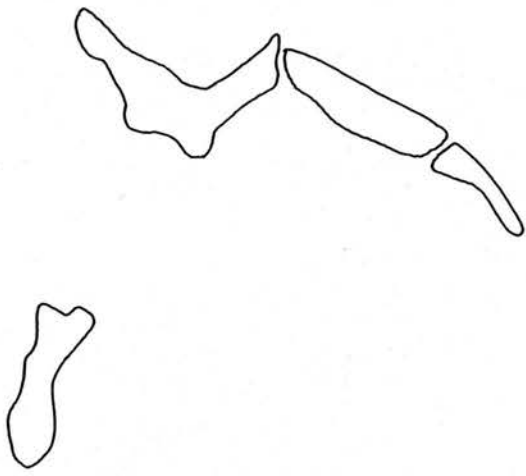
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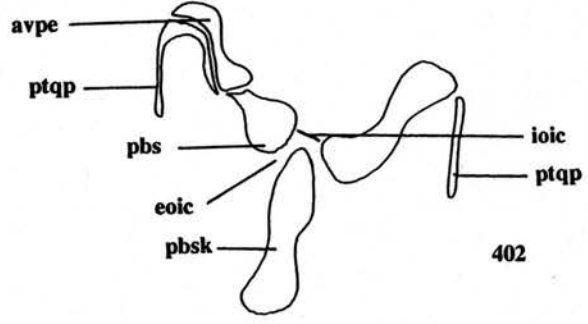
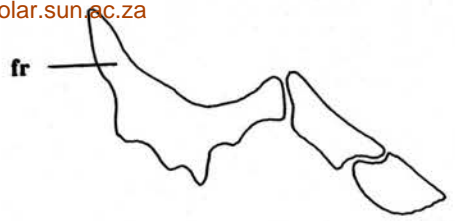


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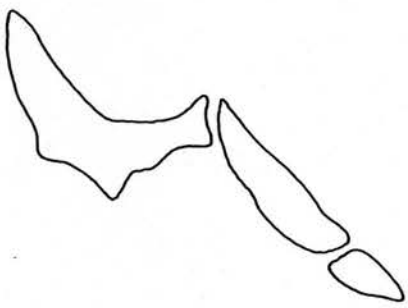
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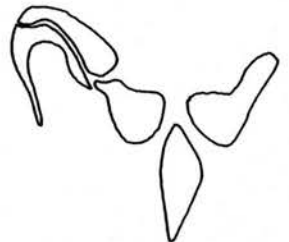
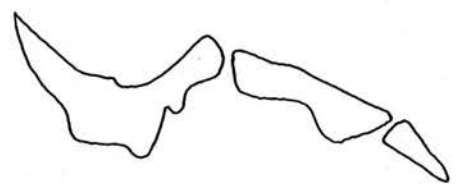
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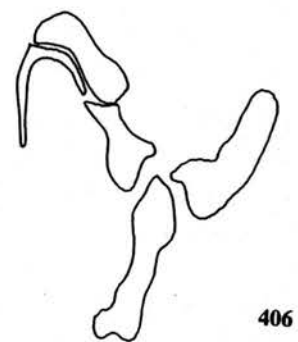
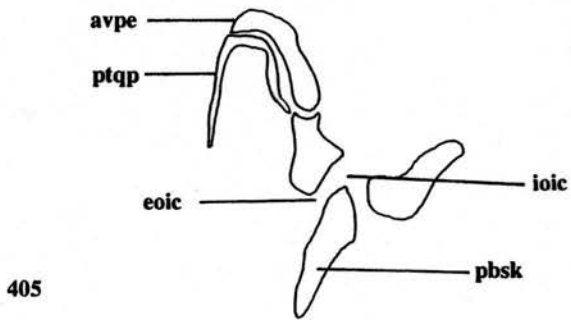
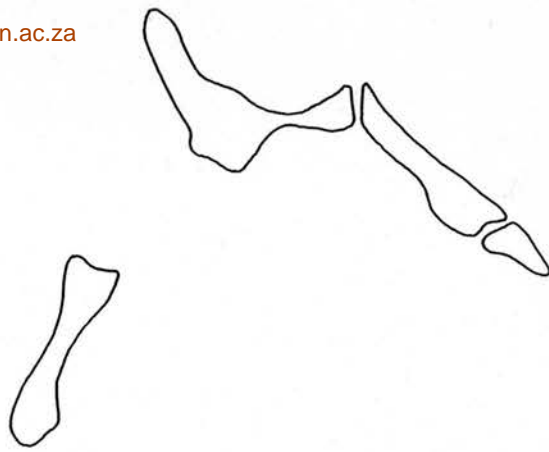
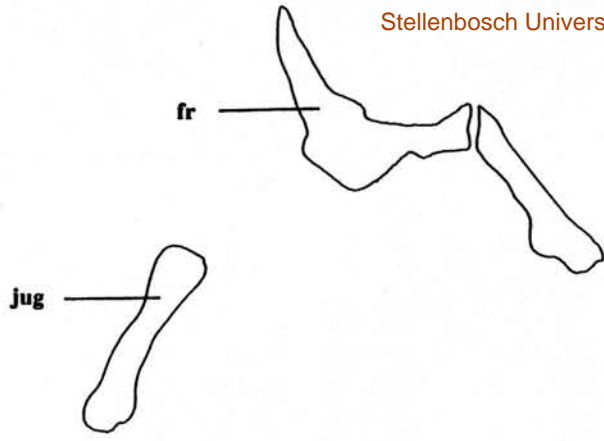
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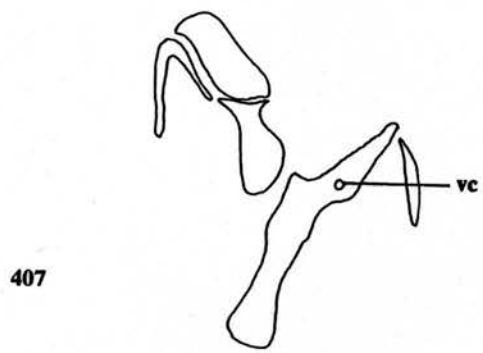
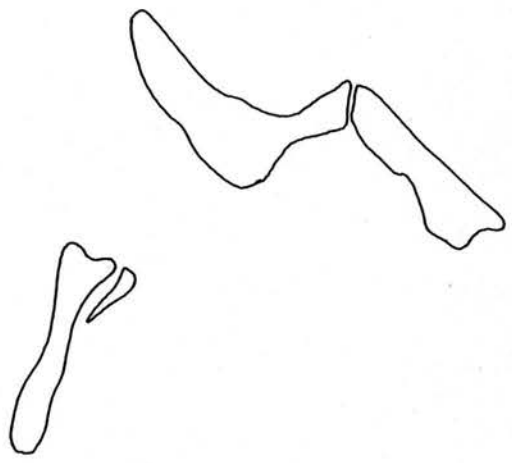
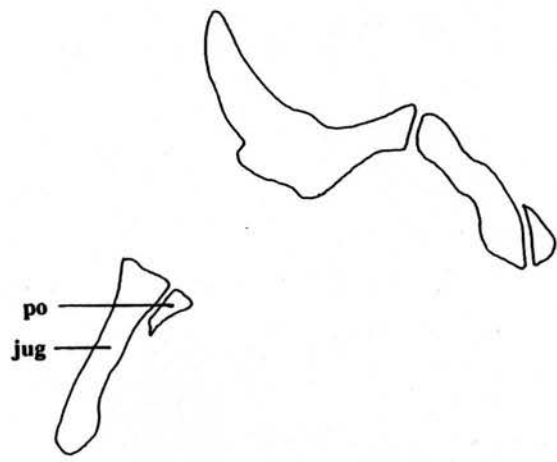
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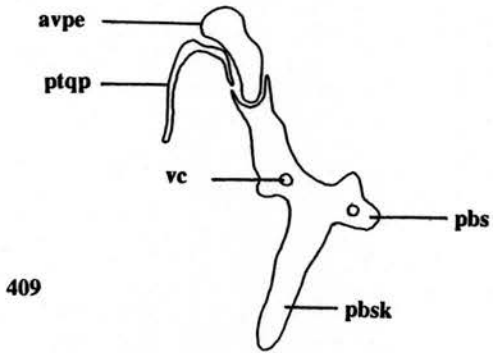
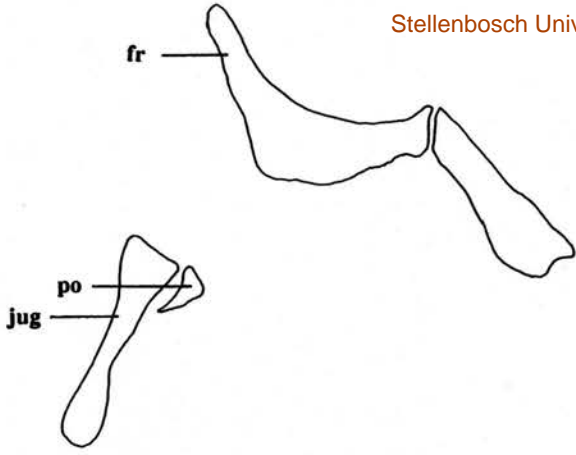
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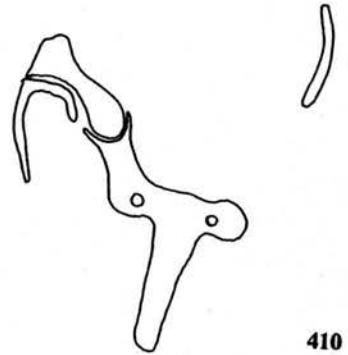
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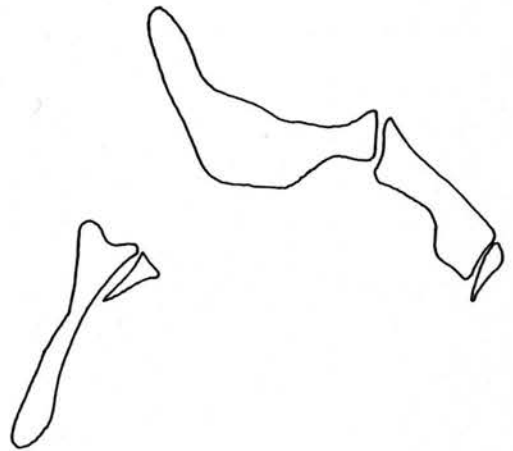
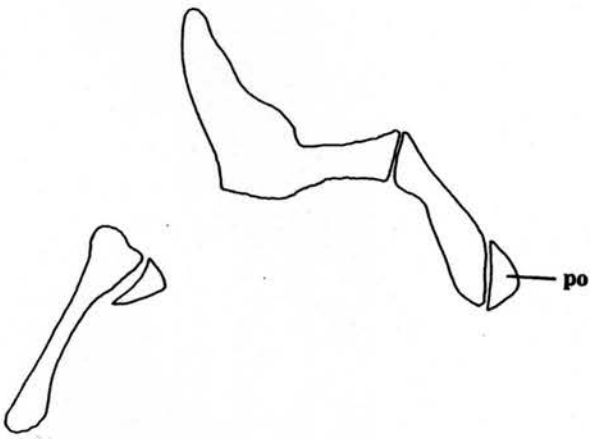
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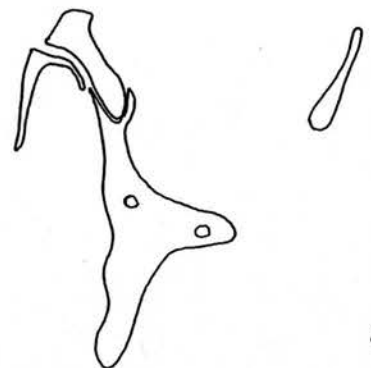
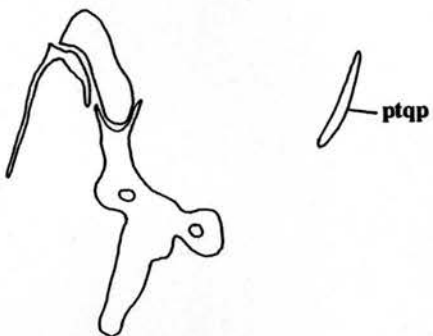
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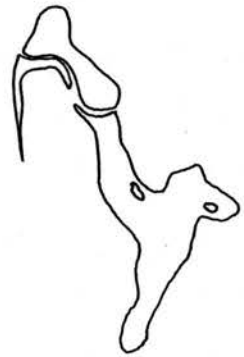
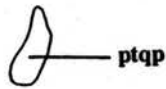
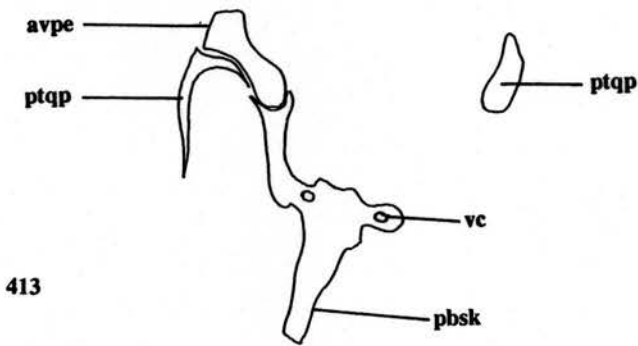
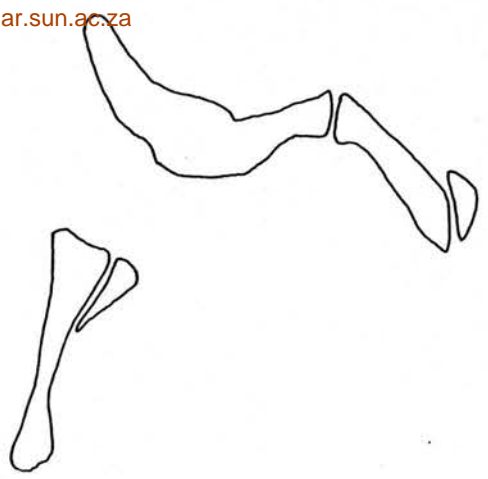
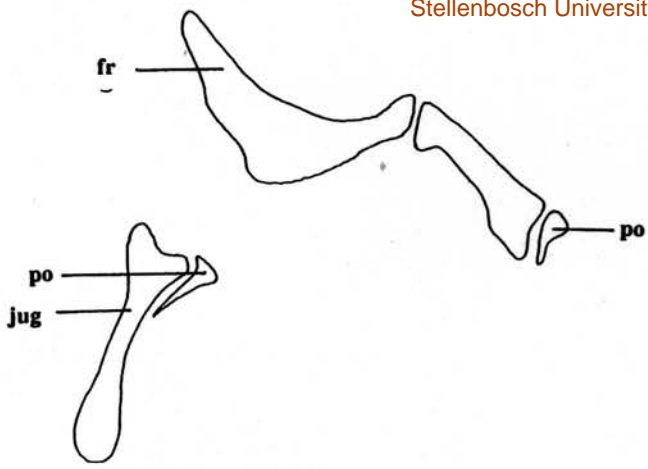
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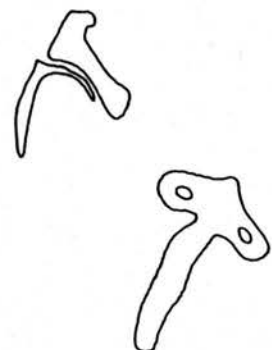
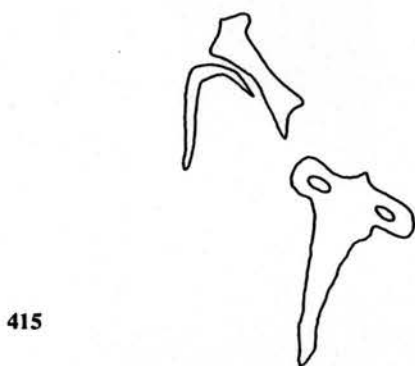
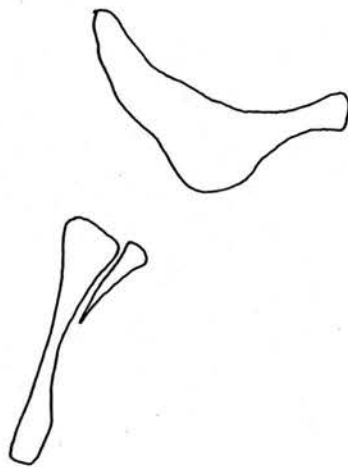
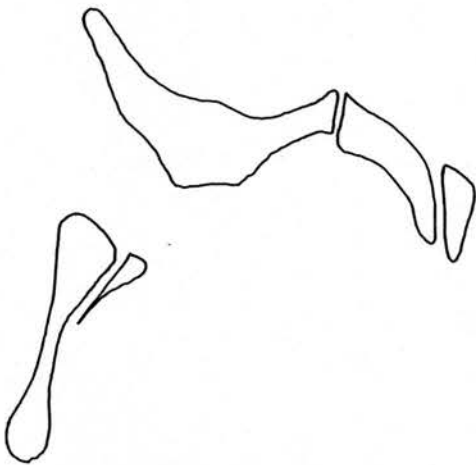
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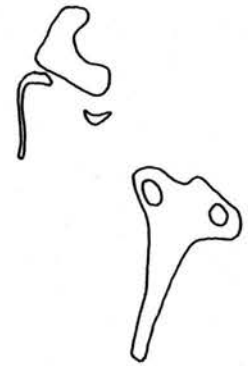
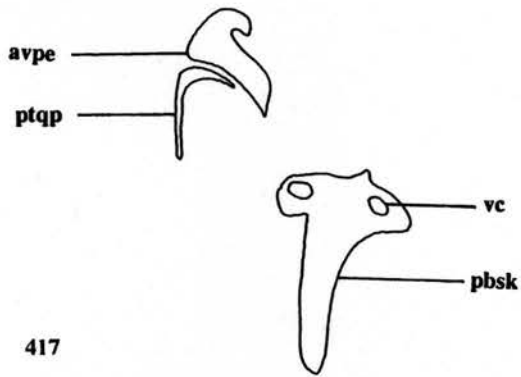
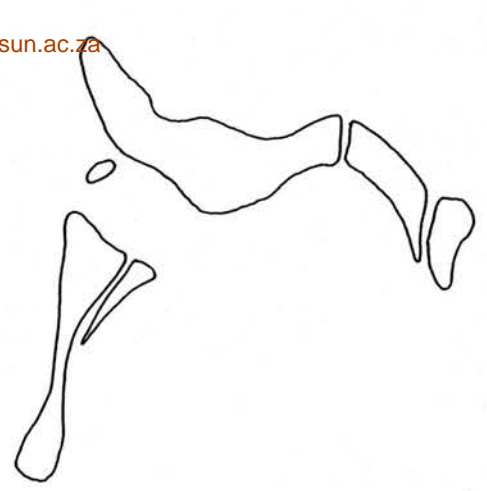
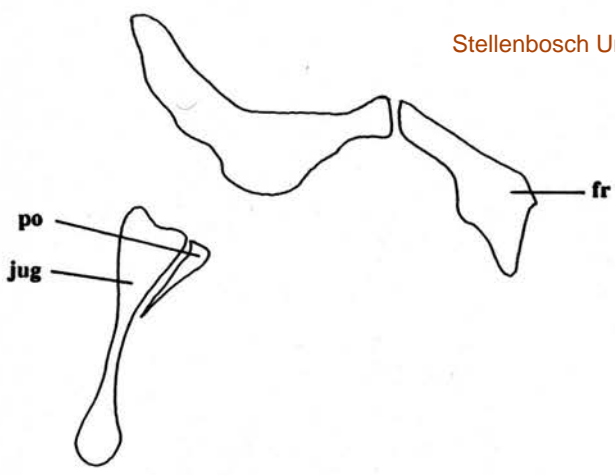
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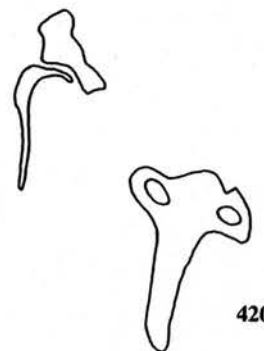
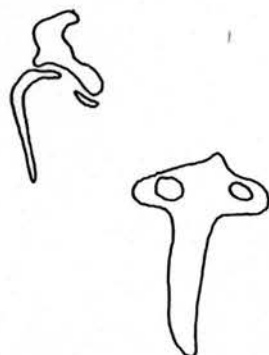
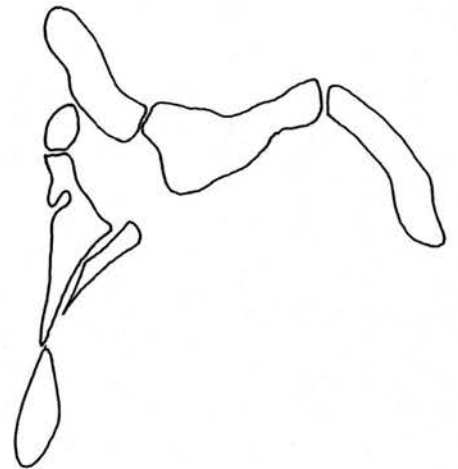
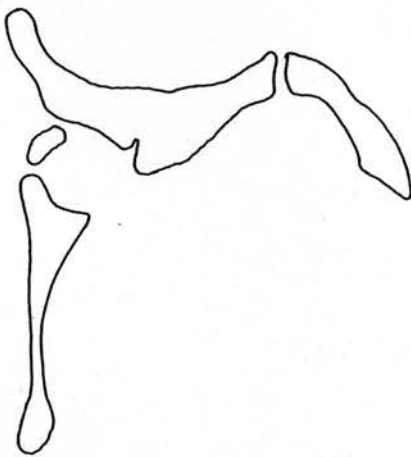
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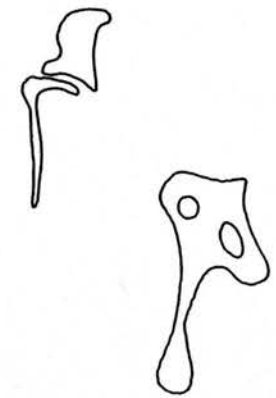
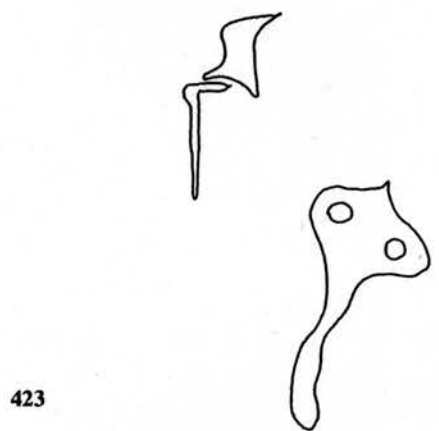
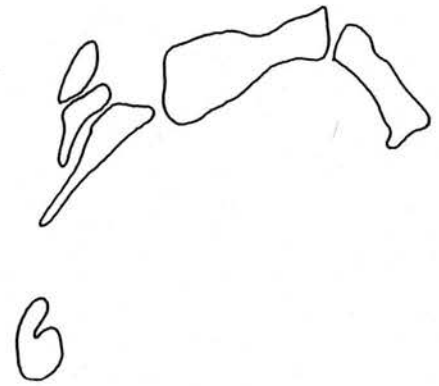
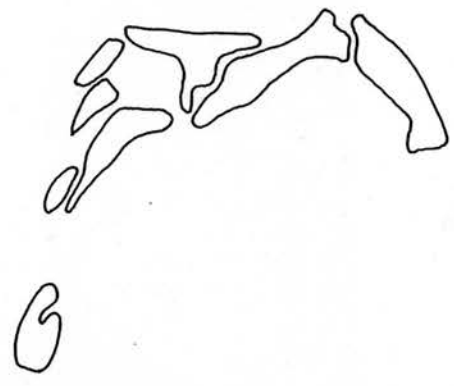
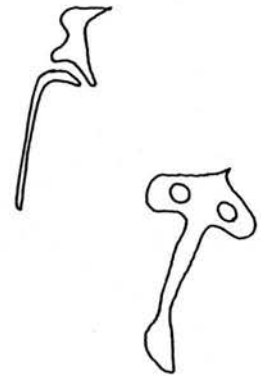
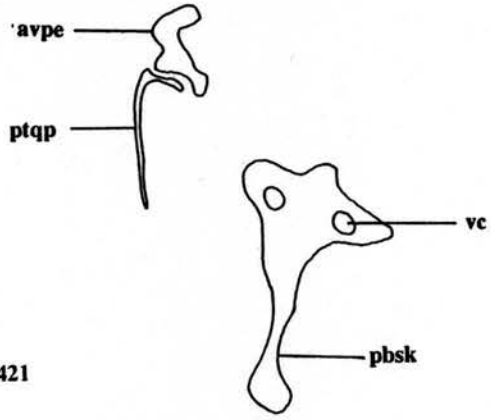
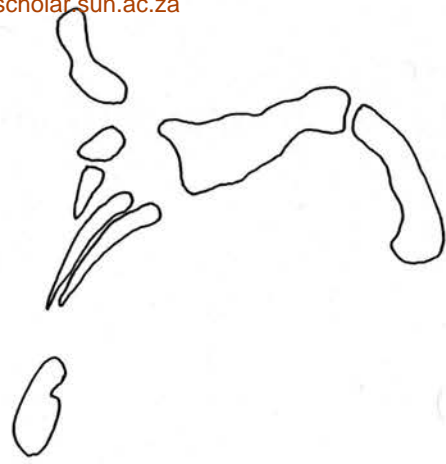
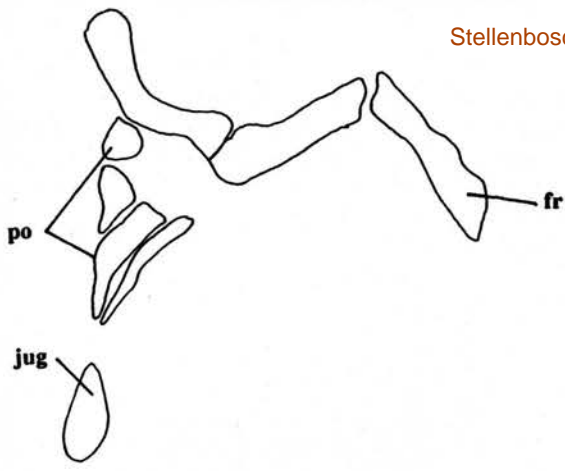


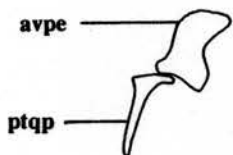
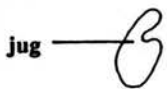
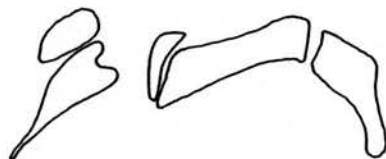
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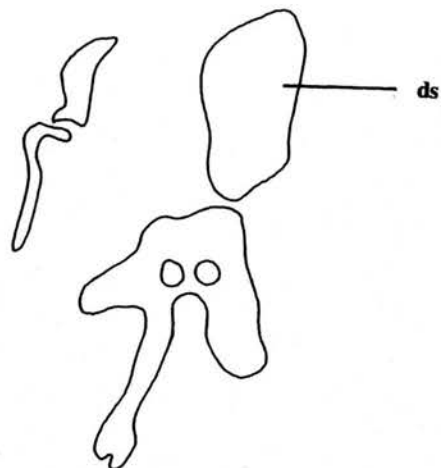
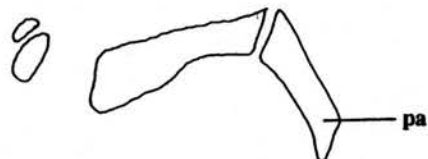
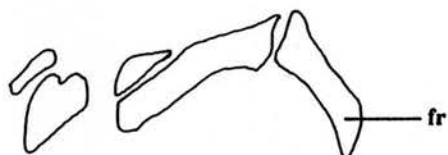
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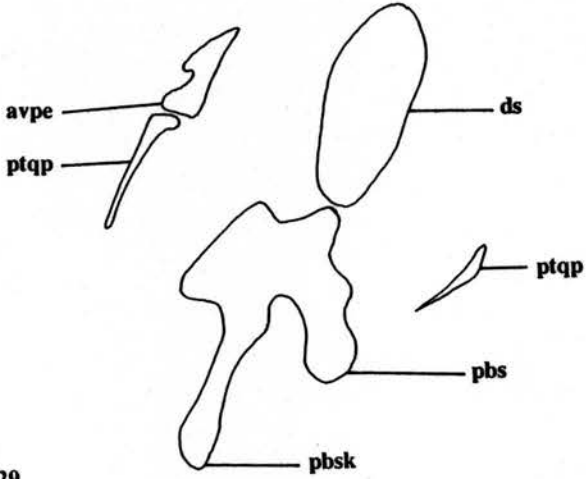
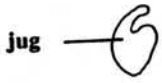
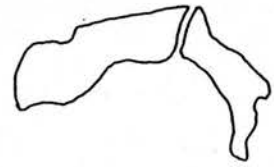
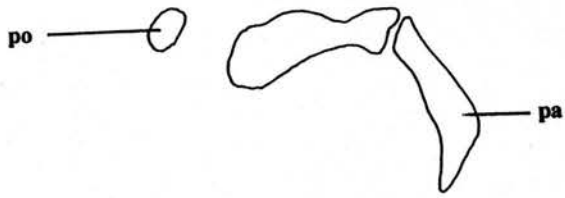


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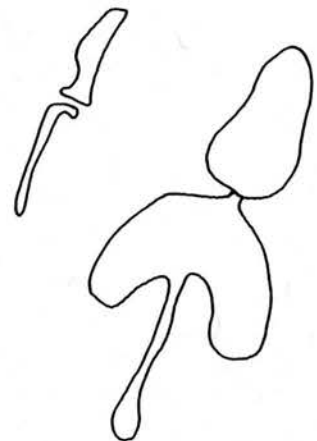
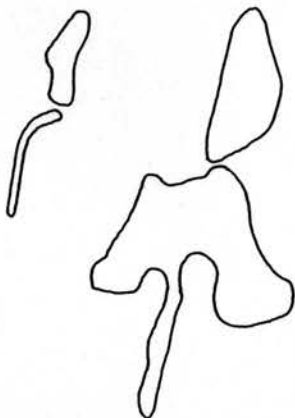
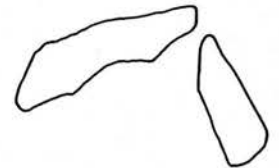
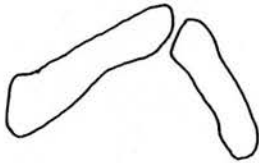
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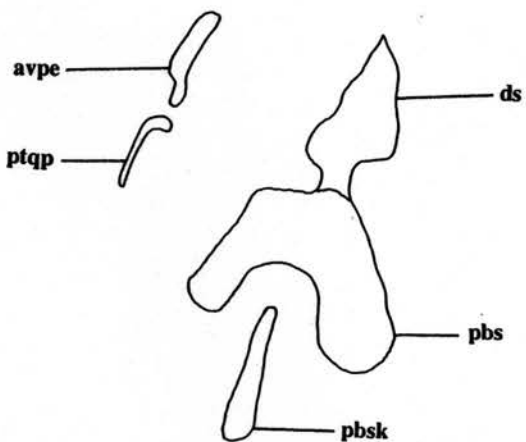
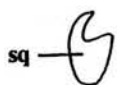
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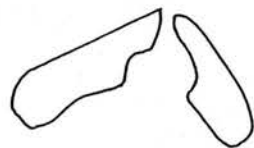
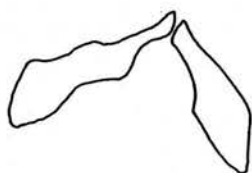
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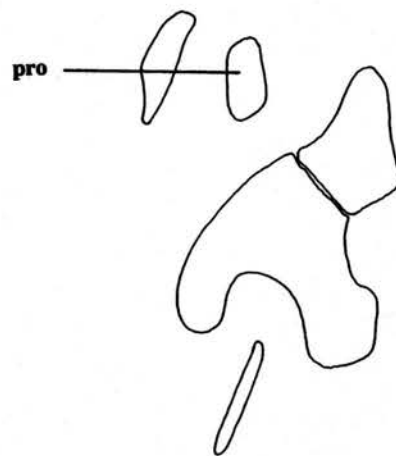
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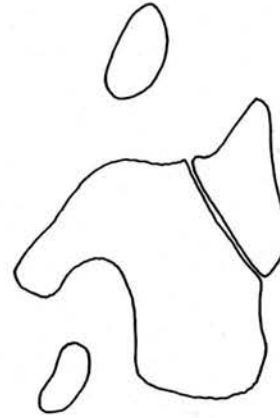
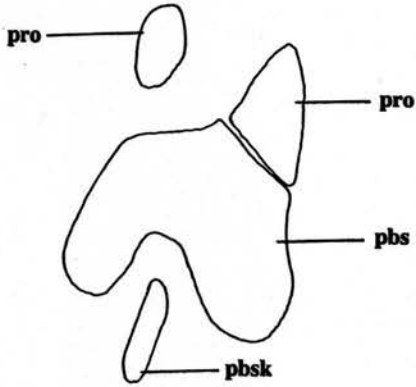
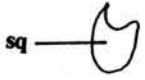
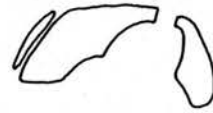
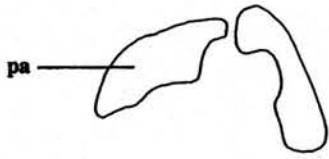
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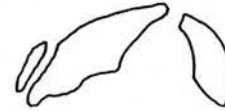
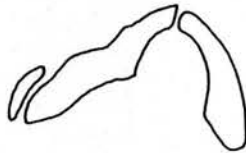


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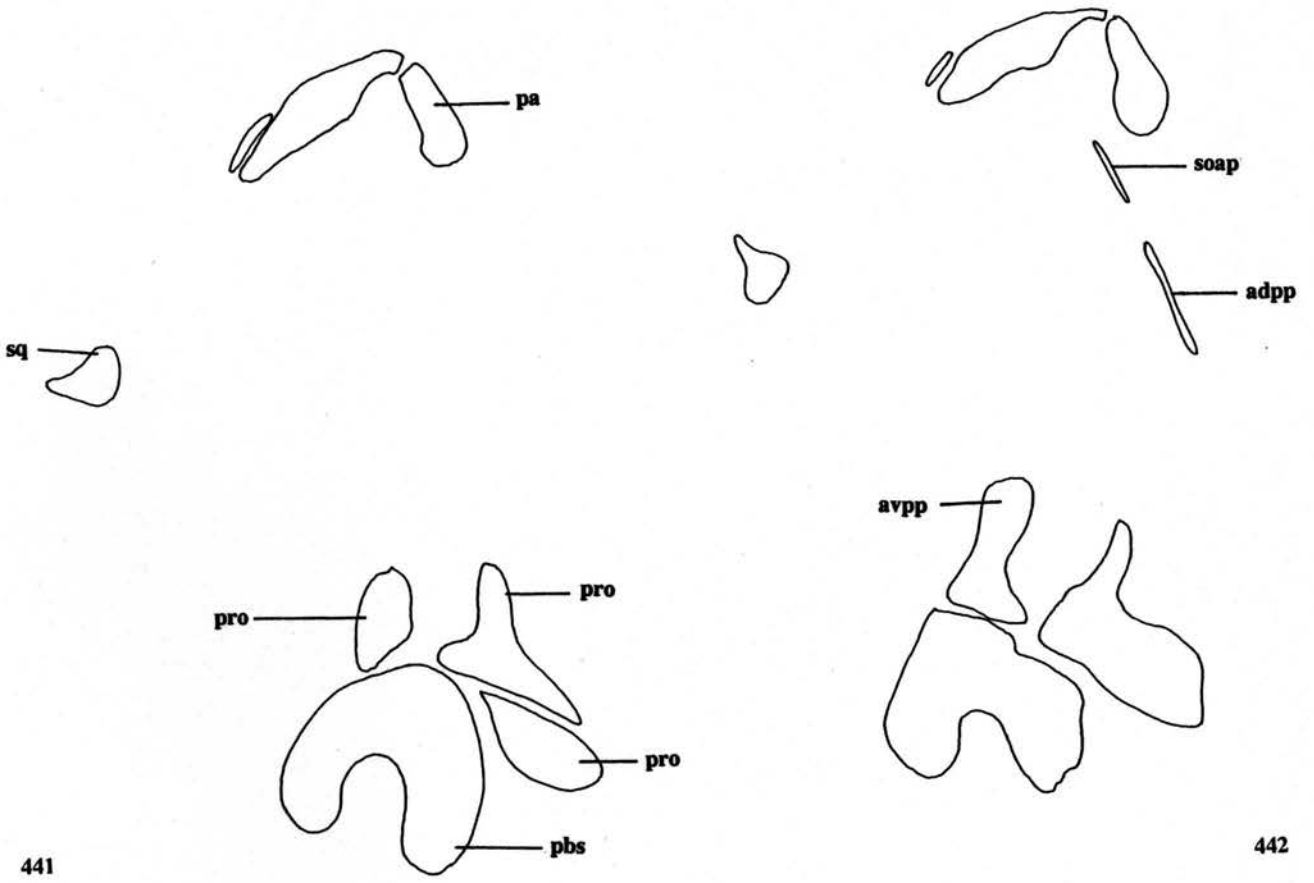
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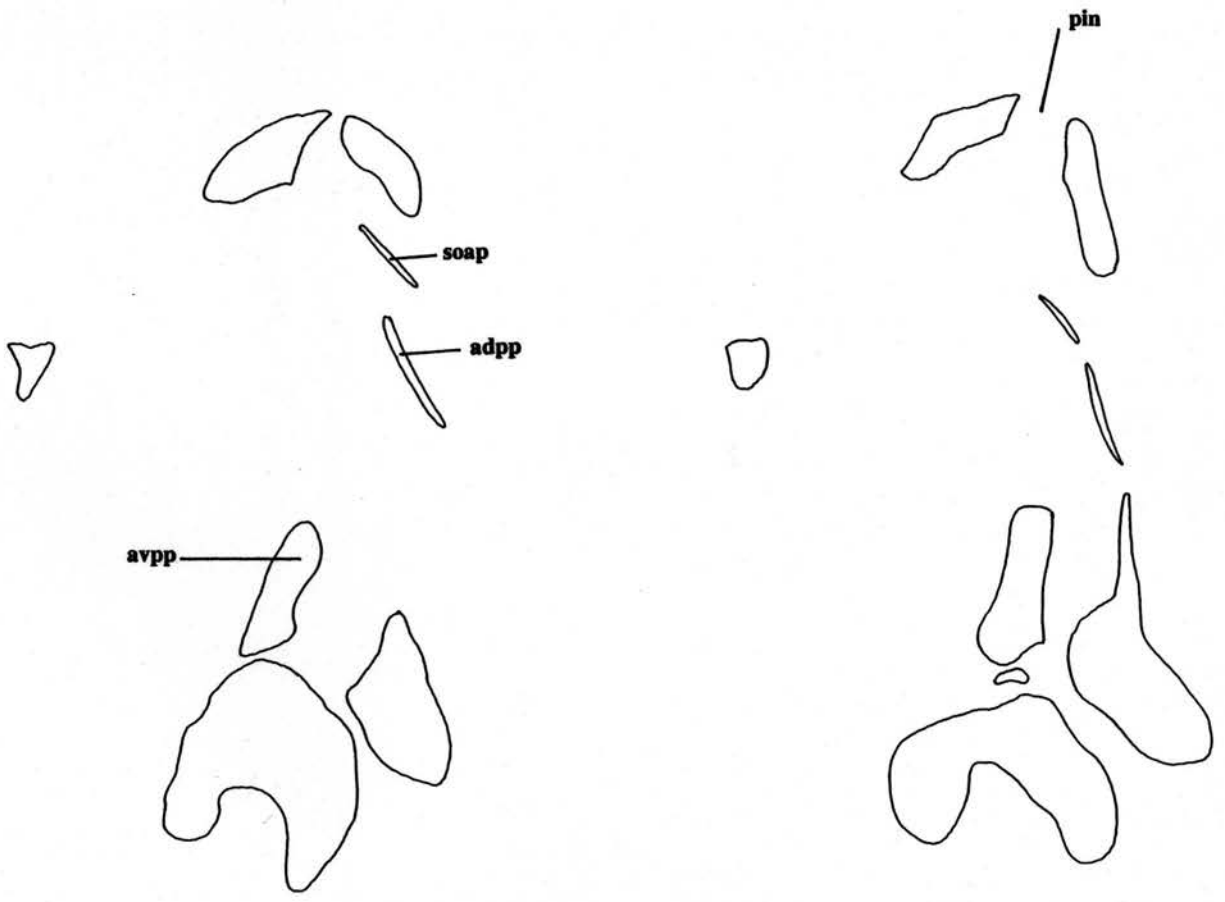
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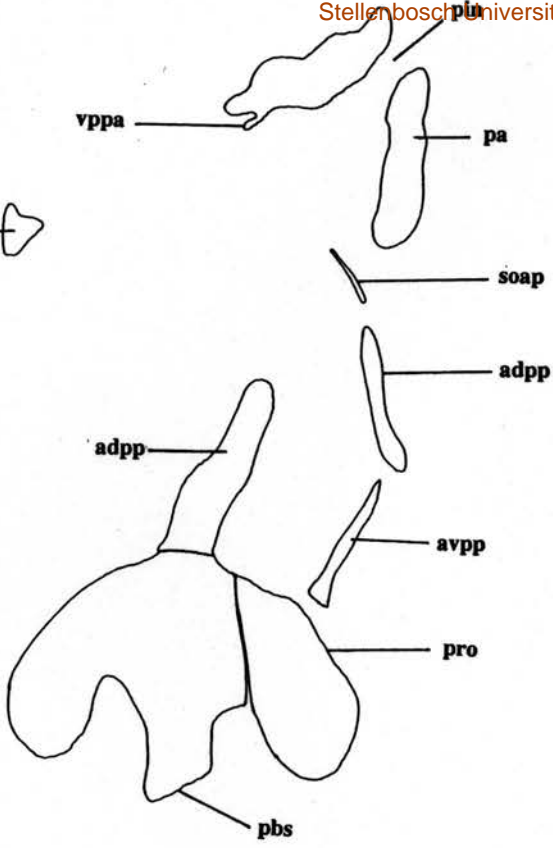
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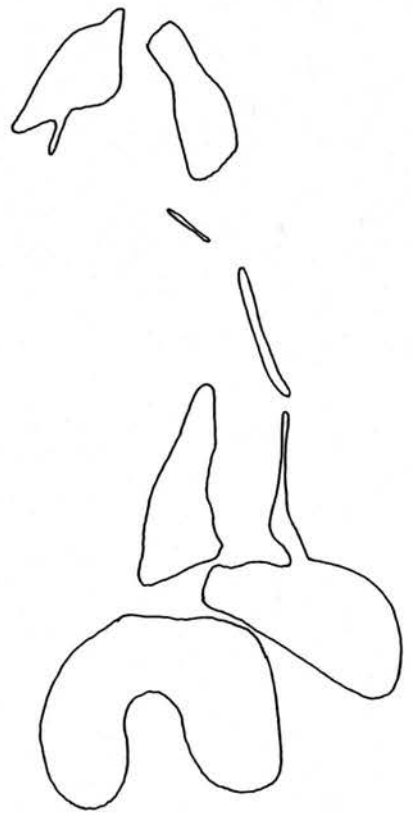
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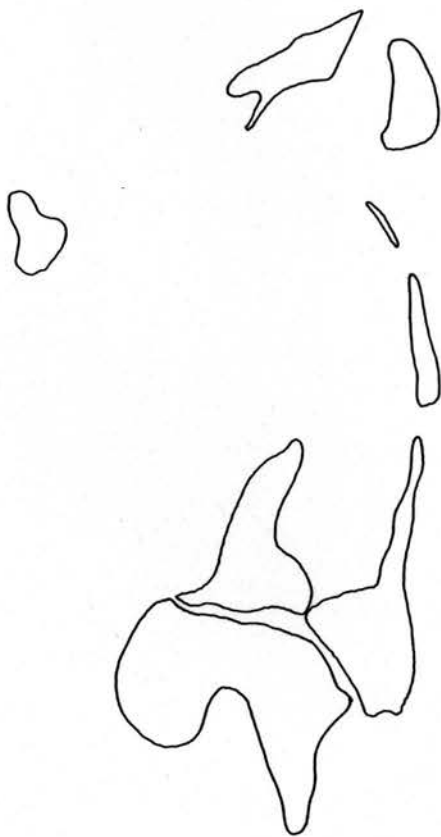
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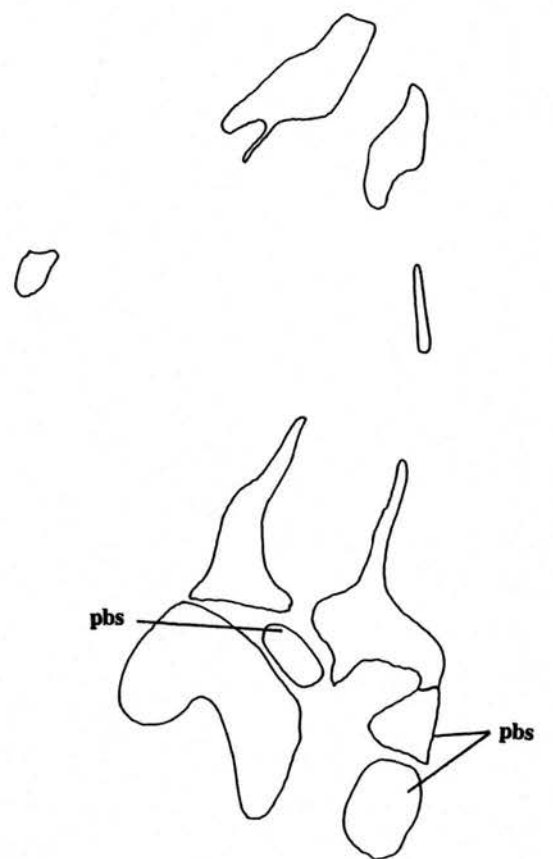
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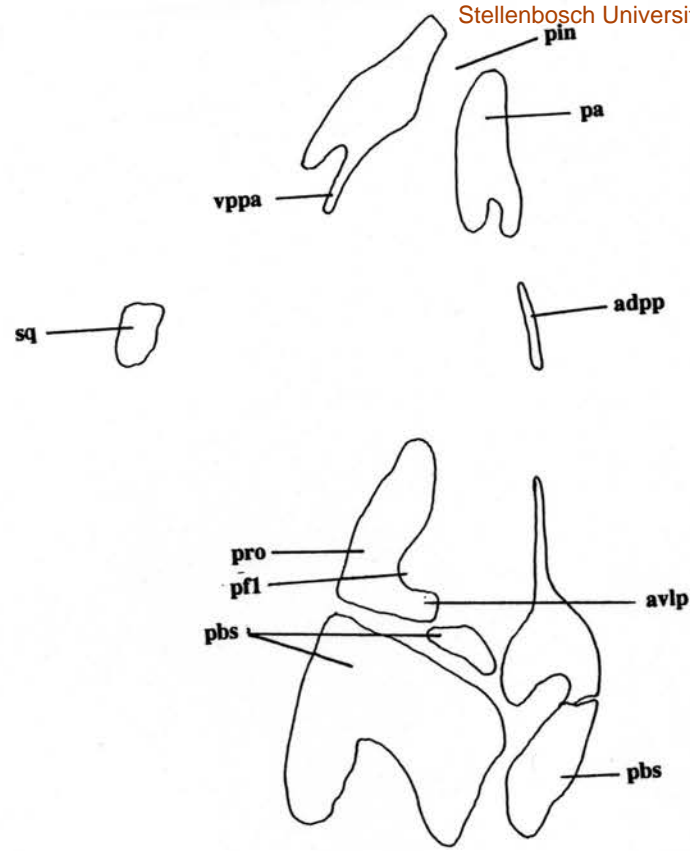
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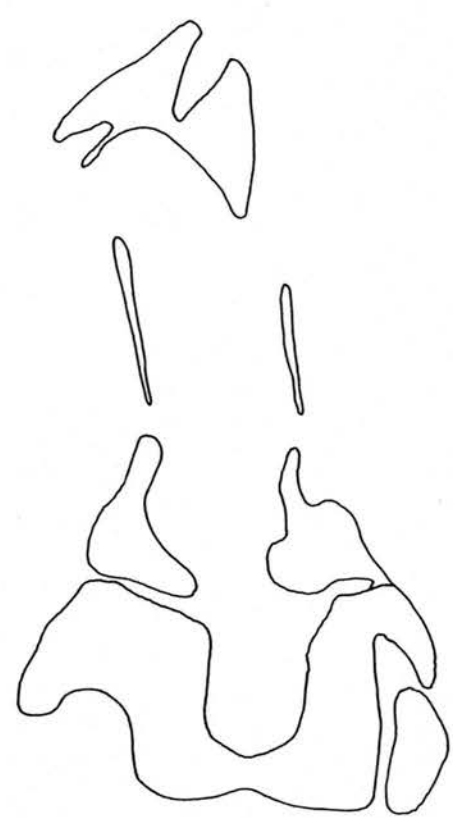
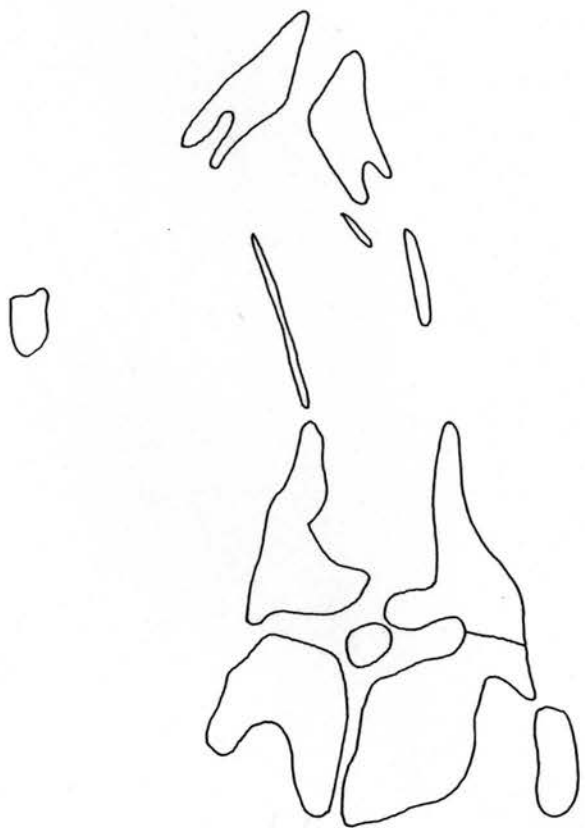


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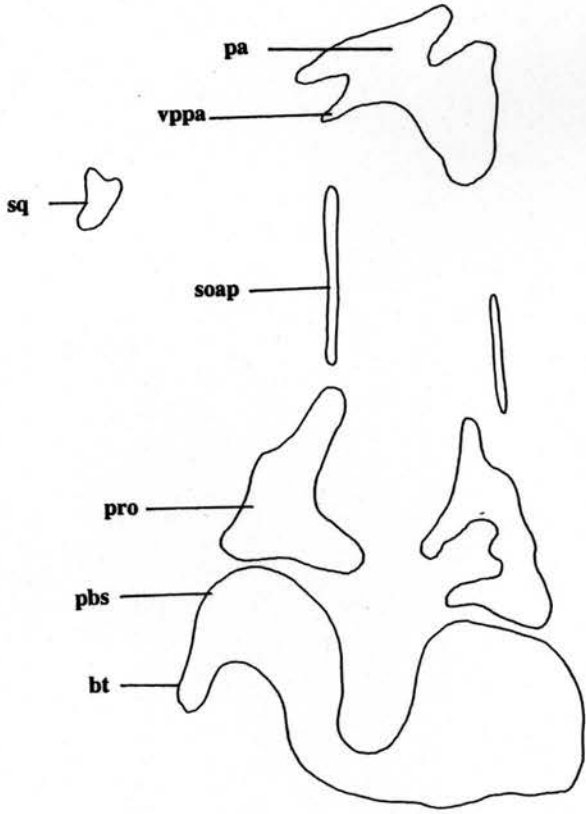
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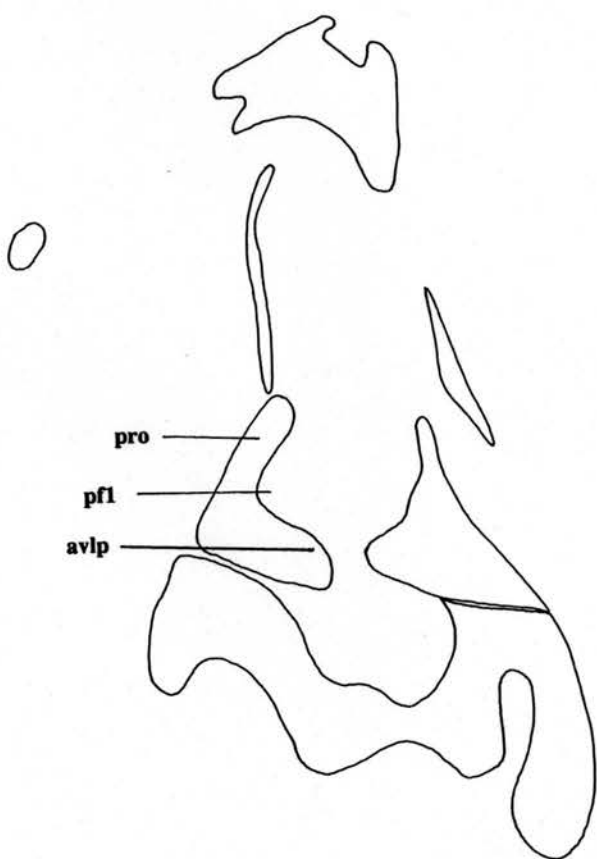
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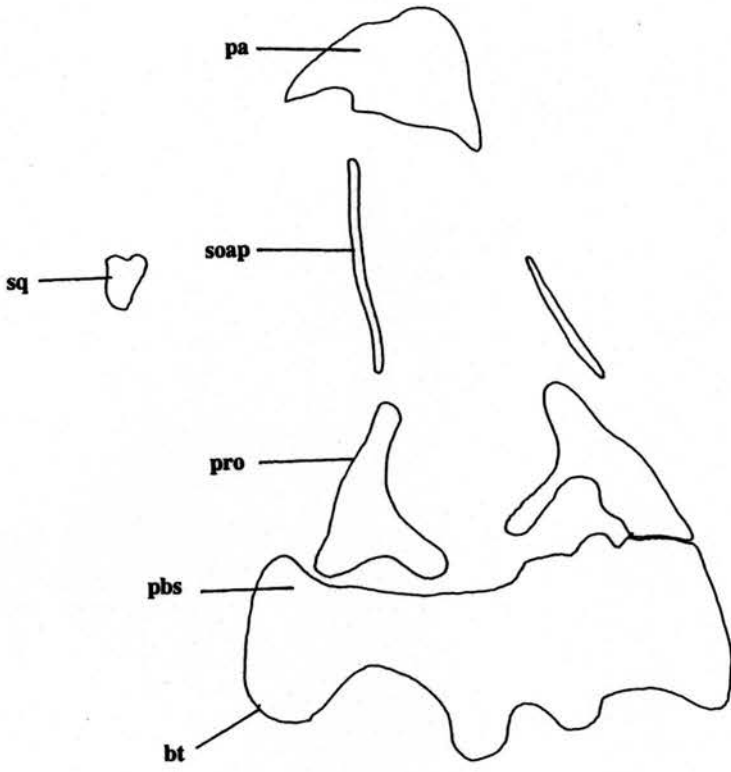
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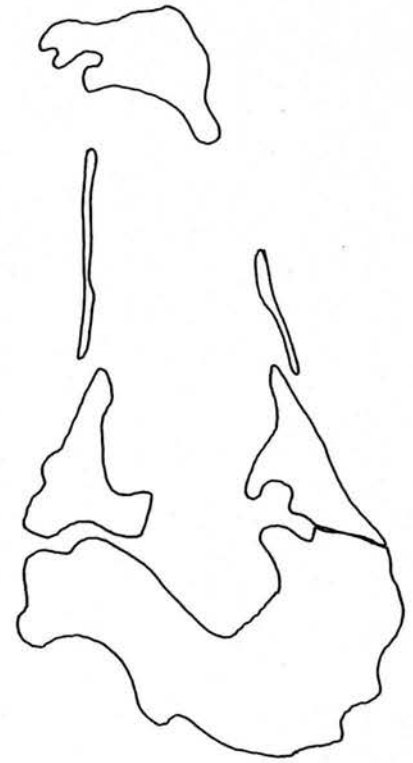
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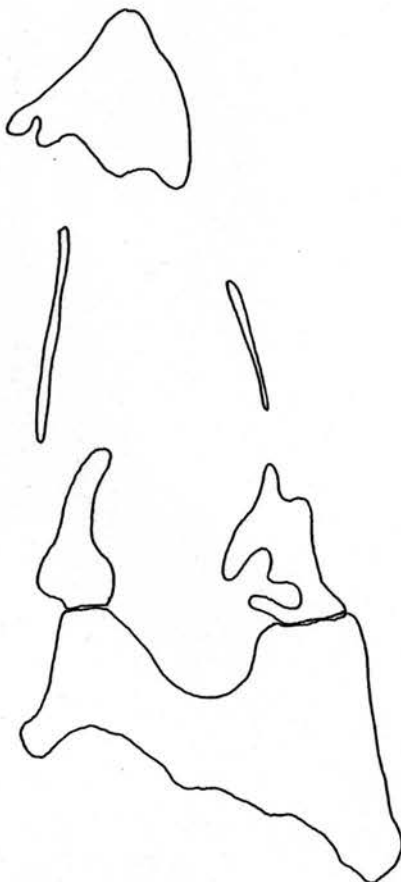
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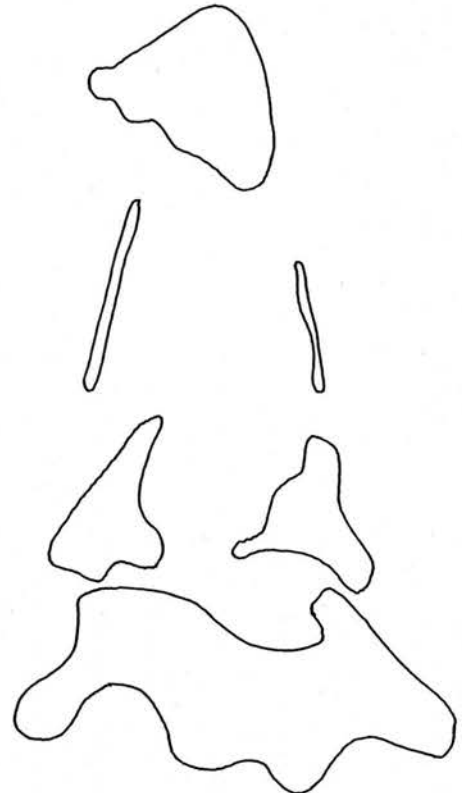
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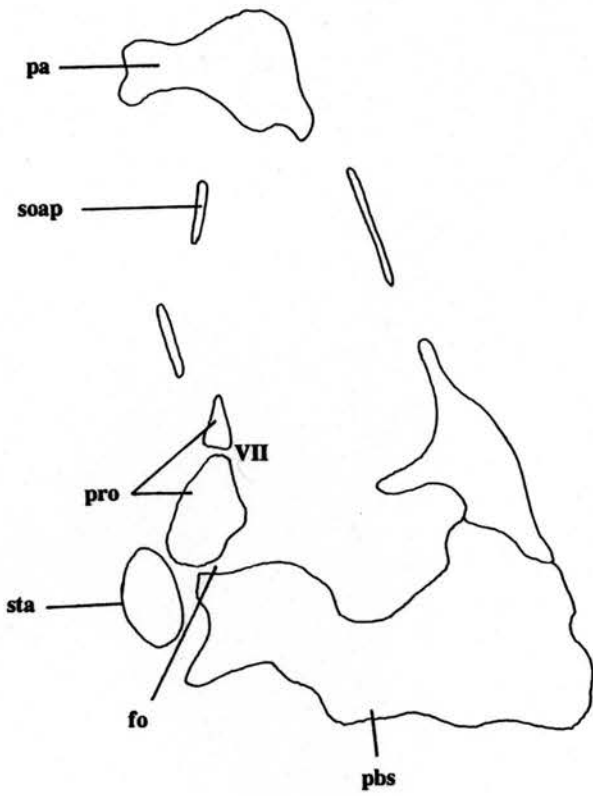
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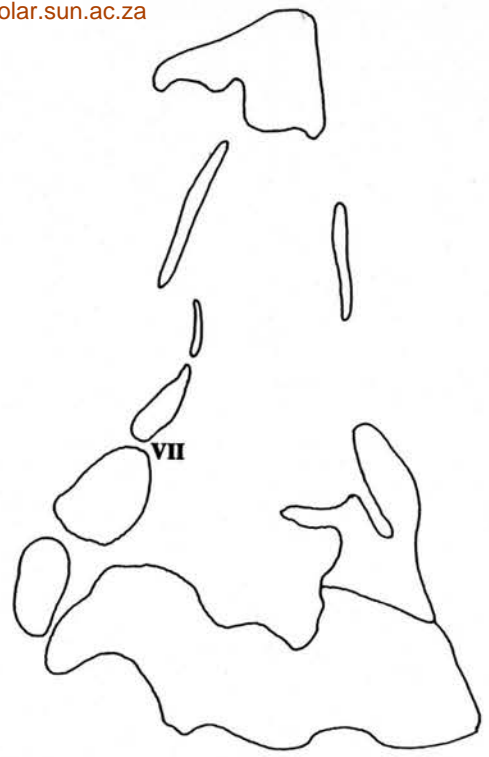
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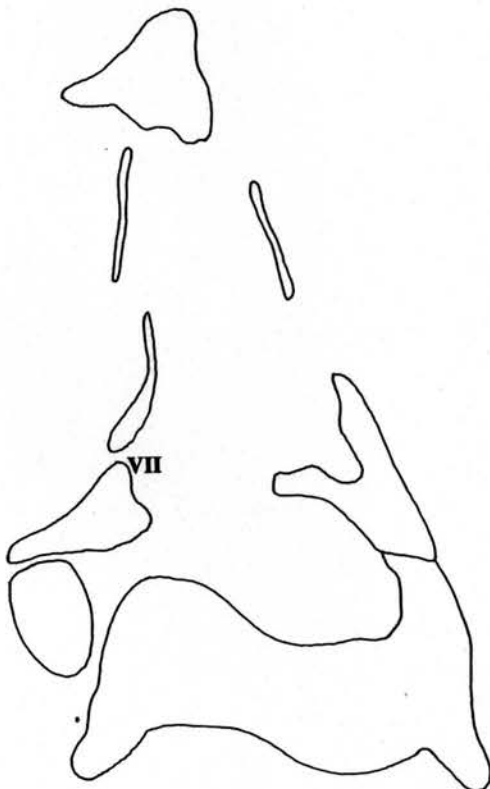
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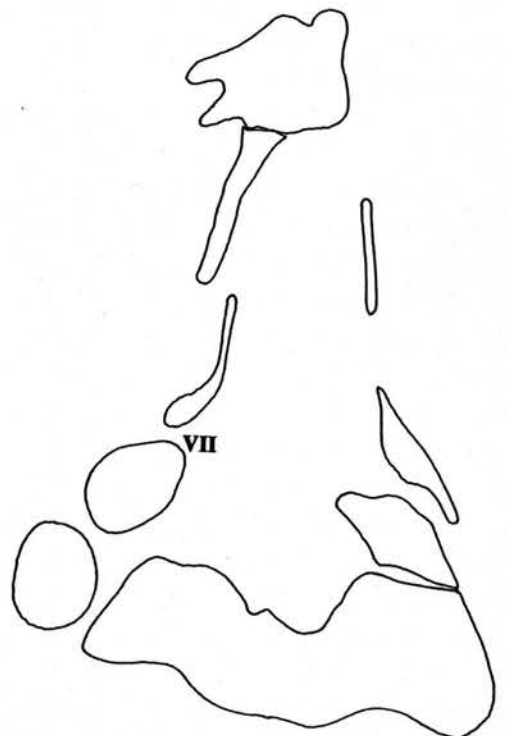
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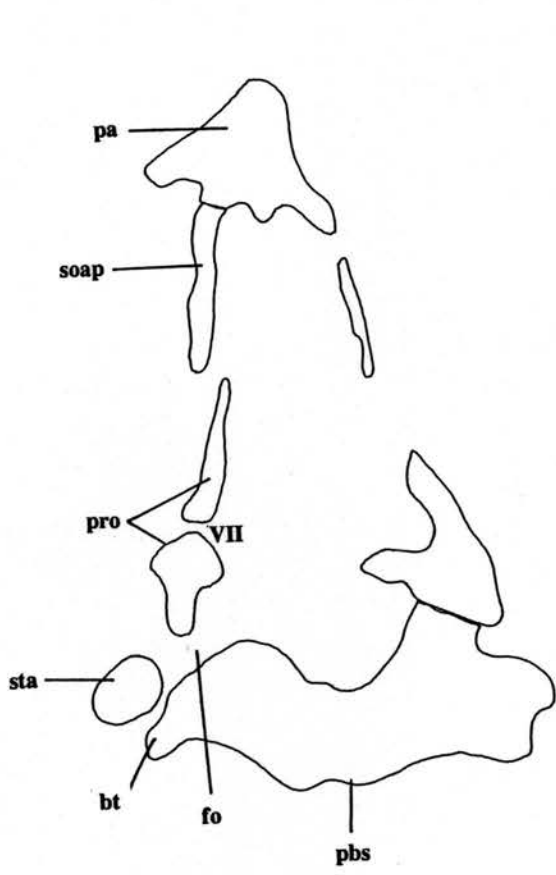
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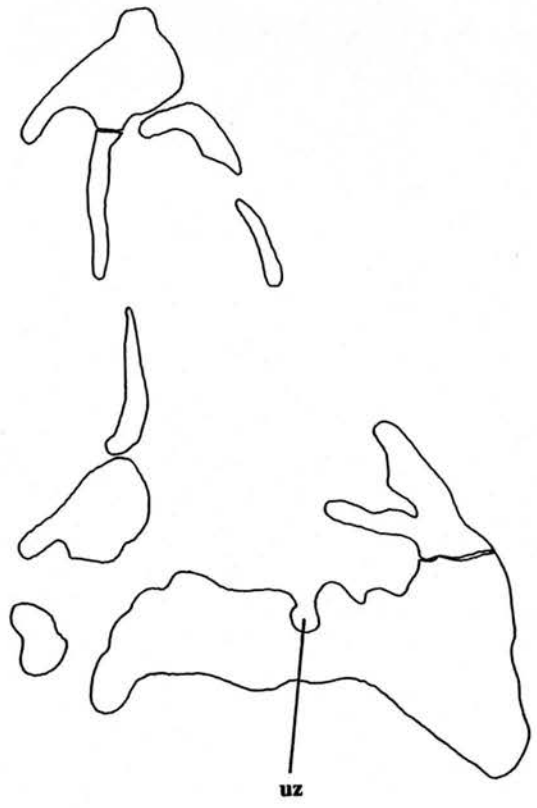
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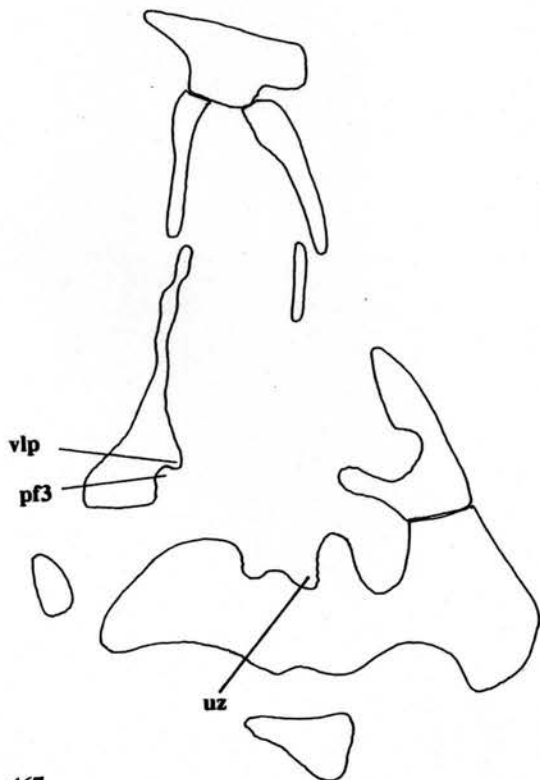
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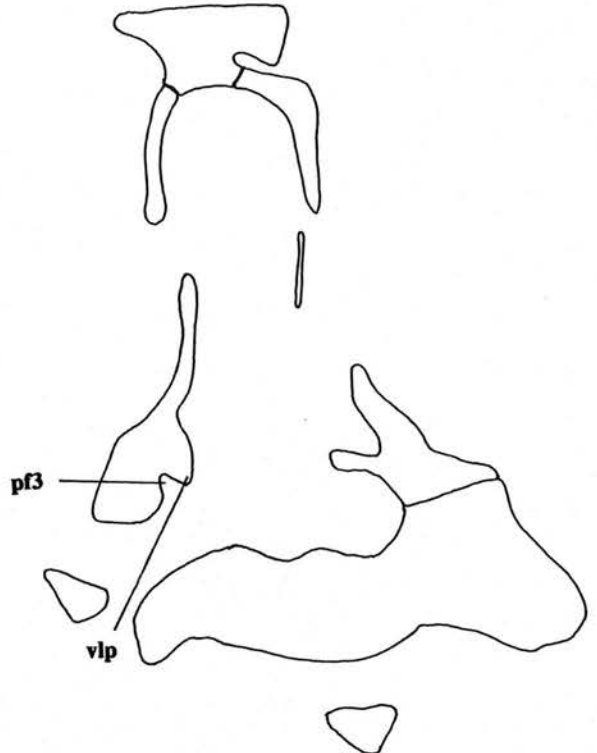
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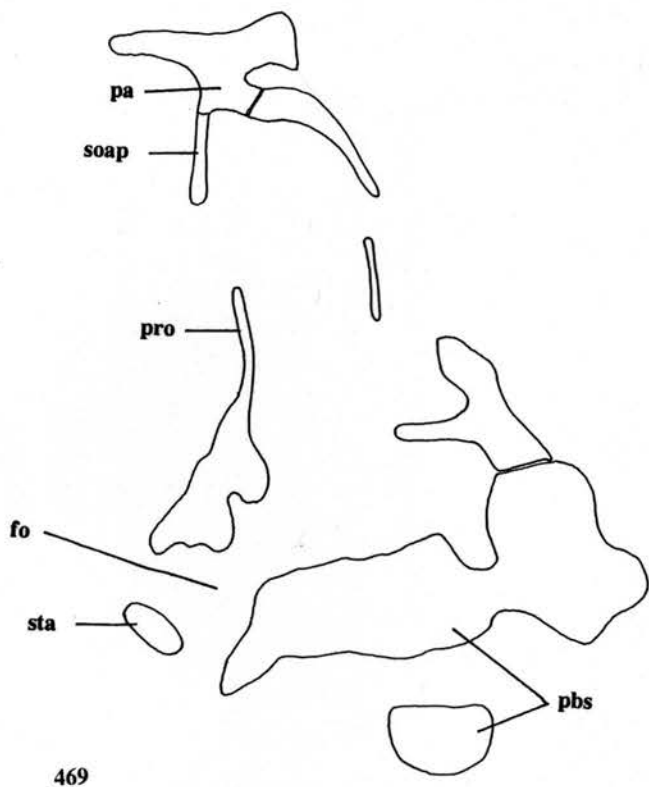
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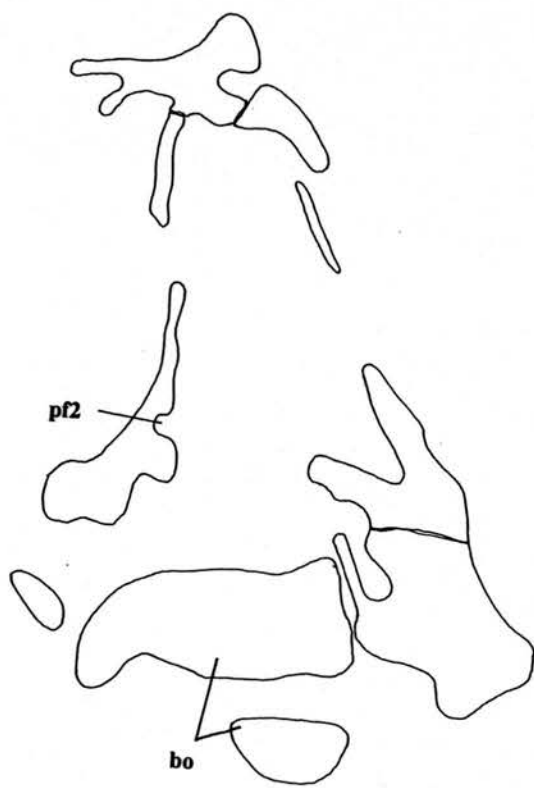
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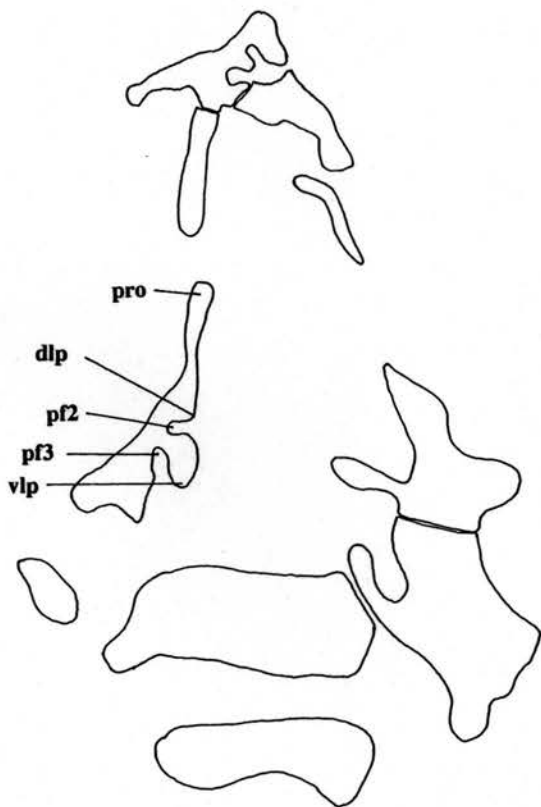
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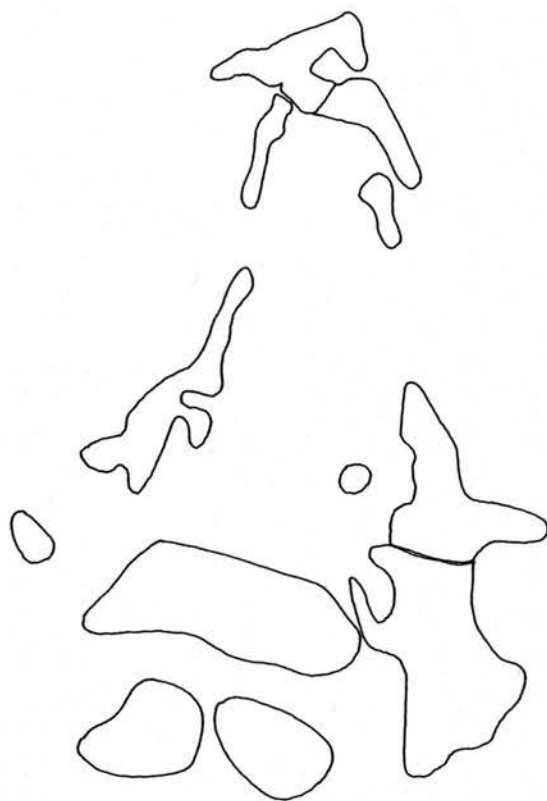
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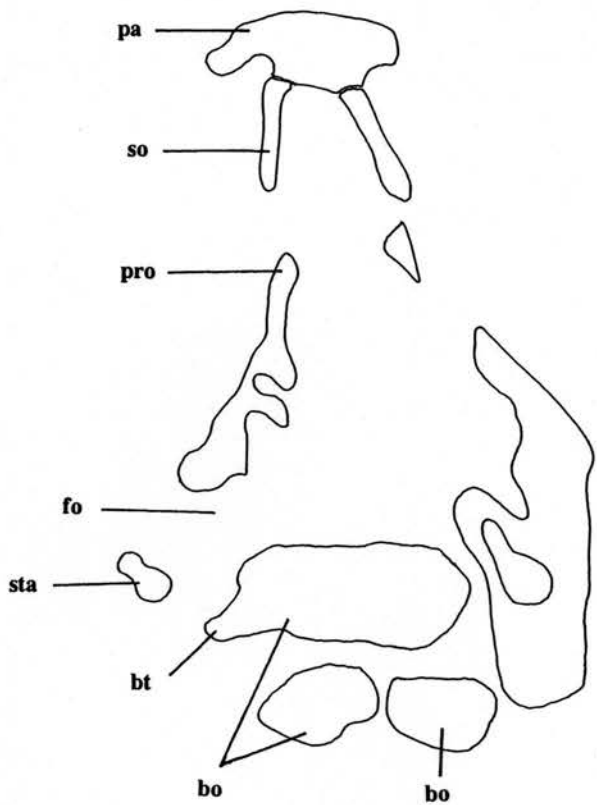
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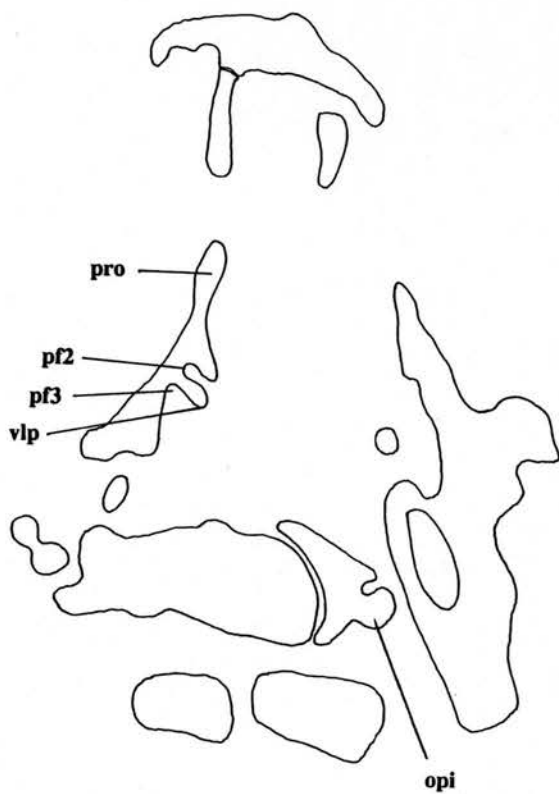
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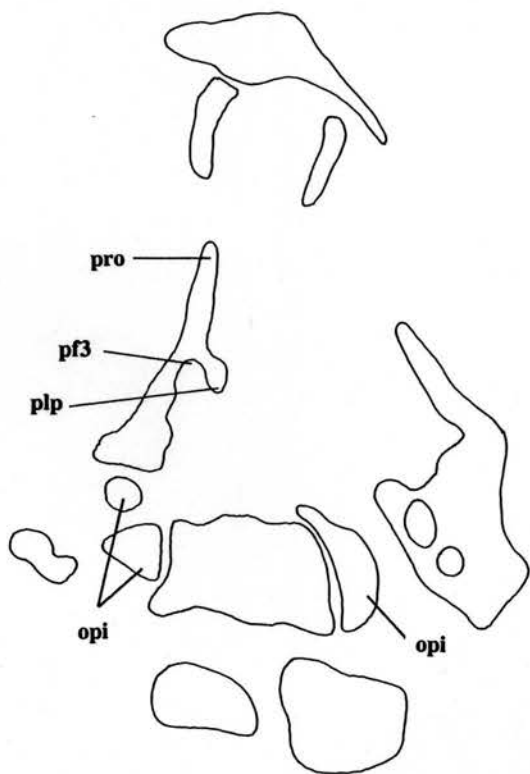
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473



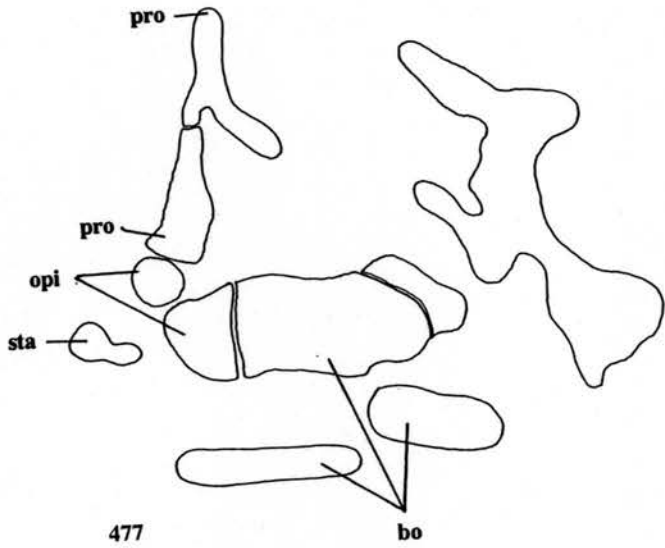
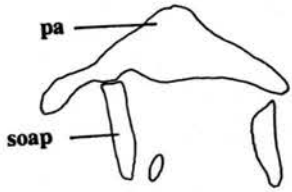
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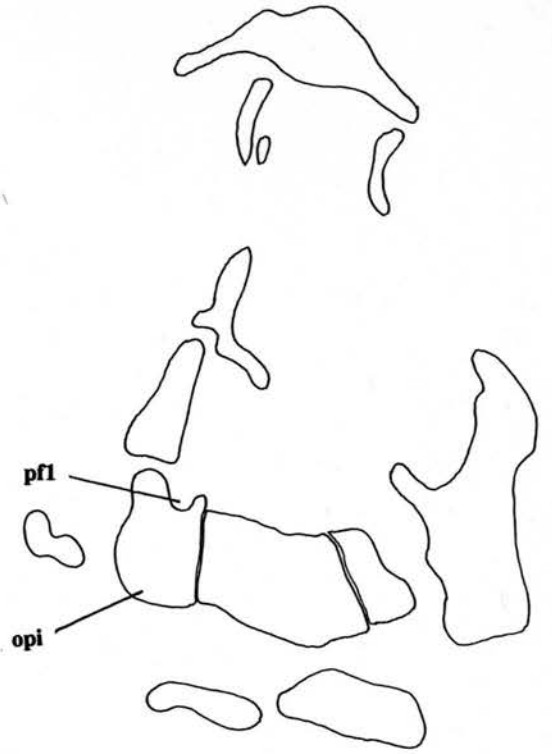
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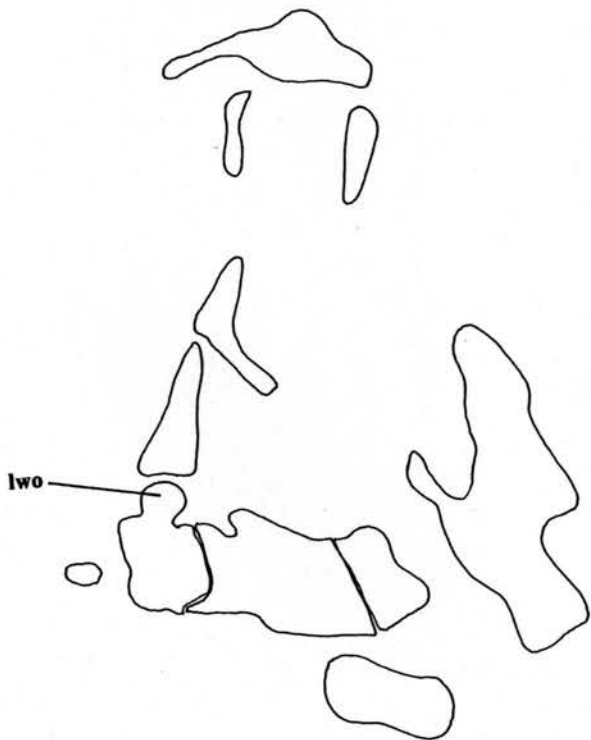
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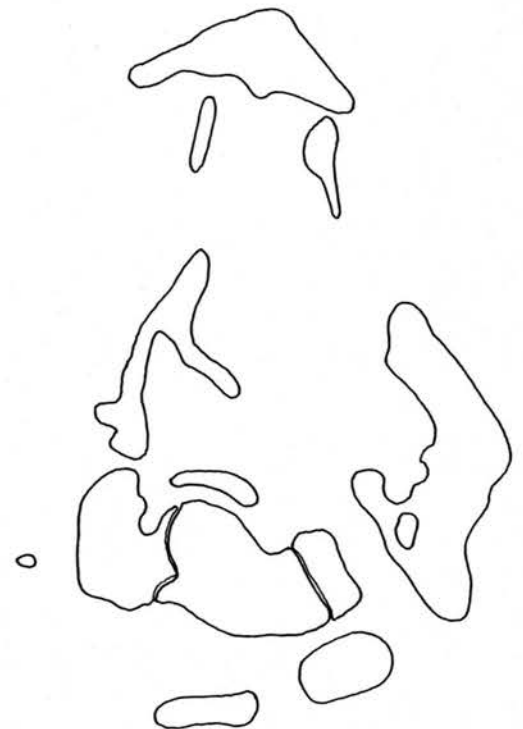
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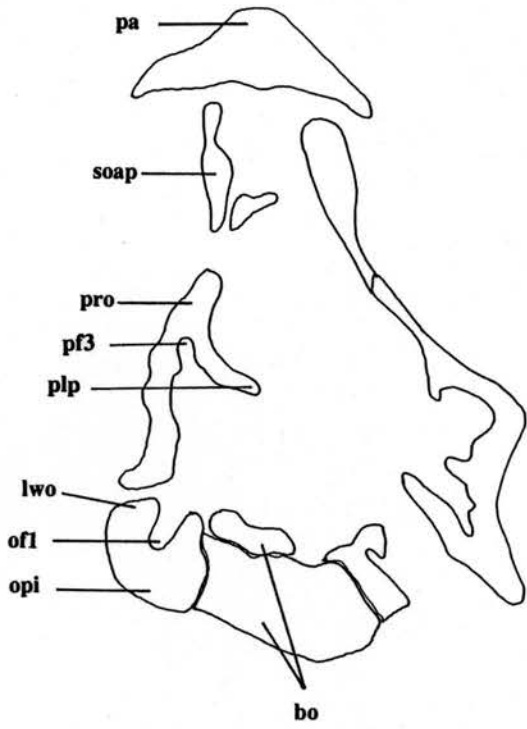
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479



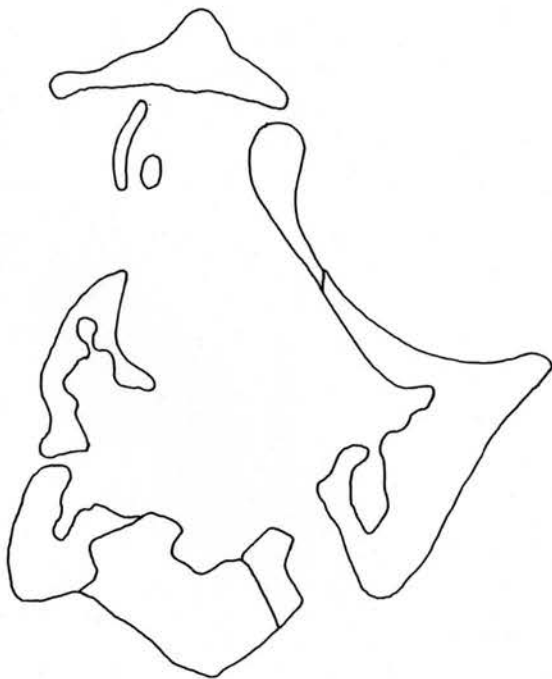
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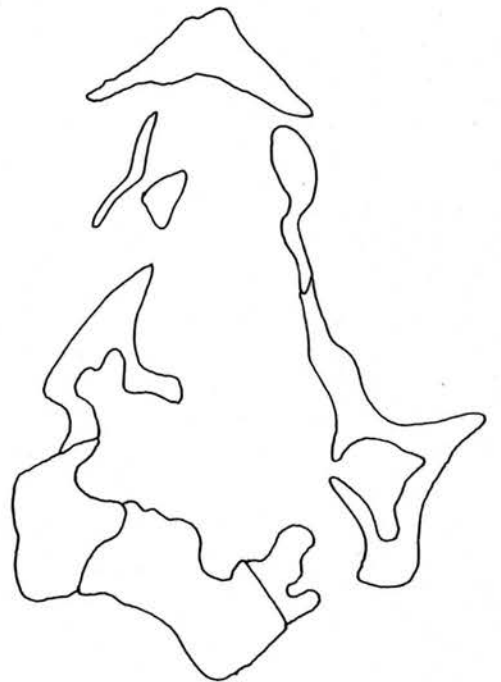
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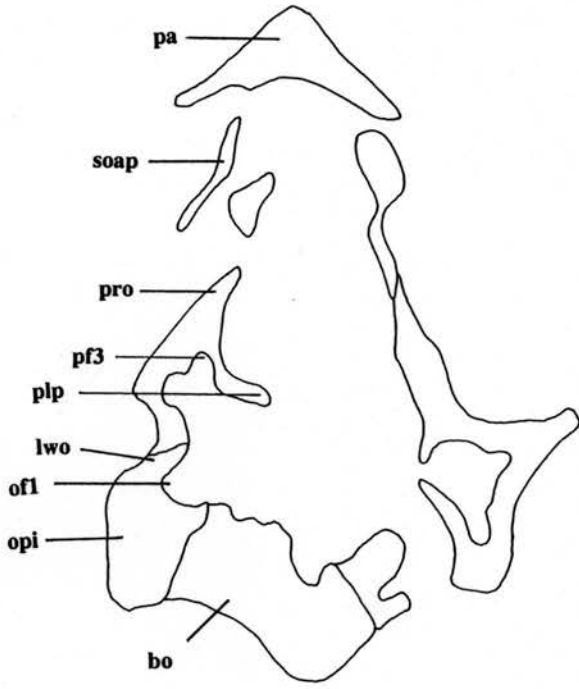
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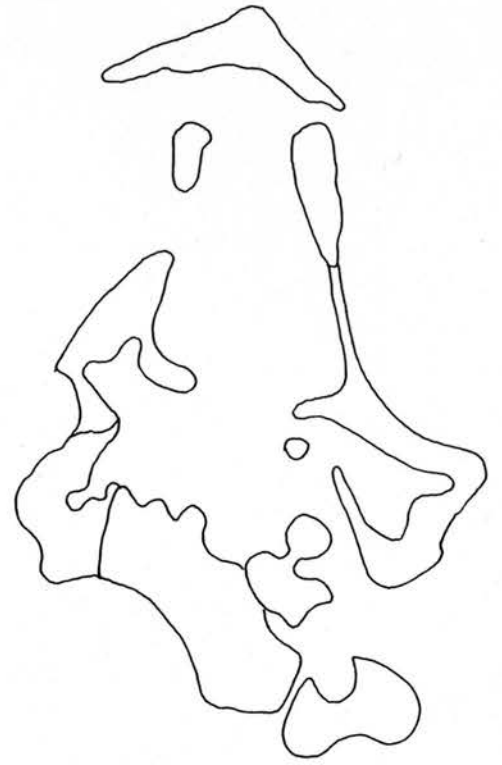
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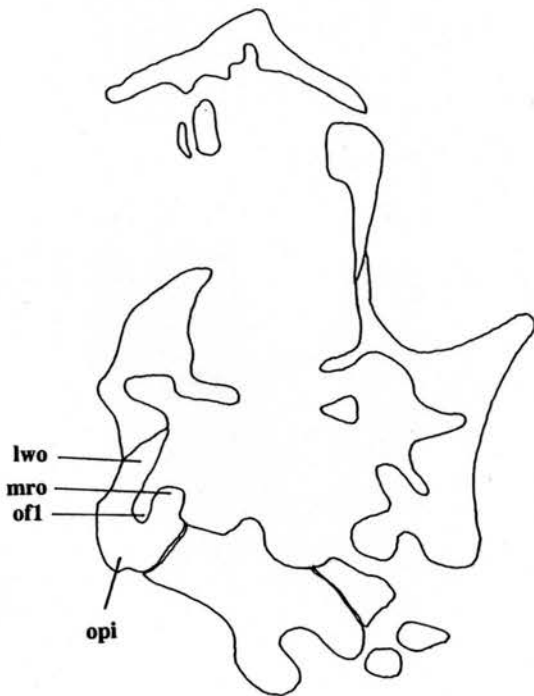
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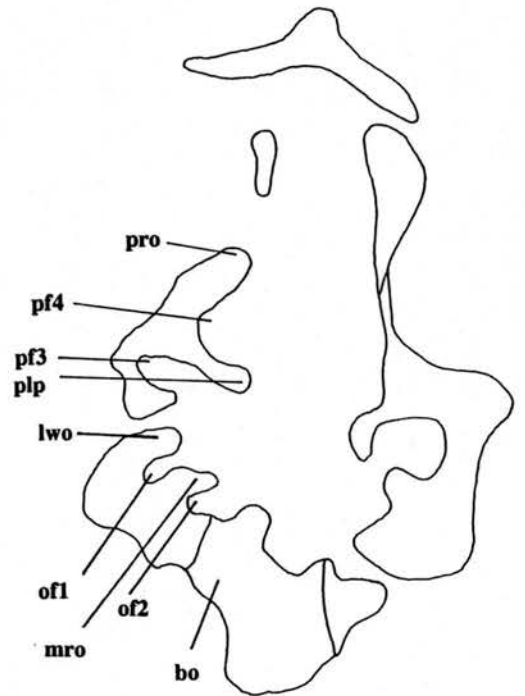
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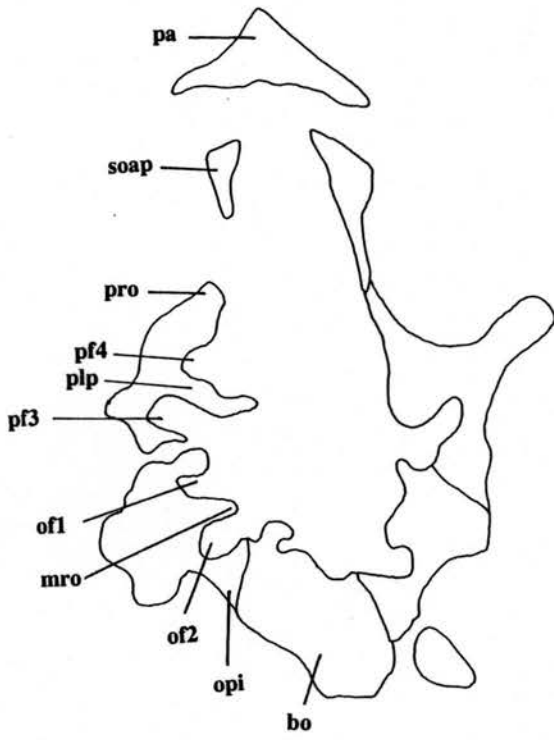
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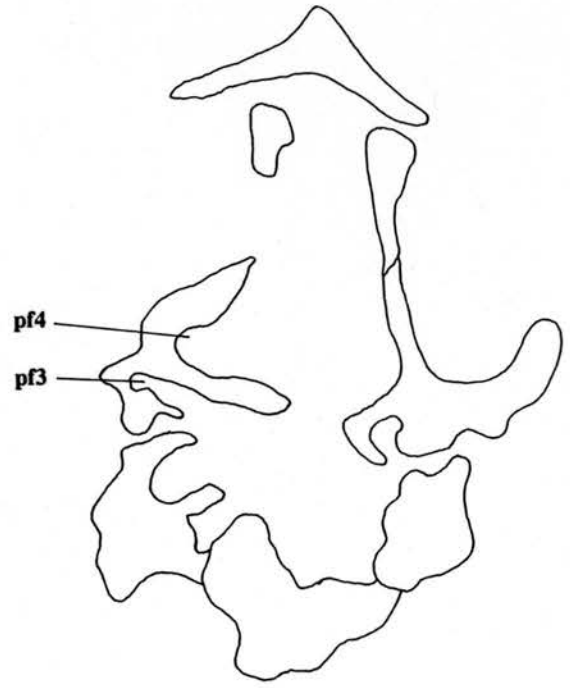
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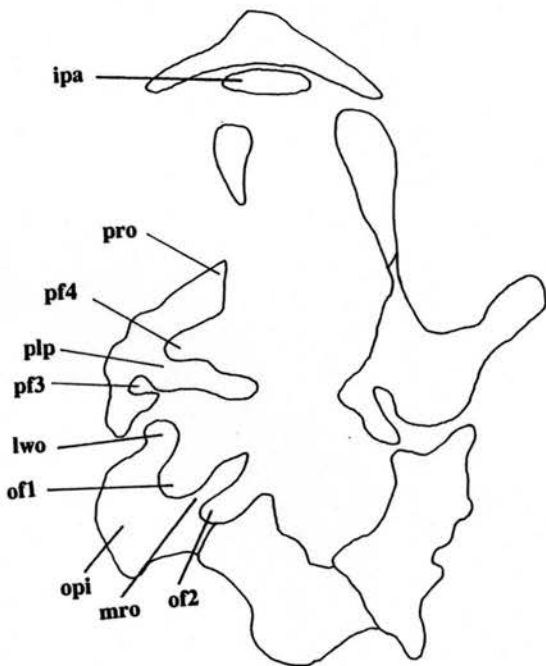
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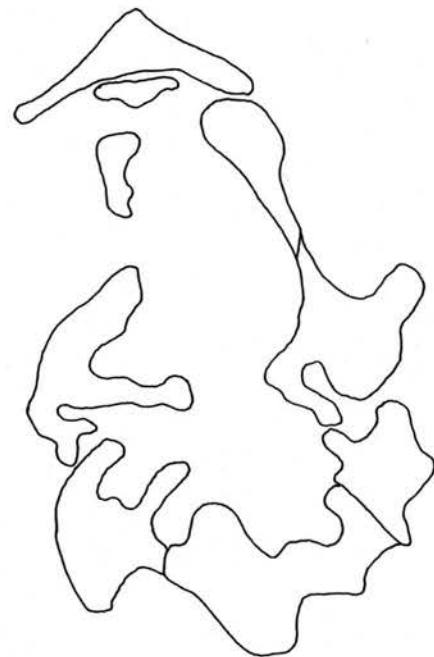
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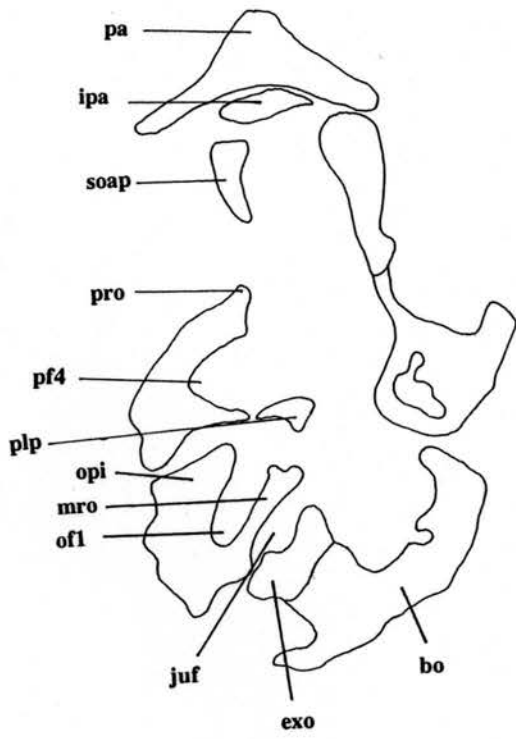
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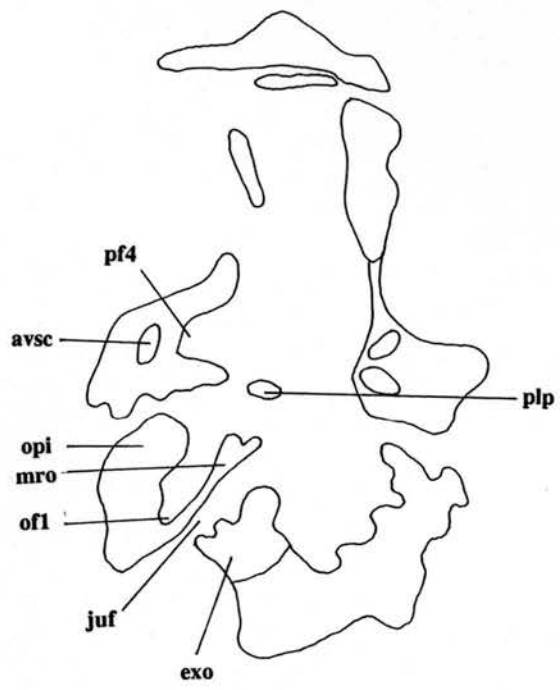
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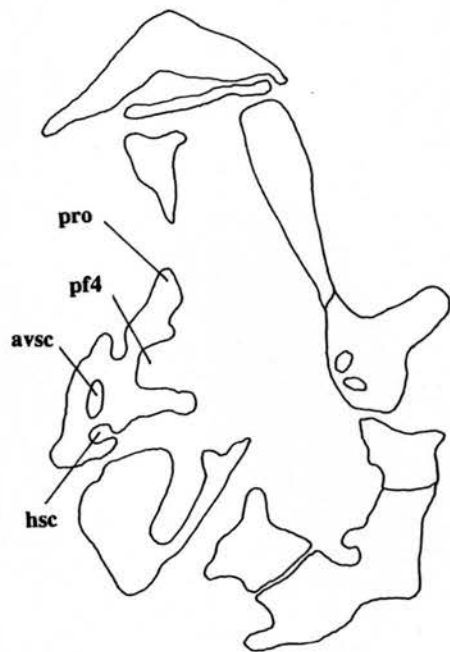
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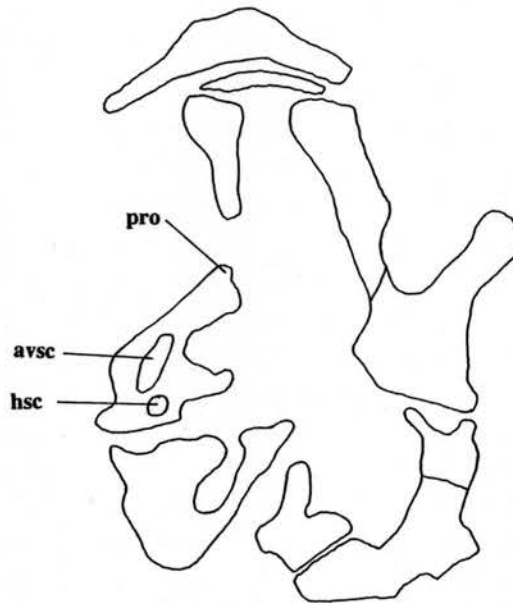
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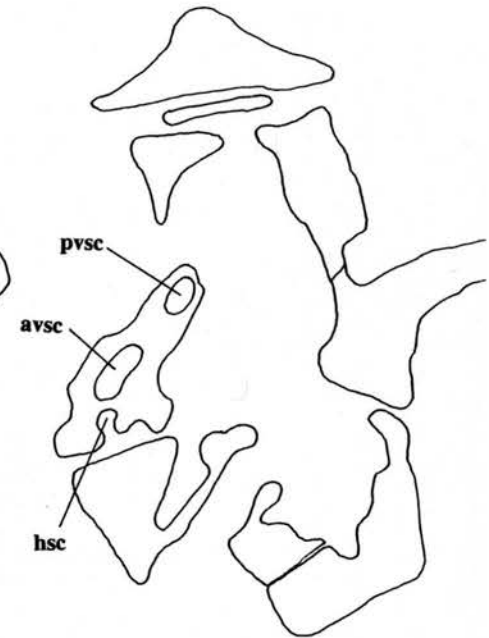
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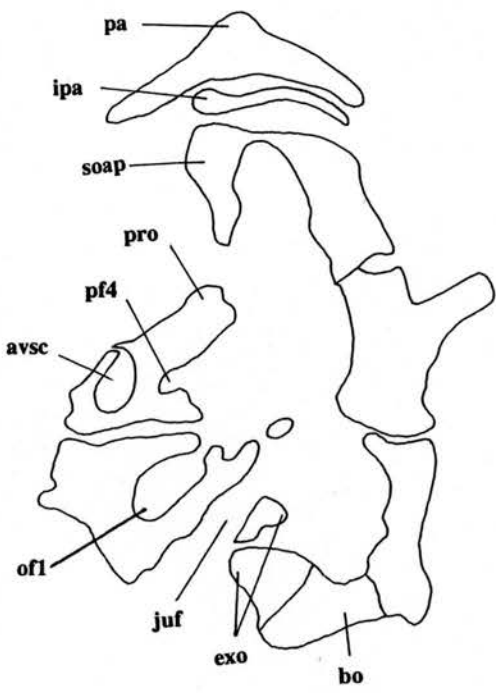
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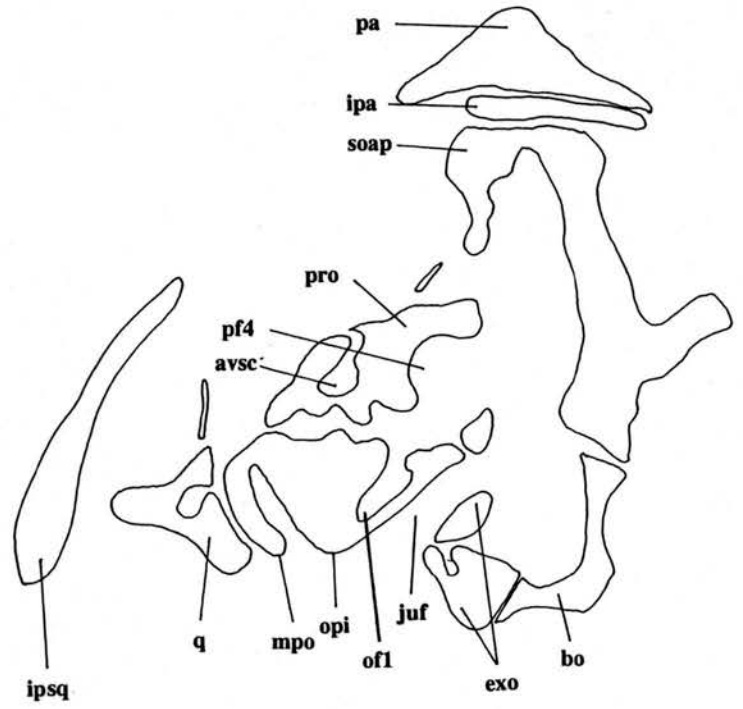
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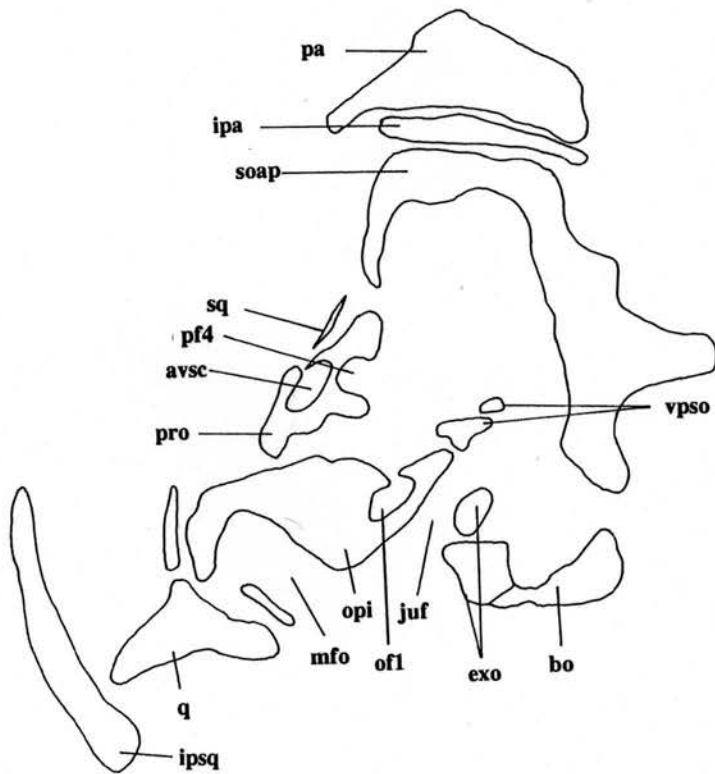
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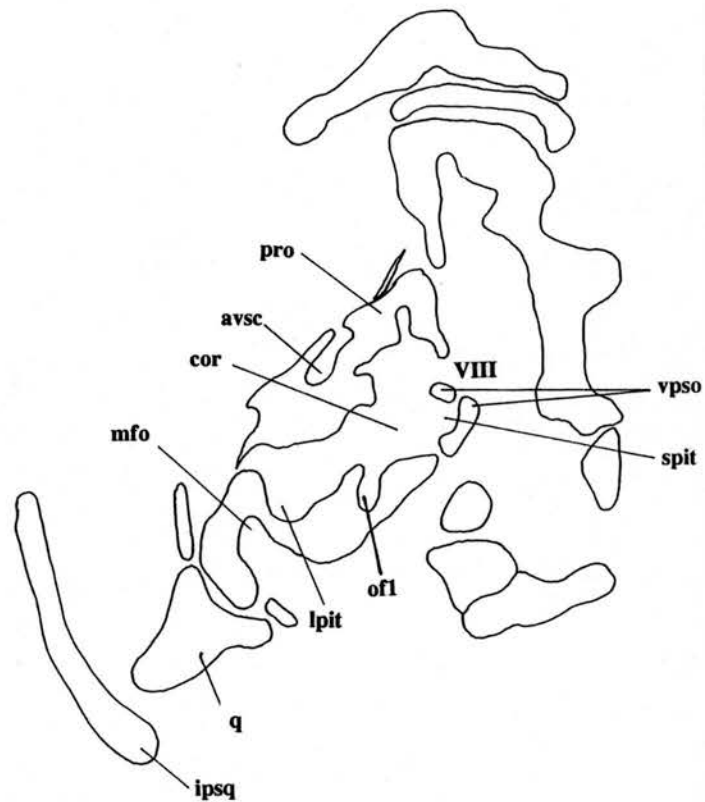
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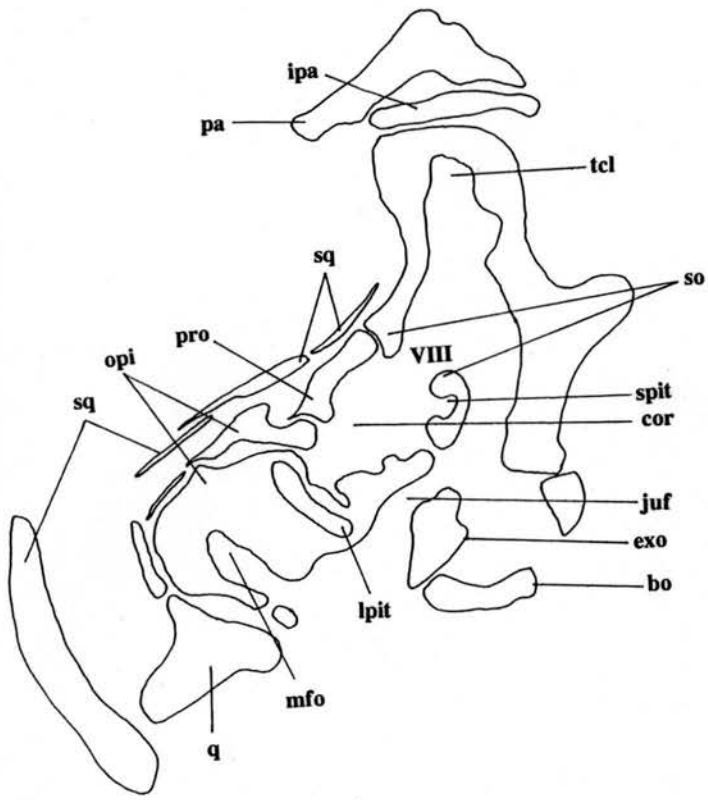
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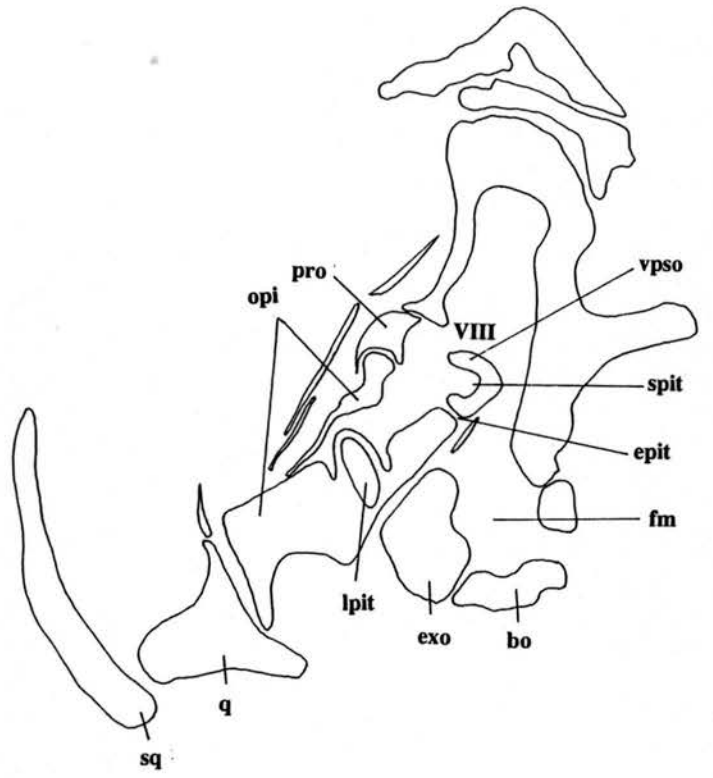
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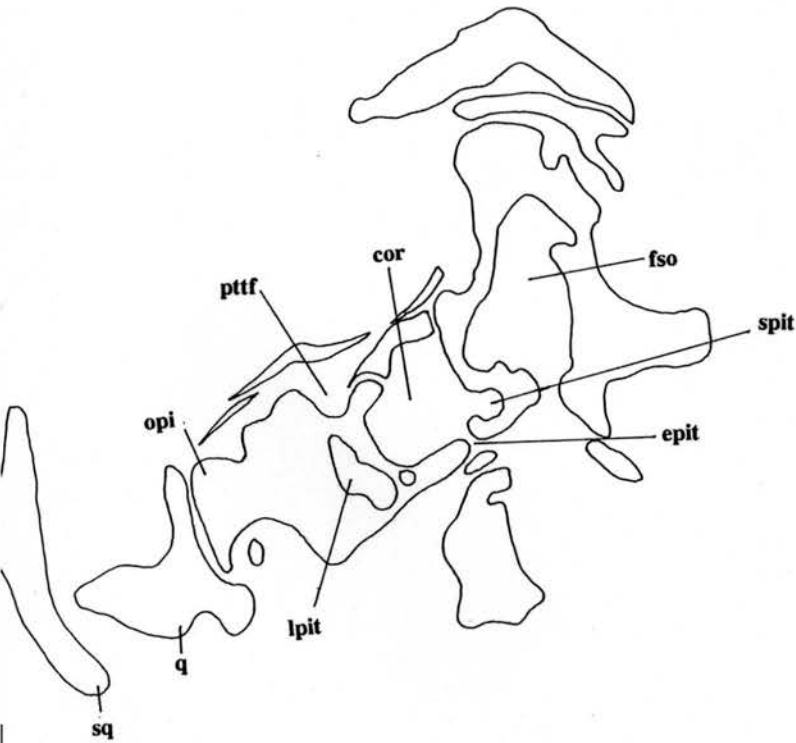
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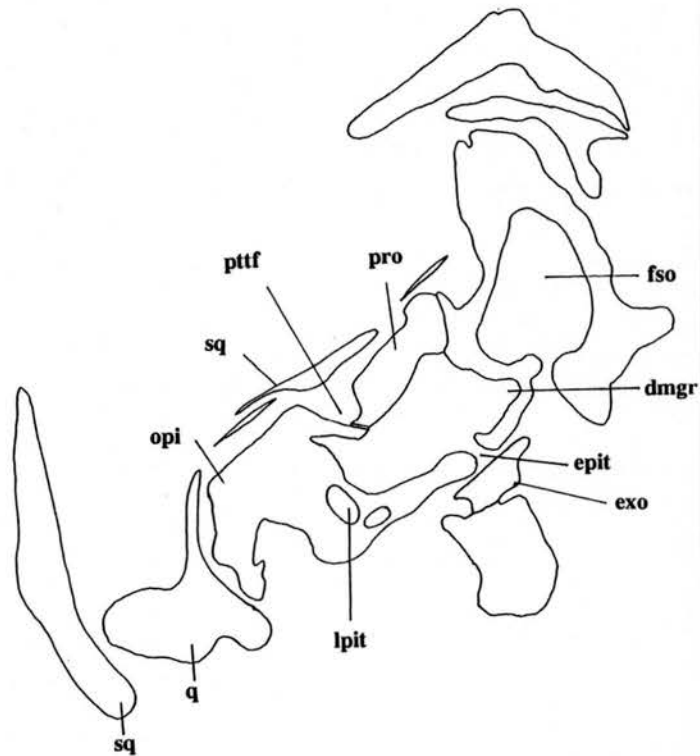
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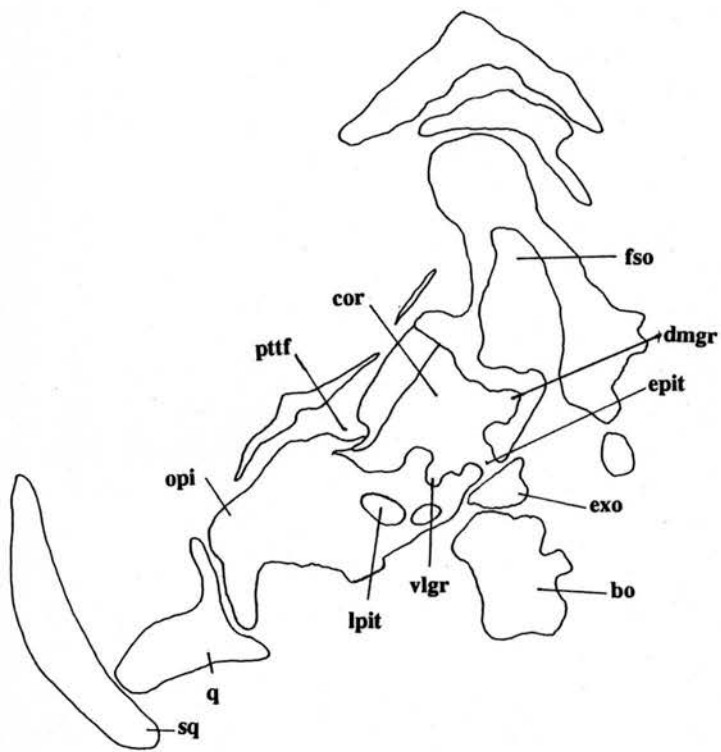
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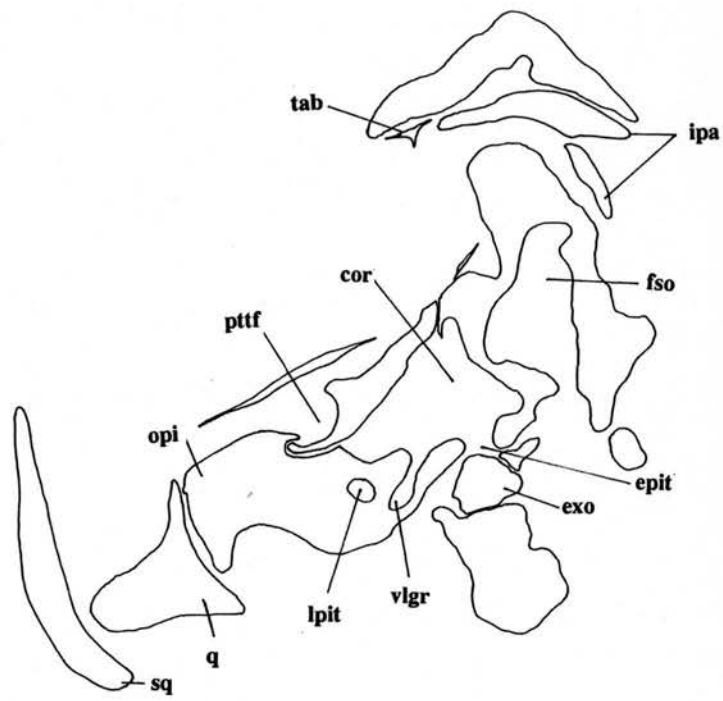
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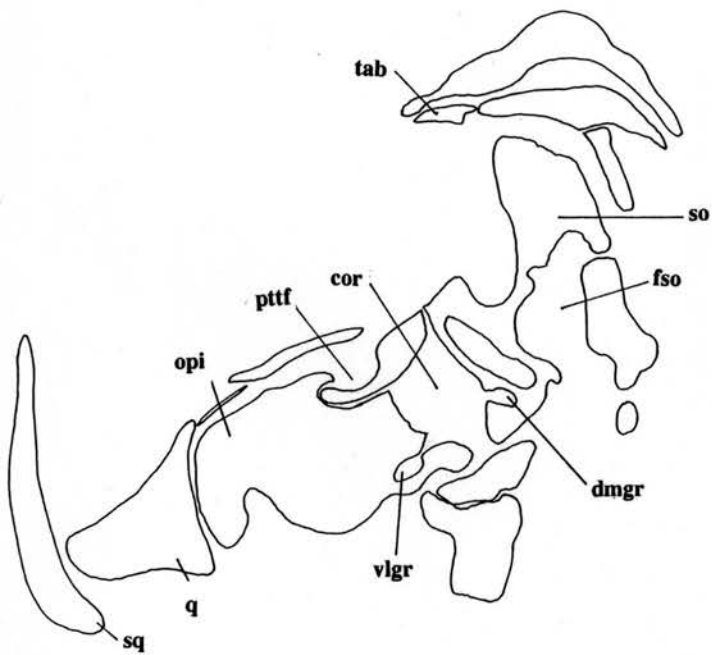
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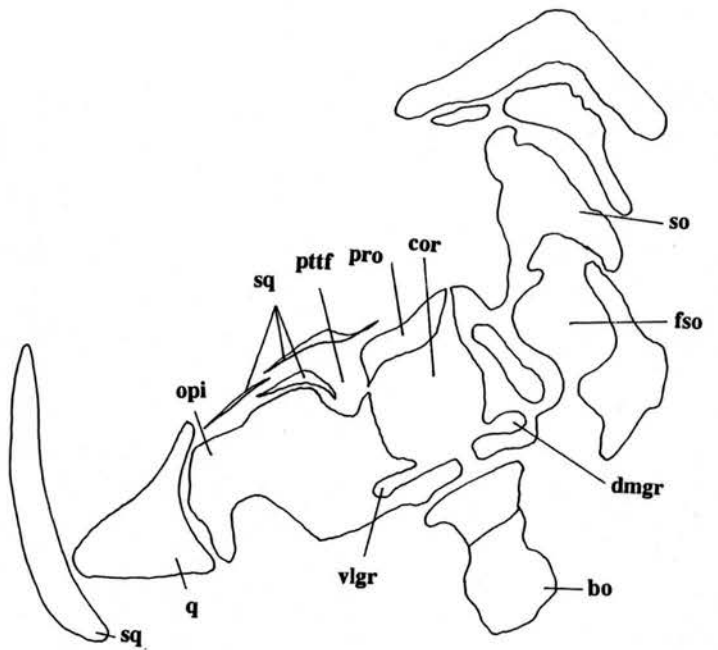
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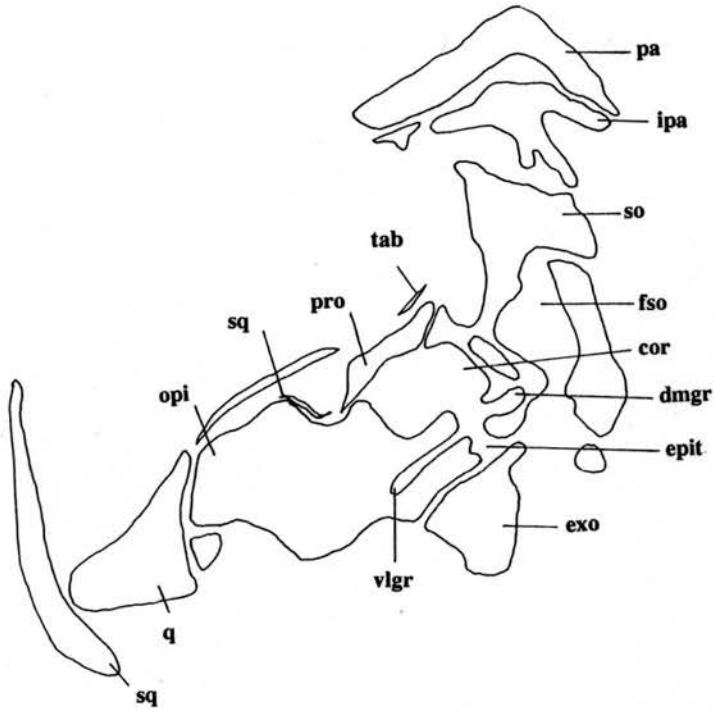
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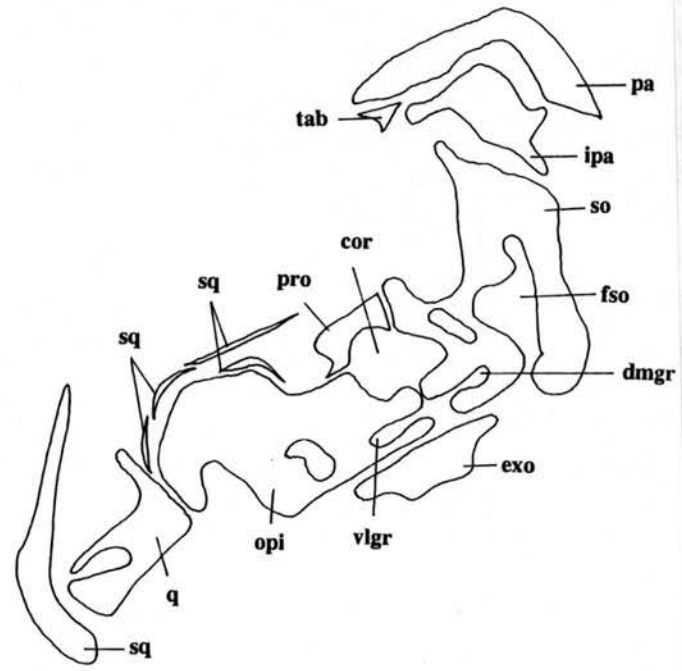
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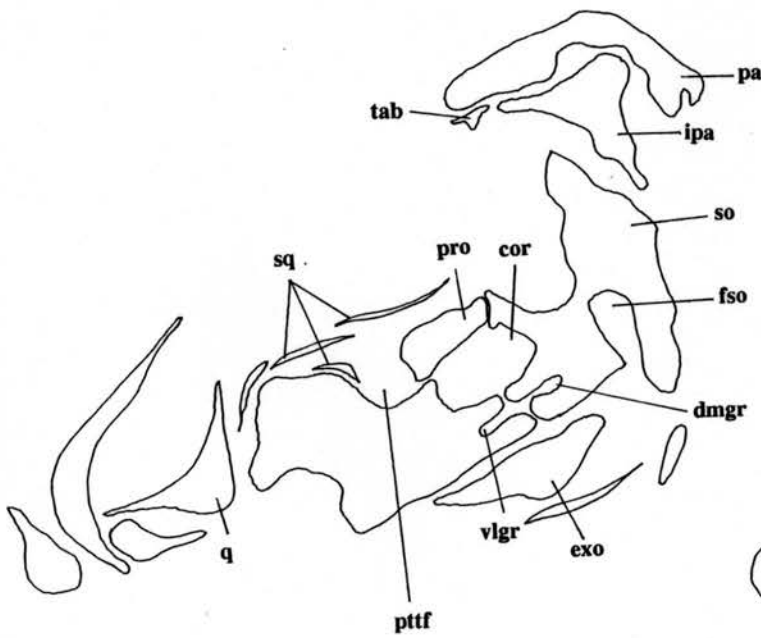
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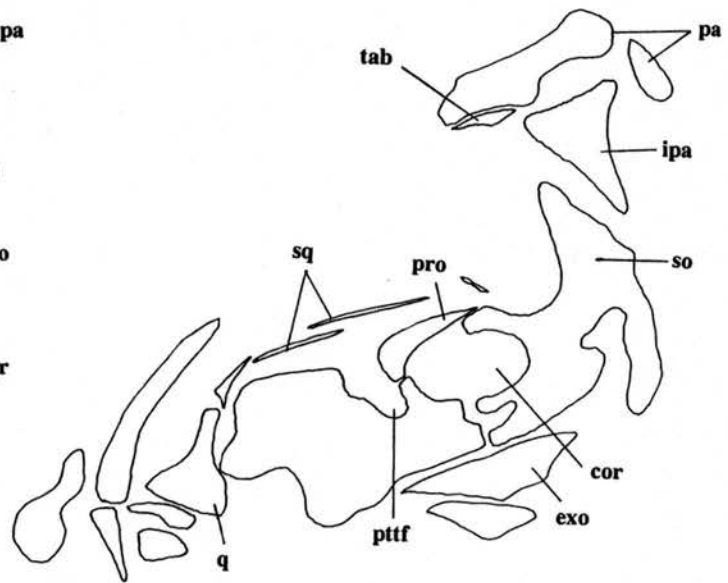
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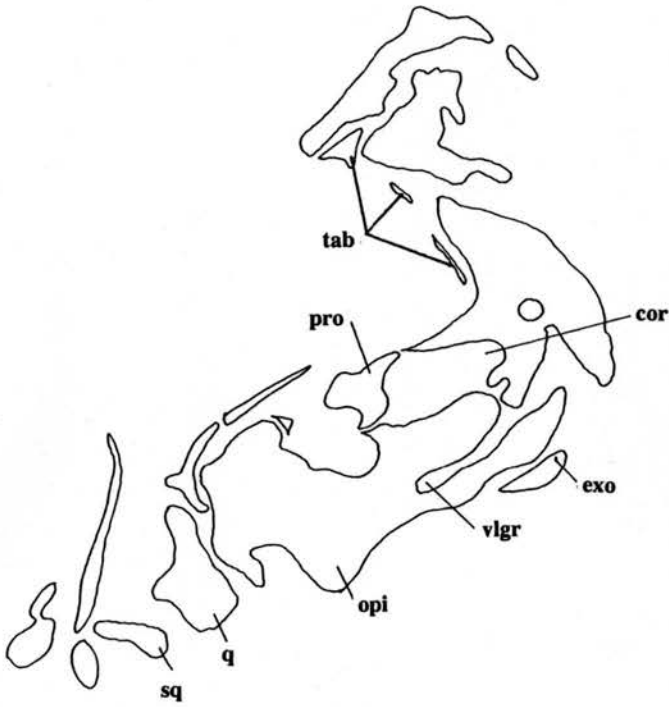
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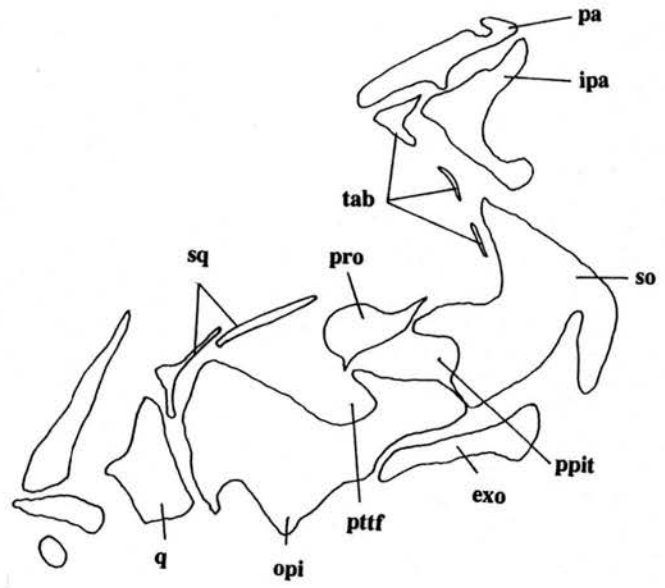
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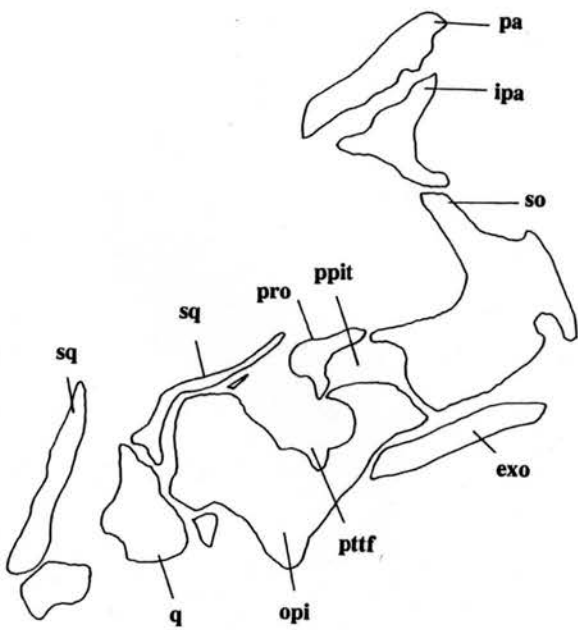
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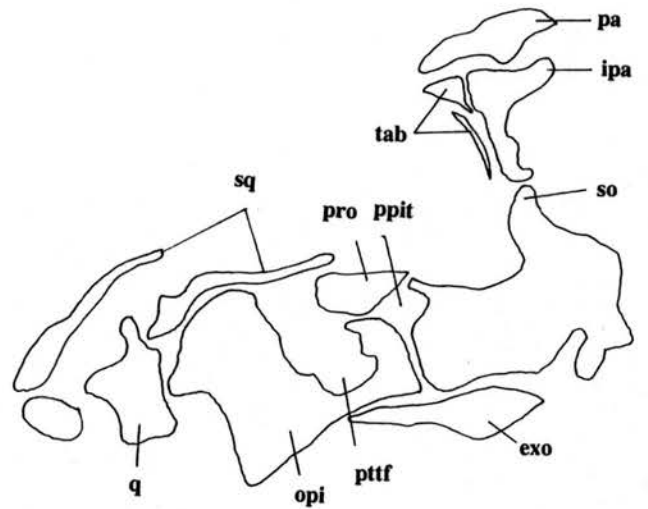
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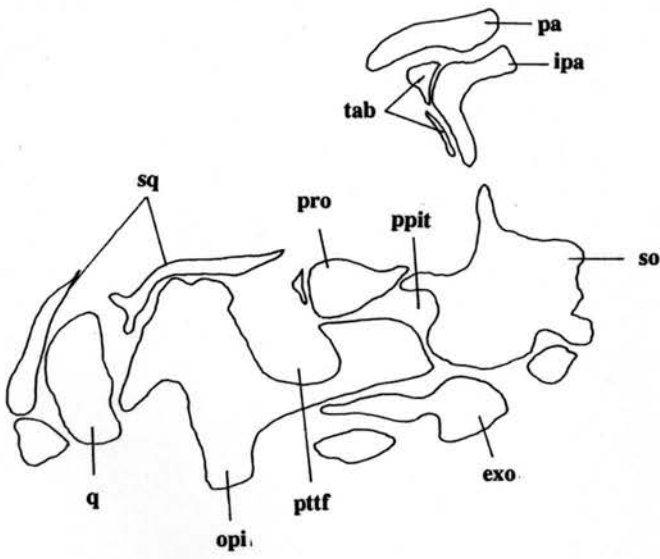
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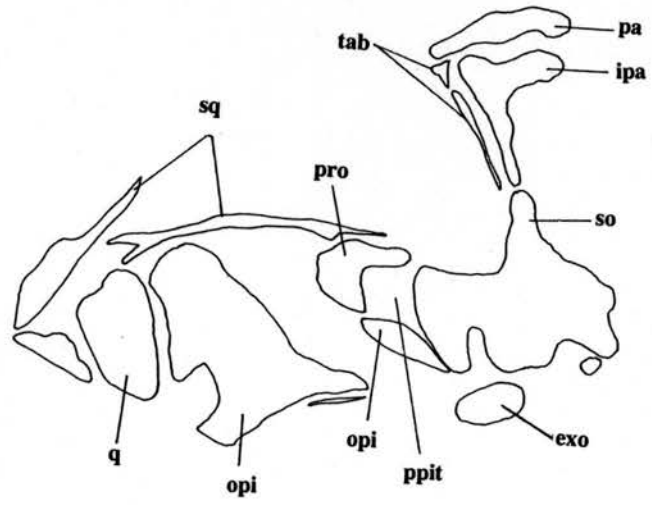
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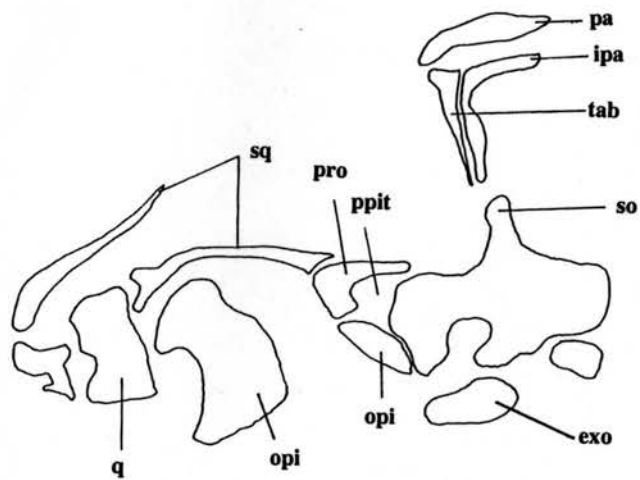
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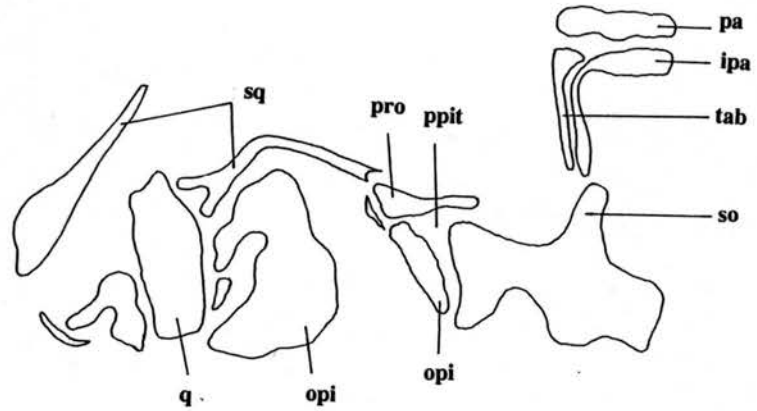
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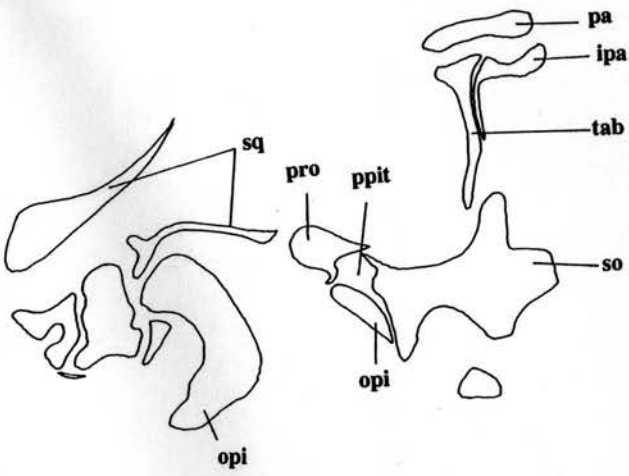
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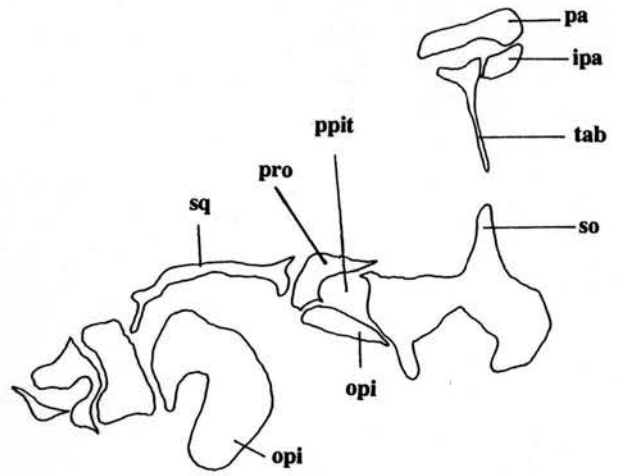
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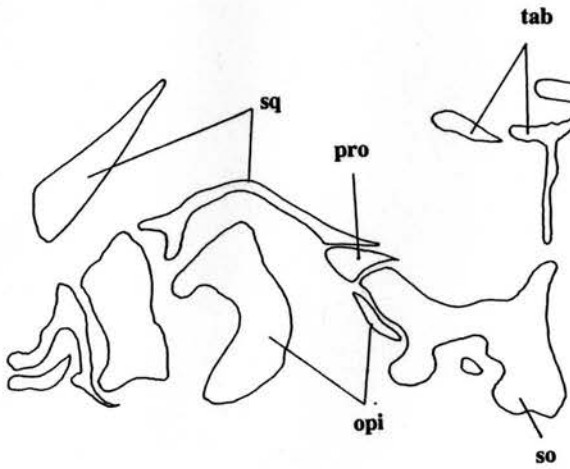
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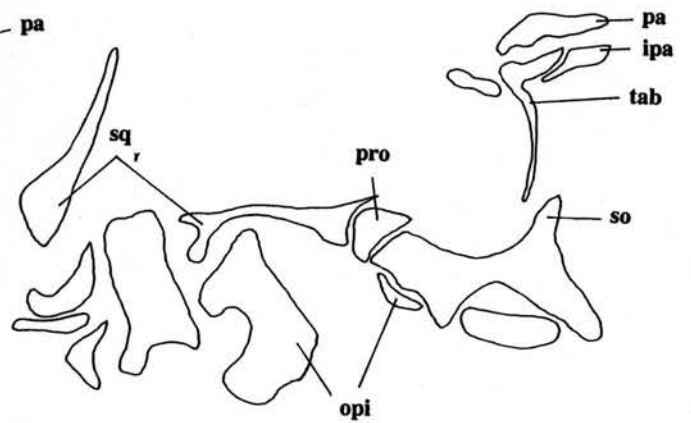
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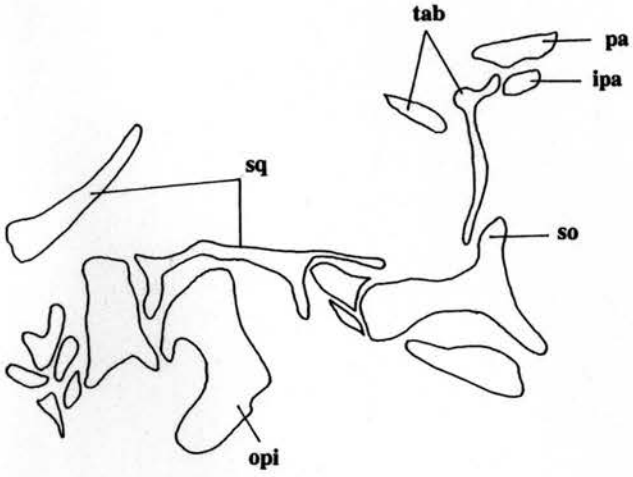
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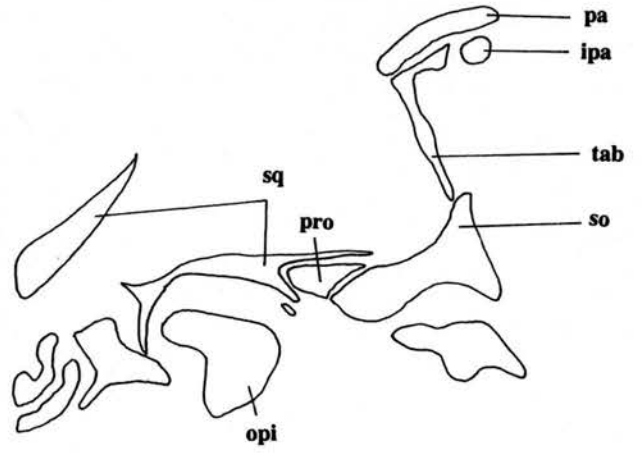
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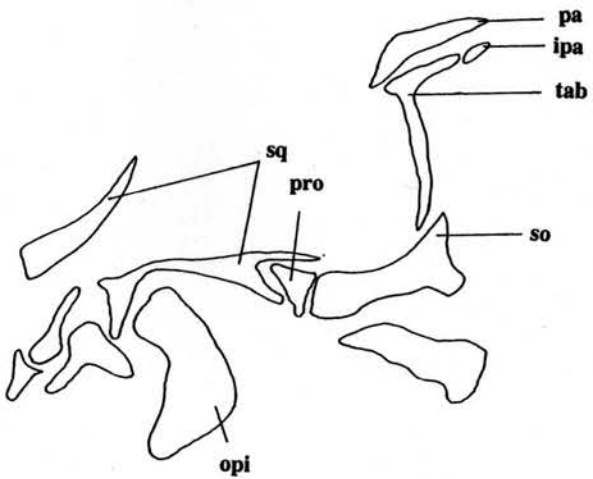
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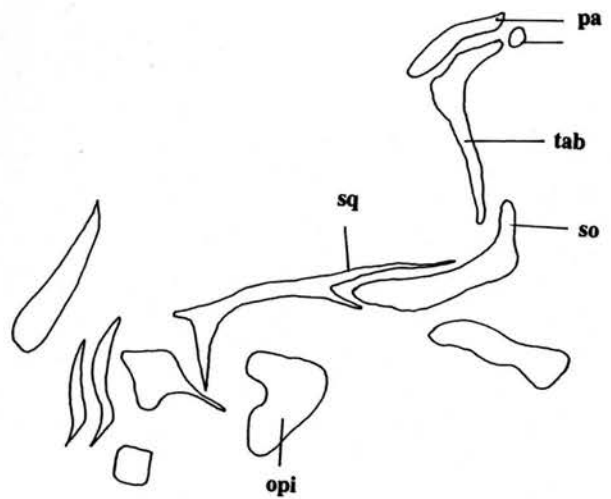
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526



527



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